Livestock Science 124 (2009) 1–8

Contents lists available at ScienceDirect

Livestock Science

journal homepage: www.elsevier.com/locate/livsci

Review article

Nest-building behaviour in sows and consequences for pig husbandry

Diane Wischner *, Nicole Kemper, Joachim Krieter

Institute of Animal Breeding and Husbandry, Christian-Albrechts-University Kiel, Olshausenstraße 40, D-24098 Kiel, Germany

ARTICLE INFO

Article history:
Received 8 September 2008
Received in revised form 22 January 2009
Accepted 23 January 2009

Keywords:
Reproduction
Crates
Maternal behaviour
Piglets
Pens

ABSTRACT

Patterns of maternal behaviour are strongly related to reproductive abilities in sows. Prepartal behaviour of sows is mainly characterised by nest-building activities, resulting in a nest that provides shelter for the piglets. In the course of domestication, sows have not lost their instinctive behaviour to nest-build, but perform at least elements of it when appropriate space and materials are available. The onset and performance of nest-building is both stimulated internally via hormones and externally via feedback from the environment. With this environmental influence, the possibilities to perform nest-building can be restricted to different extents in commercially farmed pigs. The aim of the present review is to point out the sow's need for nest-building performance as part of the natural behaviour pattern, although they are kept in different modern housing systems. With regard to increased demands for animal welfare and following changes in the legislation for pig husbandry, possible consequences for different housing systems are discussed.

Contents

1. Introduction

In modern pig husbandry, the ability of the sow to raise large litters and to meet the piglets' needs especially with regard to milk provision is essential. To reduce piglet losses and to facilitate human intervention, farrowing crates have been developed. In comparison to alternatives systems like pens, farrowing crates restrain the sow's movements during parturition and lactation and have mainly been intended to protect piglets from being crushed (Robertson et al., 1966; Edwards and Fraser, 1997). With this restriction, the performance of typical reproductive behaviour like an increased activity one to two days before farrowing (Jensen, 1986), as seen in free-ranging sows, is limited in commercially farmed pigs. One important behavioural trait before the onset of

* Corresponding author. Tel.: +49 431 880 7343; fax: +49 431 880 2588.
E-mail address: dwischner@tierzucht.uni-kiel.de (D. Wischner).

1871-1413/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.livsci.2009.01.015

parturition is nest-building as well in domesticated, feral and wild sows. Nest-building behaviour is specific and unique in members of the family *Suidae*, including the pig (*Sus scrofa*) (Lent, 1974). This behavioural pattern characterises the pig as 'hiders' (Lent, 1974), or more specifically as 'nest dwellers' (Stangel and Jensen, 1991). Nest-building is performed to provide the offspring with shelter and comfort, particularly with respect to thermoregulation. Due to a lack of brown fat tissue, the piglets demand an increased surrounding temperature (Myrcha and Jezierski, 1972; Varley and Stedmann, 1994). Their physiological thermoregulation is still developing, particularly during the first two weeks (Hurnik, 1985). Moreover, compared to other even-toed ungulates, piglets are rarely born with hair, and have an unfavourable surface-weight proportion, weighing less than 1% of their adult weights (Mayer et al., 2002). Thermoregulation is closely related to birth weight. The maintenance of the homeothermic balance in the cold is reduced in smaller piglets due to the greater surface to body mass ratio resulting in higher heat losses (Herpin et al., 2002). Without protection against climatic influences, the piglets would cool down and die. By providing a microclimate with protection against other weather effects, the nest supports the new-born piglet to perform thermoregulation and to limit rapid heat loss (Briedermann, 1986). Moreover, it offers protection against weather and predators (Pullar, 1953). In addition, piglets are kept close to the sow and away from the family group. In this way, it is ensured that the piglets are not trampled by other adults and that other piglets do not steal milk from the sow (Jensen, 1986).

Regarding the duration of staying in the nest, the classification of piglets as altricial or precocial animals is discussed controversially. Fraser (1980) classified them as precocial animals, even though they are born in large litters and spend their first days of life in the nest. On the contrary, the classification as altricial animals is justified by the long period up to seven days spent in the nest (Jensen and Redbo, 1987). This is also indicated by the fact that no rapid individual bonds with the offspring are performed, as this is not essential for nesting animals (Kilgour, 1985). Sows usually do not lick the newborn or server the umbilical cord (Randall, 1972; Fraser, 1984) and are passive during farrowing until the last piglet is born (Stangel and Jensen, 1991). On the contrary, Stangel and Jensen (1991) reported cases of sows cleaning their piglets and consuming their afterbirths. To compound the oppositional views, Portmann (1960) suggested the term 'secondary precocial' to describe the piglets' behaviour.

In the course of domestication and the associated reduced variability of the environment, sows have lost the need for protection against climatic influences, starvation and predators, as stated by Lindsay (1985). However, this position ignores the fact that extensive farming with free-roaming, domesticated animals is practised in many countries, still exposing them to various influences. Even though the influences of domestication on some behaviour patterns cannot be denied, sows in extensive housing still show behaviour more or less identical with that of wild boars when nesting material and sites are provided (Gustafsson et al., 1999). This paper reviews the pre-farrowing nest-building behaviour of sows in different housing systems and the possible consequences for pig husbandry.

2. Nest-building behaviour under natural or semi-natural environments

Both genders build and use modified nests and beds for resting and loafing (Martys, 1982). Therefore, it is possible to divide nests into sleeping nests, 'mock' nests (Jensen, 1986) and farrowing nests (Pfeffer, 1959), but only the latter are the object of this review.

In general, pigs investigate their surroundings by rooting, sniffing, biting and chewing on digestible and also indigestible items (Studnitz et al., 2007). Nest-building is a modification of this behaviour with the aim to build a nest as shelter. It is a predefined, inherited behavioural fixed action pattern shown both in male and female pigs (Eibl-Eibesfeldt, 1963). Nest-building behaviour of mammals represents an innate behaviour. Sign stimuli are necessary to perform this behaviour pattern. They represent an important starting point for the behaviour chain, determining and controlling the behaviour patterns ante and post partum, including the care of the offspring (Buß, 1972). It is shown as well in inexperienced as in experienced animals and does not have to be learnt (Lorenz, 1937). However, sows can learn how to build a better nest and improve by experience with each litter (Jensen et al., 1987).

Grandin and Deesing (1998) describe nest-building in sows as an example of the interaction between instinct and learning. Age or experience modifies nest-building behaviour (Jensen, 1989) as well as the interaction with the farrowing environment (Thodberg et al., 1999). Already at an age of six days, piglets perform basic elements of nest-building behaviour (Gundlach, 1968). In experiments, isolated piglets perform nest-building behaviour earlier to maintain their thermoregulation (Gundlach, 1968).

Nest-building behaviour is one important part in the whole process of pre and post partum maternal behaviour. During the total life-span of a sow, pre-farrowing nest-building behaviour is only performed a few times with each new pregnancy and parturition to come.

Under natural conditions, the sow limits her scope of action to a smaller home range within the last month of pregnancy and shows reduced activity (Kurz and Marchinton, 1972). One to three days prior to parturition the sow separates from the group and becomes solitary, exploring her surroundings for a suitable place to build the nest (Hafez et al., 1962; Buß, 1972; Jensen, 1986; Stolba and Wood-Gush, 1989). The sow travels distances up to 6.5 km within 6 h and stops at several places to explore the ground by sniffing and rooting (Jensen, 1986). Compared to grass areas, forest or forest border habitats are preferred as nest-sites (Stolba and Wood-Gush, 1984). Favoured sites are often situated below a slope and characterised by offering shelter against rain and wind, for instance under dense vegetation, probably in the form of a roof of branches hanging down (Gundlach, 1968; Frädrich, 1974; Stolba and Wood-Gush, 1984). These places allow an open view and provide cover on two sides (Stolba and Wood-Gush, 1984). The ground is often well-drained soil and easy to root (Jensen, 1986). Jensen (1986) reported in free-ranging sows the occurrences of 'mock nests'. These nests were built up like farrowing nests, but they were not used. A change in temperament towards unpredictable aggression, even against their own previous progeny, can be observed (Graves, 1984) as well as increased restlessness (Jones, 1966). Experienced mothers seem to be calmer than primiparae (Signoret et al., 1975). Baxter

(1982) also reported fearfulness or agitation in gilts rather than in experienced sows.

Generally, the sow starts to build the nest at approximately 24 h before parturition, showing most intensive activity 12 to 6 h before farrowing (Jensen, 1989; Cronin et al., 1994; Haskell and Hutson, 1994; Algers and Uvnäs-Moberg, 2007). Nest-building in wild boars as well as in domestic sows can be roughly classified in two consecutive phases: initially, in the first phase, the ground is rooted and pawed and a shallow hole is dug. In the second phase, the sow collects, carries and arranges the nest material along the edges of and in the nest (Jensen, 1993). In more detail, the sow roots and digs the ground by throwing the soil with her mouth and head (Gundlach, 1968). She gathers nest-building material, mainly consisting of branches, bushes and other organic material, from within a radius of 20 m (Mayer et al., 2002) and 50 m around the nest (Gundlach, 1968). The gathered material includes dry grass and leaves (Gundlach, 1968), as well as fern and moss (Snethlage, 1967).

Younger and smaller sows have a smaller radius for gathering compared to older and larger sows (Jensen, 1989; Mayer et al., 2002). Gathering is performed by breaking and biting of the material, shuffling it in the mouth and carrying it to the nest site. The sow deposits the material along the edges of the nest and, by turning her body round in circles with repeated pawing and pressing her head against the material, the edges of the nest are distinctly elevated (Gundlach, 1968). The sow fills the nest with further material by throwing smaller parts with head turns in the middle of the nest and distributes them by turning around herself. Stabilisation of the whole nest is achieved by integrating thick branches and twigs, which partially protrude over the side of the nest. After covering with finer material, such as grass, leaves and small twigs, the nest shows a stratified structure with a loose grass heap up to 1 m high and includes smaller and larger wooden parts (Gundlach, 1968).

In the finished nest, the sow keeps the material together by pawing and pushing it back with her snout. In this way, sows gradually construct an oval nest with positively correlated length and width (Mayer et al., 2002). In few cases, dome-like nest coverings have been reported (Briedermann, 1986). The sow usually leaves the nest at a certain side, and sometimes covers the nest with more material before leaving on foraging trips (Tisdell, 1982).

2.1. Influences on nest-building performance

Nest-building behaviour is both influenced by internal and external stimuli. The appropriate combination of all modulating endogenous and exogenous stimuli decides whether complete and successful nest-building will take place. With regard to these influencing stimuli, two nest-building behaviour elements can be distinguished. The initial phase of site searching and hole digging is regulated by internal hormonal changes, while the second, material-oriented phase is mainly dependent on external stimuli such as feedback from the nest site (Jensen, 1993). Hutson (1988) indicated that a successful completion of each phase is the stimulus for the next phase, like a chain or cascade of response.

Several stimuli are discussed as the starting point of this chain in the first phase. For instance, Gilbert et al. (2001) suggested that some sort of signal, resulting from foetal maturation, might initiate the cascade for nest-building behaviour. In more detail, the hormonal impact on maternal behaviour in pigs was reported by Algers and Uvnäs-Moberg (2007). In short, the onset of nest-building seems to be triggered by a rise in prolactin level (Widowski et al., 1990; Castrén et al., 1993). This rise itself is induced by a decrease in progesterone and an increase in prostaglandin (Ellendorff et al., 1979; Burne et al., 2001b; Algers and Uvnäs-Moberg, 2007). Nest-building behaviour can be induced by the administration of prostaglandin $PGF_{2\alpha}$ injections in pregnant sows (Widowski and Curtis, 1989). On the contrary, injection of the prostaglandin synthesis inhibitor indomethacin to late pregnant gilts reduces nest-building behaviour (Gilbert et al., 2001). The cessation of nest-building has been suggested to be strongly correlated with the dramatic rise in oxytocin levels 4 h prior to parturition (Castrén et al., 1993). Whether the effect of oxytocin, leading to frequent uterine contractions (Gilbert et al., 1994), stops nest-building or whether oxytocin induces the cessation at a central level still remains unknown (Algers and Uvnäs-Moberg, 2007).

The second phase, depending on external stimuli, is termed as the material-oriented phase (Jensen, 1988a). To continue the reaction chain, the sow is reliant on feedback and external stimuli. Stimuli are provided by proper nest material and therefore the availability of suitable nest material is crucial. This provision again is strongly determined by the material's suitability to stake, stuff and protect (Arey et al., 1991). The more suitable the material, the sooner nest-building is completed. For example, with access to branches, gilts terminate their nest-building sooner than without (Damm et al., 2000). Arey et al. (1991) also showed that the environment provided (e.g. provision of pre-formed nests) altered nest-building behaviour. Widowski and Curtis (1990) reported that the behaviour was directed by the nesting material as stimulus but the structure of the nesting material did not affect the activity of the sows. Stolba and Wood-Gush (1984) described that 'high standing stalks' release the behaviour. Therefore, it can be assumed that the presence of nesting material triggers nest-building behaviour in motivated sows. On the other hand, Hutson (1988) and Blackshaw (1983) claimed that nesting-material is of no importance to sows ante partum. However, Baxter (1983) hypothesised that there is a feedback stimulus to stop nest-building behaviour which was achieved via sufficient 'udder comfort' with a comfortable and flexible lying substrate area in the nest.

Habitat and season do not only influence the vegetation and thereby the nesting material, but there is evidence that nest-building behaviour is affected directly by season due to environmental temperatures (Dellmeier and Friend, 1991). The duration and intensity appears to vary with weather conditions and may be observed less frequently during hot summer weather (Damm et al., 2000). With decreasing temperatures, there is a significant increase in rooting and nest-building behaviour (Burne et al., 2001a).

However, external factors are not solely responsible for behavioural patterns in the material-oriented phase; internal, endocrine changes can influence and alter the sensitivity to external stimuli as well (Haskell and Hutson, 1994). For oxytocin, an anti-stress effect promoting calmness and reduced anxiety is described by Uvnäs-Moberg et al. (2001), but the detailed interplay of these factors still has to be investigated.

2.2. Influences of domestication

Buß (1972) described various morphological, physiological and psychological changes in the course of domestication which resulted in behavioural characteristics. Behavioural and other, especially physiological, changes caused by domestication are often based on innate behaviour (Lorenz, 1959). Stressors, such as those usually experienced in the natural environment, are limited in surroundings where locomotion is reduced as food is supplied and protection against predators is given (Lorenz, 1959). Modification of old phylogenetic behavioural elements allows new variances of behavioural patterns, for example, a shortened flight distance. Increased variability in these patterns is reported in domestic animals (Schulz-Scholz, 1963). As a consequence, a possible alteration of nest-building behaviour in domesticated pigs could be assumed. Therefore, the argument that modern sows do not necessarily build nests due to domestication has been used to doubt confinement in farrowing crates (Algers and Uvnäs-Moberg, 2007). These housing systems, established since the late 1950s, were designed to minimise piglet losses by crushing and to improve management (Edwards and Fraser, 1997). Additionally, Grauvogel (1958) postulated that a 'nest feeling' is provided by the enclosed crate and no negative effects on the sows have to be expected. First studies on nest-building behaviour in domestic pigs under semi-natural conditions were investigated in the 1980s (Stolba and Wood-Gush, 1989; Jensen, 1986; Algers and Jensen, 1990). Domestic sows, even with experience of four farrowings in confinement, were able to build nests identical to those of wild boars (Gustafsson et al., 1999). This led to the conclusion that domestication has not given rise to any changes in the performance of nest-building behaviour. Due to only few differences between maternal behaviour in wild and domesticated sows, Mignon-Grastreau et al. (2005) suggested that maternal behaviour is relatively robust in pigs. This statement is supported by Jensen (2002) who described similar behaviour patterns for free-ranging sows and wild boars. On the contrary, Price (1999) mentioned behavioural changes associated with the process of domestication. Through selection, inbreeding and genetic drift animals have been domesticated and forced to adapt to the provided housing and management. Given this adaptation, it might be expected that because nest-building is no longer needed, its associated behaviour would have vanished. However, domestication has not given rise to major changes in the performance of nest-building behaviour. This fact clearly underlines how innate this behaviour is, and highlights its importance.

3. Nest-building behaviour in different housing systems

All elements of nest-building are performed by female pigs in their environment as far as possible (Hutson and Haskell, 1990; Jensen and Toates, 1993). In commercially farmed pigs, maternal behaviour is usually strongly restricted (von Borell et al., 2007). In order to reduce piglet losses due to crushing, and to facilitate human intervention, systems to control sow movement were developed and farrowing crates were introduced on a large scale (Fraser and Broom, 1990; Edwards, 2002). Different types and systems have been created since then, but most of them without considering the natural periparturient behaviour of sows (Damm et al., 2003).

3.1. Housing in crates

Farrowing crates and concrete floors prevent much of the nest-building behaviour, but many of the motor elements are still present. In intensive pig production, most exogenous stimuli are excluded and in most cases only provided if regulated by legislation. In confinement, feedback from the nest site, necessary to continue successful nest-building in the material-oriented phase, is and can lead to prolonged, but futile nest-building motivation (Damm et al., 2000, 2003). In general, nest-building-like behaviour is shown, even in absence of exogenous stimuli. However, compared to sows housed in pens, nest-building in crates is performed only in a small variation and in more fragmented and longer phases (Damm et al., 2003). In the crates, animals may grind their teeth, bite and root at the rails and change position frequently between standing and lying (Heckt et al., 1988). In comparison to a turn-around crate and an open pen, frequency and duration of standing is greatest in the standard crate and increase gradually until the sow changes position every few minutes (Heckt et al., 1988). Sows housed in farrowing crates stand up more often before the onset of parturition compared to sows in pens (Hansen and Curtis, 1980). These activities are accompanied by intermittent grunting, champing of the jaws and increased respiratory rate (Heckt et al., 1988). Rooting with the nose and pawing with the front hooves is shown by sows on concrete floor during 'nest' preparation (Hartsock and Barczewski, 1997; Thodberg et al., 1999). Heckt et al. (1988) and Cronin et al. (1994) reported that crated gilts tended to paw more than gilts in open pens. The sow's drive to gather nesting material with the mouth results in rooting and mouthing pipes and waterers, as only these items are available for oral manipulation (Hartsock and Barczewski, 1997). In a study dealing with sows in crates and pens, the increase of plasma cortisol as stress indictor in crated sows was related to the interruption of pre-parturient behaviour like nest-building (Lawrence et al., 1997). Pre-partal stress may be coupled with slow parturition and lactation problems (Poe, 1960). Event though the adaption to the behavioural restriction in crates increases from parity to parity, this adaptation has not completely reduced the elevation of stress hormones (Jarvis et al., 2001). Of course it has to be considered that parturition itself influences the release of stress-indicators like cortisol (Lawrence et al., 1994). In general, confined sows show increased activity (Jarvis et al., 2001) and substrate directed-behaviour like interacting with floor and fixtures of the crate (Lawrence et al., 1997). As further possible indicators of stress or frustration, oral or nasal stereotypes are described, such as bar biting (Jensen, 1988b), repetitive pressing of the snout against a surface (Vestergaard, 1984), and straw chewing (Grauvogel, 1958; Horrel et al., 2001). Distinguishing between stereotypes and indirect nest-building behaviour is difficult, since biting and chewing on systemic equipment may be analogous to the act of gathering and carrying branches and twigs to the nest (Jensen, 1993; Hartsock and Barczewski, 1997). Farrowing in crates tends to be more stressful than in pens, even if adaptation to the crate environment occurs (Jarvis et al., 2001). Unsatisfied behavioural needs and idle activities can cause injuries and apparent exhaustion in the sow (Hansen and Curtis, 1980). Additionally, the lack of feedback can result in higher heart rates before farrowing (Jensen and Toates, 1993). Environmental stress of sows inhibits oxytocin and this may compromise the welfare of the sow and the piglet, because oxytocin influences the

maternal behaviour (Jarvis et al., 1997). Jarvis et al. (2004) found no relationship between space or substrate and oxytocin, but a positive relationship between oxytocin and unresponsiveness to piglets. Furthermore, Jarvis et al. (2004) described lower levels of oxytocin and higher ACTH concentrations in crated gilts, and these gilts showed more savaging as well as more activity and responsiveness towards their piglets. However, the environment did not affect the cortisol concentration (Jarvis et al., 1998). Ahlstrom (1997) reported a higher responsiveness of crated gilts to their piglets during early stages of farrowing, but a higher probability to savage their piglets. Sows in crates without nest materials have been reported to be less responsive to piglet screams one to three days postpartum (Thodberg et al., 2002a) and vocalise less to piglets on day 1 postpartum in comparison to sows in pens with nest materials (Cronin et al., 1996). On the other hand, Damm et al. (2002) found no effect of the housing environment on the timing of termination of nest-building behaviour during parturition or the course of parturition in gilts.

3.2. Housing in pens

The first study on nest-building behaviour in sows in pens was done by Buß (1972). The phases of nest-building were found to be similar to wild boars (Gundlach, 1968), but restricted by the provision of space and nesting material. In comparison to wild sows, sows housed in pens lack orientation, endurance and purposive directness within their instinctive acts. Explicit exploration behaviour could not be performed and the possibility for digging the hole was not given; therefore these elements were described as 'degraded behaviour' because of the lack of exogenous stimuli (Buß, 1972).On the contrary, all observed sows showed an overemphasis in padding out the nest with the straw provided and an exaggerated moving of straw to cover their body (Buß, 1972). In contrast to Hafez et al. (1962), Buß (1972) did not observe the sows cleaning the nest.

Sows housed in pens with straw perform more nest-building behaviour than pigs housed in pens with straw removed (Burne et al., 2000). Sows turn and walk more frequently during 24 h before farrowing in pens compared to the restricted possible activities in farrowing crates (Hartsock and Barczewski, 1997). Furthermore, Thodberg et al. (2002b) found more elaborated nest-building behaviour in 'get-away-pens' in comparison to crates and the pre-partum rooting period started significantly sooner with a longer duration. 'Nesting-like' behaviour occurred more frequently in penned than in crated sows (Cronin et al., 1994). Andersen et al. (2005) described significantly more nest-building activity of sows in pens that had not crushed one single piglet within the first 4 days. Herskin et al. (1998) showed that provision of nest material to loose-housed sows increased the response to piglet screams one to three days postpartum. The provision of space, even without straw, encourages the performance of maternal behaviour during parturition (Jarvis et al., 2004). Against this background, several attempts to develop alternative farrowing accommodation have been made. Although there are several alternative farrowing pens, most of the recent research has been carried out in the 'Schmid' or the 'Werribee farrowing pens'.

Schmid constructed a farrowing pen isolating the sow from other pigs while allowing nest-building behaviour (Schmid, 1991a,b). Under Swiss production circumstances, piglet mortality in these pens is comparable to that of farrowing crates (Schmid, 1991a, 1992, 1993). In these so-called 'Schmid pens' the duration of nest-building is with 8 h shorter than that in crates with 10.5 h (Damm et al., 2003). Even if the whole period is shorter, sows perform a greater variety of behaviour including more pawing, nodding, collecting, depositing and packing (Damm et al., 2003). Another attempt to offer more possibilities for the expression of nest-building behaviour is the 'Werribee farrowing pen' (WFP) (Cronin et al., 1996). This pen is twice as large as a usual crate and consists of two compartments, a 'nest' and a 'non-nest' area. The width of these pens affects nest-building behaviour, and an appropriately wide WFP is recommended (Cronin et al., 1998).

4. Discussion: consequences for modern sow management

As a major part of reproduction, the sow's pre-farrowing behaviour is strongly associated with piglet survival because it affects parturition (Heckt et al., 1988; McGlone et al., 1996; Cronin et al., 1993). Explicit nest-building behaviour can clearly be classified as a behavioural need for the pre-partum sow. It is a natural adaptation and even domesticated sows are highly motivated to perform this behaviour pattern. Allowing the sow to perform nest-building, or at least some elements of it, leads to better health and welfare of both the sow and the piglets (Algers, 1994). For instance, increased litter sizes were reported to be positively correlated with more nest-building behaviour (Pedersen et al., 2006). Additionally, a higher responsiveness to piglet distress calls and a lower mortality rate in piglets until weaning is documented in sows with better nest-building performance (Cronin and van Amerongen, 1991). When the opportunity for nest-building is given, the duration of sucking periods is increased and the number of sucking periods terminated by the sow is decreased (Herskin et al., 1998). Therefore, the possibility to perform nest-building behaviour should be offered to all sows in modern management systems. For this possibility, space and the provision of adequate nest-building material are two relevant pre-requisites. Under confinement, activities that need space like standing or walking can hardly be realized.

Denying sows space and material at the time of strong nest-building motivation is associated with negative consequences like reduced piglet survival or savaging of piglets (Hötzel et al., 2005) and results in physiological stress in the sow (Lawrence et al., 1994). With the implementation of the EU Directive 2001/88/EC, this stress might even have increased because all sows have to be loose-housed during the majority of gestation and the subsequent confinement can be a radical change (Boyle et al., 2000). The effects of stress on reproduction are a matter of scientific discussion. While some authors claim that sows are resistant to the effects of single or repeated stressors (Turner et al., 2002, 2005), more commonly it is expected that in pigs experiencing stress, reproduction is negatively affected (Varley and Stedmann, 1994; von Borell, 1995; Einarsson et al., 1996). In this way, a prolonged duration of the farrowing period after restricted nest-building is either caused directly by the less optimal conditions for nest-building or indirectly by the subsequent stress (Vestergaard and Hansen, 1984). The restraint-stillbirth hypothesis, first established by Baxter and Petherick (1980), claimed that the stress caused by the restriction of normal pre-farrowing behaviour in crates induces changes in the endocrine system leading to delayed births and raised stillbirth. On the contrary,

Fraser et al. (1997) hypothesised that stimulating the sows' pre-farrowing activity by pen-mates or human activity results in a lower stillbirth rate and suggested therefore a positive influence of stress towards the sows.

In pens and farrowing huts, the design can improve maternal behaviour and increase the sows' welfare, which is proposed to lead to a better survival and growth of the piglets (Algers, 1994; Damm et al., 2003). From a holistic point of view, ranking of the motivational effects of internal and external factors of nest-building behaviour is pointless (Jensen and Toates, 1993), but more moves to adapt the present farrowing systems to these behavioural needs are required. Farrowing accommodation restraining the sow's movements has repeatedly been shown to improve piglet survival (Edwards and Fraser, 1997), but for both economical and ethical reasons these systems require reconsideration (Edwards, 2002). Alternative housings systems resulted in similar piglet mortality rates compared to conventional systems (Weber et al., 2007; Wechsler and Weber, 2007), but the number of crushed piglets was significantly higher in pens with loosed housed sows (Weber et al., 2007). In loose-farrowing systems, piglet's mortality by crushing can be further reduced by a careful selection of environments and sows showing a genetic determination of positive maternal behaviour (Johnson et al., 2007).

Furthermore, not only space, but the use of nest-building material is restricted in confinement. This restriction results in the sow's inability to get external stimuli for the performance of nest-building behaviour. As shown, this behaviour is influenced both by internal and external stimuli (Blackshaw, 1983; Jensen, 1988a, 1993; Boulton et al., 1997; Burne et al., 1999; Thodberg et al., 1999). However, mainly external stimuli are crucial to express satisfactory nest-building. The act of nest building alone is more important than the provision of a nest (Widowski and Curtis, 1990). When pre-constructed nests are offered, the sows still show nest-building behaviour (Arey et al., 1991). In crates, sawdust bedding triggers a more active nesting-like 'behaviour' before farrowing, but once farrowing has started, sows are more passive (Cronin et al., 1993). This decreases the risk of crushing piglets during farrowing (Thodberg et al., 1999). Furthermore, these sows had a shorter duration of parturition (Cronin et al., 1994), and more piglets born alive, compared to sows that do not receive sawdust bedding (Cronin et al., 1993). McGlone et al. (1996) found that sows housed in farrowing crates with access to a cloth tassel that could be manipulated during the pre-farrowing period, tend to have a reduced incidence of stillbirth. Hötzel et al. (2005) noticed that providing confined sows with enough space and material decreased some of the negative effects of confinement, but did not eliminate them completely.

In the last years, legislation has assessed the welfare benefits of loose-farrowing systems and the implicated positive effects. The intention of several European Commission Directives, such as Directive 2001/88/EC regarding loose-housing, or Directive 2001/93/EC regarding rooting material, is to improve the welfare of pigs, but the sows' maternal behaviour has not yet been adequately considered in the legislation. In this regard, not only the piglets' survival, health and welfare have to be taken into account, but also the sows' health and welfare, including the reproduction performance.

An enriched environment in crates and a greater space for movement are first steps towards the reconsideration and integration of behavioural maternal needs in modern pig management. Therefore, following actions should be put into practice:

(i) in sow management: even though crates might be with no alternative in the following years, all chances to integrate the sows' behavioural needs should be taken. Under consideration of management, economic, health and hygiene factors, suitable material and space for nest-building-performance should be provided in the pre-partal period.
(ii) in research: alternative pens and nest-building material should be tested in detail with regard to practicability, application and effects on sows and piglets. Individual characteristics of single sows like maternal behaviour should be examined with respect to their genetic determination in order to breed sows better adapted to more open farrowing surroundings (Grandinson et al., 2003; Grandinson, 2005).
(iii) in legislation: results from research should be implemented into consistent EU-Regulations, considering space and material requirements in enriched environments.

Practice, research and legislation together should concentrate on management tools to realise an improvement of the sow's need for nest-building performance, not only in order to optimise the sows' health and welfare, but also for the following positive effects on consumer perception and price building.

5. Conclusion

A better understanding of behaviour patterns in general and farrowing behaviour, including nest-building in sows, is essential for an economically successful pig production. Compared to their ancestor, the wild boar, domestic sows perform nest-building as part of maternal behaviour in a nearly unmodified way. However, the pre-parturient behaviour is considerably affected by the husbandry system and is only shown to its full extent when environmental circumstances allow it. If the sow cannot follow her natural behavioural need, for instance when no material is available, she redirects her nest-building behaviour towards the pen or crate equipment. This results in stereotypes and stress, followed by a reduced reproduction performance. With regard to animal health and welfare, loose farrowing systems provide a good alternative while maintaining a high production performance. As long as these systems are not implemented, the farmers should provide at least suitable nest-building material like straw. Concluding, further research should evaluate and promote alternative enriched systems in order to support the economic use of these systems for the farmers.

Acknowledgement

The manuscript has benefited from the critical and helpful comments of an anonymous reviewer.

References

Ahlstrom, S., 1997. Assessing maternal behaviour in domestic pig. M.Sc. Thesis. University of Edinburgh.
Algers, B., 1994. Health, behaviour and welfare of outdoor pigs. Pig News Inf. 15 (4), 113N–115N.

Algers, B., Jensen, P., 1990. Thermal microclimate in winter farrowing nests of free-ranging domestic pigs. Livest. Prod. Sci. 25, 177–181.
Algers, B., Uvnäs-Moberg, K., 2007. Maternal behavior in pigs. Horm. Behav. 52, 78–85.
Andersen, I.L., Berg, S., Bøe, K.E., 2005. Crushing of piglets by the mother sow (*Sus scrofa*)—purely accidental or a poor mother? Appl. Anim. Behav. Sci. 93, 229–243.
Arey, D.S., Petchey, A.M., Fowler, V.R., 1991. The periparturient behaviour of sows in enriched pens and the effect of pre-formed nests. Appl. Anim. Behav. Sci. 31, 61–68.
Baxter, M.R., 1982. The nesting behaviour of sows and its disturbance by confinement of farrowing. In: Bessei, W. (Ed.), Disturbed Behaviour in Farm Animals. Seminar in the EEC Program of Coordination of Research in Animal Welfare at the University of Hohenheim, pp. 101–114.
Baxter, M.R., 1983. Ethology in environmental design for animal production. Appl. Anim. Ethol. 9, 207–220.
Baxter, M.R., Petherick, J.C., 1980. The effect of restraint on parturition in the sow. Proceedings of the International Pig Veterinary Society, vol. 6, p. 84.
Blackshaw, J.K., 1983. Prostaglandin-F-2-α induced nest-building behaviour in the nonpregnant sow, and some welfare considerations. Int. J. Study Anim. Probl. 4, 299–304.
Boulton, M.-I., Wickens, A., Goode, J.A., Gilbert, C.L., 1997. Prostaglandin F2-α-induced nest-building in pseudopregnant pigs. I. Effects of environment on behaviour and cortisol secretion. Physiol. Behav. 62, 1071–1078.
Boyle, L.A., Leonard, J.L., Lynch, P.B., Brophy, P., 2000. Influence of housing system during gestation on the behavior and welfare of gilts in farrowing crates. Anim. Sci. 71, 561–570.
Briedermann, L., 1986. Schwarzwild. VEB Deutscher Landwirtschaftsverlag, Berlin, DDR, pp. 269–270.
Burne, T.H.J., Murfitt, P.J.E., Goode, J.A., Boulton, M.I., Gilbert, C.L., 1999. Effects of oestrogen supplementation and space restriction on $PGF_2\alpha$-induced nest-building in pseudopregnant gilts. Anim. Reprod. Sci. 55, 255–267.
Burne, T.H.J., Murfitt, P.J.E., Gilbert, C.L., 2000. Deprivation of straw bedding alters $PGF_2\alpha$-induced nesting behaviour in female pigs. Appl. Anim. Behav. Sci. 69, 215–225.
Burne, T.H.J., Murfitt, P.J.E., Gilbert, C.L., 2001a. Influence of environmental temperature on $PGF_2\alpha$-induced nest building in female pigs. Appl. Anim. Behav. Sci. 71, 293–304.
Burne, T.H.J., Murfitt, P.J.E., Johnston, A.N.B., 2001b. $PGF_2\alpha$-induced nest building and choice behaviour in female domestic pigs. Appl. Anim. Behav. Sci. 73 (4), 267–269.
Buß, K.-D., 1972. Ein Vergleich des Nestbauverhaltens beim Wildschwein und Hausschwein, Dissertation, Hannover.
Castrén, H., Algers, B., de Passillé, A.-M., Rushen, J., Uvnäs-Moberg, K., 1993. Periparturient variation in progesterone, prolactin, oxytocin and somatostatin in relation to nest building in sows. Appl. Anim. Behav. Sci. 38, 91–102.
Cronin, G.M., van Amerongen, G., 1991. The effects of modifying the farrowing environment on sow behaviour and survival and growth of piglets. Appl. Anim. Behav. Sci. 30, 287–298.
Cronin, G.M., Schirmer, B.N., McCallum, T.H., Smith, J.A., 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 interpartum stillborn piglets. Appl. Anim. Behav. Sci. 36, 301–315.
Cronin, G.M., Smith, J.A., Hodge, F.M., Hemsworth, P.H., 1994. The behaviour of primiparous sows around farrowing in response to restraint and straw bedding. Appl. Anim. Behav. Sci. 39, 269–280.
Cronin, G.M., Simpson, G.J., Hemsworth, P.H., 1996. The effects of the gestation and farrowing environment on sow and piglet behaviour and piglet survival and growth in early lactation. Appl. Anim. Behav. Sci. 46, 175–192.
Cronin, G.M., Duntsmore, B., Lesson, E., 1998. The effect of farrowing nest size width on sow and piglet behaviour and piglet survival. Appl. Anim. Behav. Sci. 60, 331–345.
Damm, B.I., Vestergaard, K.S., Schrøder-Petersen, D.L., Ladewig, J., 2000. The effects of branches on prepartum nest building in gilts with access to straw. Appl. Anim. Behav. Sci. 69, 113–124.
Damm, B.I., Bildsøe, M., Gilbert, C., Ladewig, J., Vestergaard, K.S., 2002. The effect of confinement on periparturient behaviour and circulating prolactin, prostaglandin $F_{2\alpha}$ and oxytocin in gilts with access to a variety of nest materials. Appl. Anim. Behav. Sci. 76, 135–156.
Damm, B.I., Lisborg, L., Vestergaard, K.S., Vanicek, J., 2003. Nest-building behavioural disturbances and heart rate in farrowing sows kept in crates and Schmid pens. Livest. Prod. Sci. 80 (3), 175–187.
Dellmeier, G.R., Friend, T.H., 1991. Behaviour and extensive management of domestic sows (*Sus scrofa*) and litters. Appl. Anim. Behav. Sci. 29, 327–341.
Edwards, S.A., 2002. Perinatal mortality in the pig: environmental or physiological solutions? Livest. Prod. Sci. 78, 3–12.
Edwards, S.A., Fraser, D., 1997. Housing systems for farrowing and lactation. Pig J. 39, 77–89.
Eibl-Eibesfeldt, I., 1963. Angeborenes und Erworbenes im Verhalten einiger Säuger. Z. Tierpsychol. 20, 705–754.
Einarsson, S., Madej, A., Tsuma, V., 1996. The influence of stress on early pregnancy in pig. Anim. Reprod. Sci. 42, 165–172.
Ellendorff, F., Taverne, M., Elsaesser, F., Forsling, M., Parvizi, N., Naaktgeboren, C., Smidt, D., 1979. Endocrinology of parturition in the pig. Anim. Reprod. Sci. 2, 323–334.
Frädrich, H., 1974. A Comparison of Behaviour in the Suidae. . New Series, vol. 24. IUCN, Morges, pp. 133–143.
Fraser, D., 1980. A review of the behavioural mechanism of milk ejection of the domestic pig. Appl. Anim. Ethol. 6, 247–255.
Fraser, D., 1984. The role of behaviour in swine production: a review of research. Appl. Anim. Ethol. 11, 317–339.
Fraser, A.F., Broom, D.M., 1990. Farm Animal Behaviour and Welfare. Bailliére Tindall, London, p. 437.
Fraser, D., Phillips, P.A., Thompson, B.K., 1997. Farrowing behaviour and stillbirth in two environments: an evaluation of the restraint-stillbirth hypothesis. Appl. Anim. Behav. Sci. 55, 51–66.
Gilbert, C.L., Goode, J.A., McGrath, T.J., 1994. Pulsatile secretion of oxytocin during parturition in the pig: temporal relationship with fetal expulsion. J. Physiol. 475 (1), 129–137.
Gilbert, C.L., Murfitt, P.J.E., Burne, T.H.J., 2001. Effects of prostaglandin $F2_\alpha$ treatment of pseudopregnant pigs on nest building and interactions with newborn piglets. Horm. Behav. 39, 206–215.
Grandin, T., Deesing, M.J., 1998. Behavioral genetics and animal science. In: Grandin, T. (Ed.), Genetics and the Behavior of the Domestic Animals. Academic Press, San Diego, pp. 1–30.
Grandinson, K., 2005. Genetic background of maternal behaviour and its relation to offspring survival. Livest. Prod. Sci. 93, 43–50.
Grandinson, K., Rydhmer, L., Strandberg, E., Thodberg, K., 2003. Genetic of on-farm tests of maternal behaviour in sows. Livest. Prod. Sci. 83, 141–151.
Grauvogel, A., 1958. Über das Verhalten des Hausschweines unter besonderer Berücksichtigung des Fortpflanzungsverhaltens. Vet. Med. Diss., Berlin, p. 69.
Graves, H.B., 1984. Behavior and ecology of wild and feral swine (*Sus scrofa*). J. Anim. Sci. 58, 482–492.
Gundlach, H., 1968. Brutfürsorge, Brutpflege, Verhaltensontogenese und Tage-speriodik beim Europäischen Wildschwein. Z. Tierpsychol. 25, 955–995.
Gustafsson, M., Jensen, P., de Jonge, F.H., Illman, G., Špinka, M., 1999. Maternal behaviour of domestic sows and crosses between domestic sows and wild boar. Appl. Anim. Behav. Sci. 65, 29–42.
Hafez, E.S.E., Sumpton, L.J., Jakway, J.S., 1962. The behaviour of swine. In: Hafez, E.S. E. (Ed.), The Behaviour of Domestic Animals. Bailliére, Tindall and Cox, London.
Hansen, K.E., Curtis, S.E., 1980. Prepartal activity of sows in stall or pen, J. Anim. Sci. 51, 456–460.
Hartsock, T.G., Barczewski, R.A., 1997. Prepartum behaviour in swine: effects of pen size. J. Anim. Sci. 75, 2899–2904.
Haskell, M.J., Hutson, G.D., 1994. Pre-farrowing behaviour of sows and gilts with access to space for locomotion. Aust. J. Exp. Agric. 34, 1099–1105.
Heckt, W.L., Widowski, T.M., Curtis, S.E., Gonyou, H.W., 1988. Pre-partum behaviour of gilts in three farrowing environments. J. Anim. Sci. 66, 1378–1385.
Herpin, P., Damon, M., Le Dividich, J., 2002. Development of thermoregulation and neonatal survival in pigs. Livest. Prod. Sci. 78, 25–45.
Herskin, M.S., Jensen, K.H., Thodberg, K., 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.
Horrel, R.I., A'Ness, P.J., Edwards, S.A., Edison, J.C., 2001. The use of nose-rings in pigs: consequences for rooting, other functional activities, and welfare. Anim. Welf. 10 (1), 3–22.
Hötzel, M.J., Machado Filho, L.C.P., Dalla Costa, O.A., 2005. Behaviour of pre-parturient sows housed in intensive outdoor or indoor systems. Pesqui. Agropecu. Bras. 40, 169–174.
Hurnik, J.F., 1985. A review of periparturient behaviour in swine. Can. J. Anim. Sci. 65, 777–788.
Hutson, G.D., 1988. Do sows need straw for nest-building? Aust. J. Exp. Agric. 28, 187–194.
Hutson, G.D., Haskell, M.J., 1990. The behaviour of farrowing sows with free and operant access to an earth floor. Appl. Anim. Behav. 26, 363–372.
Jarvis, S., McLean, K.A., Chirnside, J., Deans, L.A., Calvert, S.K., Molony, V., Lawrence, A.B., 1997. Opioid-mediated changes in nociceptive threshold during pregnancy and parturition in the sow. Pain 72, 153–159.
Jarvis, S., Lawrence, A.B., McLean, K.A., Chirnside, J., Deans, L.A., Calvert, S.K., 1998. The effect of environment on plasma cortisol and β-endorphin in the parturient pig and the involvement of endogenous opioids. Anim. Reprod. Sci. 52, 139–151.
Jarvis, S., Van der Vegt, B.J., Lawrence, A.B., McLean, K.A., Deans, L.A., Chirnside, J., Calvert, S.K., 2001. The effect of parity and environmental restriction on behavioural and physiological responses of pre-parturient pigs. Appl. Anim. Behav. Sci. 71, 203–216.
Jarvis, S., Reed, B.T., Lawrence, A.B., Calvert, S.K., Stevenson, J., 2004. Peri-natal environmental effects on maternal behaviour, pituitary and adrenal activation, and the progress of parturition in the primiparous sow. Anim. Welf. 13 (2), 171–181.

Jensen, P., 1986. Observations on the maternal behaviour of free-ranging domestic pigs. Appl. Anim. Behav. Sci. 16, 131–142.
Jensen, P., 1988a. Maternal behaviour of free-ranging domestic pigs, 1. Result of a three-year study. Report 23. Swedish University of Agricultural Sciences, Skara, p. 56.
Jensen, P., 1988b. 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.
Jensen, P., 2002. Behaviour of pigs. In: Jensen, P. (Ed.), The Ethology of Domestic Animals. CABI Publishing, Wallingford, UK, pp. 159–172.
Jensen, P., Redbo, I., 1987. Behaviour during nest leaving in free-ranging domestic pigs. Appl. Anim. Behav. Sci. 18, 355–362.
Jensen, P., Toates, F.M., 1993. Who needs 'behavioural needs'? Motivational aspects of the needs of animals. Appl. Anim. Behav. Sci. 37, 161–181.
Jensen, P., Florén, K., Hobroh, B., 1987. Peri-parturient changes in behaviour in free-ranging domestic pigs. Appl. Anim. Behav. Sci. 17, 69–76.
Johnson, A.K., Morrow, J.L., Dailey, J.W., McGlone, J.J., 2007. Preweaning mortality in loose-housed lactating sows: behavioural and performance differences between sows who crush or do not crush piglets. Appl. Anim. Behav. Sci. 105, 59–74.
Jones, J.E.T., 1966. Observations on parturition in the sow. I. The pre-partum phase. Brit. Vet. J. 122, 420–426.
Kilgour, R., 1985. Imprinting in farm animals. In: Fraser, A.F. (Ed.), Ethology of Farm Animals. World animal sciences A, Basic information, vol. 5. Elsevier, Amsterdam, p. 143.
Kurz, J.C., Marchinton, R.L., 1972. Radiotelemetry studies of feral hogs in South Carolina. J. Wildl. Manage. 36, 1240–1248.
Lawrence, A.B., Petherick, J.C., McLean, K.A., Deans, L.A., Chirnside, J., Vaughan, A., Clutton, E., Terlouw, E.M.C., 1994. The effect of environment on behaviour, plasma cortisol and prolactin in parturient sows. Appl. Anim. Behav. Sci. 39, 313–330.
Lawrence, A.B., McLean, K.A., Jarvis, S., Gilbert, C.L., Petherick, J.C., 1997. Review. Stress and parturition in the pig. Reprod. Domest. Anim. 32, 231–236.
Lent, P.C., 1974. Mother–infant spatial relationships in ungulates. In: Geist, V., Walther, F. (Eds.), The Behaviour of Ungulates and its Relationship to Management. New Series. IUCN, Morges, Switzerland, pp. 14–55.
Lindsay, D.R., 1985. Behavioural drives. In: Fraser, A.F. (Ed.), Ethology of Farm Animals. World animal sciences A, Basic information, vol. 5. Elsevier, Amsterdam, pp. 103–108.
Lorenz, K., 1937. Über die Bildung des Instinktbegriffes. Naturwissenschaften 25, 289–331.
Lorenz, K., 1959. Psychologie und Stammesgeschichte in Herberer: Die Evolution der Organismen. Fischer-Verlag, Stuttgart.
Martys, M., 1982. Gehegebeobachtungen zur Geburts- und Reproduktionsbiologie des Europäischen Wildschweins (*Sus scrofa* L.). Z. Säugetierkd. 47, 100–113.
Mayer, J.J., Martin, F.D., Brisbin, I.L., 2002. Characteristics of wild pig farrowing nests and beds in the upper Coastal Plain of South Carolina. Appl. Anim. Behav. Sci. 78, 1–17.
McGlone, J.J., Widowski, T.M., Stricklen, K.D., Mitchell, D., Curtis, S.E., 1996. Sow access to tassel pre-farrowing: preliminary evidence of stillbirth rate. J. Anim. Sci. 74 (1), 127.
Mignon-Grastreau, S., Boissy, A., Bouix, J., Faure, J.-M., Fisher, A.D., Hinch, G.N., Jensen, P., Le Neindre, P., Mormède, P., Prunet, P., Vandeputte, M., Beaumont, C., 2005. Genetics of adaption and domestication in livestock. Livest. Prod. Sci. 93, 3–14.
Myrcha, A., Jezierski, W., 1972. Metabolic rate during the postnatal development of wild boars. Acta Theriol. XVII (33), 443–452.
Pedersen, L.J., Jørgensen, E., Heiskanen, T., Damm, B.I., 2006. Early piglet mortality in loose-housed sows related to sow and piglet behaviour and to the progress of parturition. Appl. Anim. Behav. Sci. 96, 215–232.
Pfeffer, P., 1959. Biologie et migrations du sanglier de Borneo (*Sus barbatus*). Mammalia 23, 277–303.
Poe, E.R., 1960. Round stall for farrowing. Nebrasks Exp.Sta. Quarterly, vol. 7, p. 12.
Portmann, A., 1960. Kindheit der Säugetiere. Documenta Geigy, Nr. 3, Basel.
Price, E.O., 1999. Behavioral development in animals undergoing domestication. Appl. Anim. Behav. Sci. 65, 245–271.
Pullar, E.M., 1953. The wild (feral) pigs of Australia: their origin, distribution and economic importance. Mem. Nat. Mus. Melb. 18, 7–23.
Randall, G.C.B., 1972. Observations on parturition in the sow. I. Factors associated with the delivery of the piglets and their subsequent behaviour. Vet. Rec. 90, 178–182.
Robertson, J.B., Laired, R., Hall, J.K.S., Forsyth, R.J., Thomson, J.M., Walker-Love, J., 1966. A comparison of two indoor farrowing systems of sows. Anim. Prod. 8, 171–177.
Schmid, H., 1991a. Verhaltensgerechte Abferkelbucht nach Schmid. FAT, Nutztierethologie Universität Zürich-Irchel, p. 2.
Schmid, H., 1991b. Arttypische Strukturierung der Abferkelbucht. Aktuelle Arbeiten zur artgemäßen Tierhaltung 1991. KTBL-Schr. 351, 27–36.
Schmid, H., 1992. Abferkelbuchten: ein neues Konzept. FAT-Ber. 417, 8.
Schmid, H., 1993. Ethological design of a practicable farrowing pen. Proceedings of the international Congress on Applied Ethology, Berlin 1993, pp. 238–242.
Schulz-Scholz, J., 1963. Über den Einfluß verschiedener Verhaltensweisen auf die Lernfähigkeit von Haushühnern. Z. Wiss. Zool. 168.
Signoret, J.P., Baldwin, B.A., Fraser, D., Hafez, E.S.E., 1975. The behaviour of swine. In: Hafez, E.S.E. (Ed.), The Behaviour of Domestic Animals. Baillière, Tindall and Cox, London.
Snethlage, K., 1967. Das Schwarzwild. Verlag Paul Parey, Hamburg und Berlin.
Stangel, G., Jensen, P., 1991. Behaviour of semi-naturally kept sows and piglets (except suckling) during 10 days postpartum. Appl. Anim. Behav. Sci. 31, 211–227.
Stolba, A., Wood-Gush, D.G.M., 1984. The identification of behavioural key features and their incorporation into a housing design for pigs. Ann. Rech. Vet. 15 (2), 287–298.
Stolba, A., Wood-Gush, D.G.M., 1989. The behaviour of pigs in a semi-natural environment. Anim. Prod. 48, 419–425.
Studnitz, M., Jensen, M.B., Pedersen, L.J., 2007. Why do pigs root and what will they root? A review on the exploratory behavior of pigs in relation to environmental enrichment. Appl. Anim. Behav. Sci. 107, 183–197.
Thodberg, K., Jensen, K.H., Herskin, M.S., Jørgensen, E., 1999. Influence of environmental stimuli on nest-building and farrowing behaviour in domestic sows. Appl. Anim. Behav. Sci. 63, 131–144.
Thodberg, K., Jensen, K.H., Herskin, M.S., 2002a. Nursing behaviour, post partum activity and reactivity in sows: effects of farrowing environment, previous experience and temperament. Appl. Anim. Behav. Sci. 77, 53–76.
Thodberg, K., Jensen, K.H., Herskin, M.S., 2002b. Nest building and farrowing in sows: relation to the reaction pattern during stress, farrowing environment and experience. Appl. Anim. Behav. Sci. 77, 21–42.
Tisdell, C.A., 1982. Wild Pigs: Environmental Pest or Economic Resource? Pergamon Press, New York, p. 24.
Turner, A.I., Hemsworth, P.H., Tilbrook, A.J., 2002. Susceptibility of reproduction in female pigs to impairment by stress and the role of the hypothalamo-pituitary-adrenal axis. Reprod. Fertil. Dev. 14, 377–391.
Turner, A.I., Hemsworth, P.H., Tilbrook, A.J., 2005. Susceptibility of reproduction in female pigs to impairment by stress or elevation of cortisol. Domest. Anim. Endocrinol. 29, 398–410.
Uvnäs-Moberg, K., Johansson, B., Lupoli, B., Svennersten-Sjaunja, K., 2001. Oxytocin facilitates behavioural, metabolic and physiological adaptations during lactation. Appl. Anim. Behav. Sci. 72, 225–234.
Varley, M., Stedmann, R., 1994. Stress and reproduction. In: Cole, D.J.A., Wiseman, J., Varley, M.A. (Eds.), Principles of Pig Science. Nottingham University Press, UK, pp. 277–296.
Vestergaard, K., 1984. Adfærd hos opbundne og løse søounder drægtighed og faring. Doctoral dissertation. The Royal Veterinary and Agricultural University, Department of Animal Science and Animal Health, Kopenhagen, Denmark, pp. 216.
Vestergaard, K., Hansen, L.L., 1984. Tethered versus loose sows: ethological observations and measures of productivity. I. Ethological observations during pregnancy and farrowing. Ann. Rech. Vet. 15, 245–256.
von Borell, E., 1995. Neuroendocrine integration of stress and significance of stress for the performance of farm animals. Appl. Anim. Behav. Sci. 44, 219–227.
von Borell, E., Dobson, H., Prunier, A., 2007. Stress, behaviour and reproductive performance in female cattle and pigs. Horm. Behav. 52, 130–138.
Weber, R., Keil, N.M., Fehr, M., Horat, R., 2007. Piglet mortality on farms using farrowing systems with or without crates. Anim. Welf. 16 (2), 227–279.
Wechsler, B., Weber, R., 2007. Loose farrowing systems: challenges and solutions. Anim. Welf. 16 (3), 295–307.
Widowski, T.M., Curtis, S.E., 1989. Behavioral responses of periparturient sows and juvenile pigs to prostaglandin F2α. J. Anim. Sci. 67, 3266–3276.
Widowski, T.M., Curtis, S.E., 1990. The influence of straw, cloth tassel, or both on the prepartum behaviour of sows. Appl. Anim. Behav. Sci. 27, 53–71.
Widowski, T.M., Curtis, S.E., Dziuk, P.J., Wagner, W.C., Sherwood, O.D., 1990. Behavioural and endocrine responses of sows to prostaglandin F2-alpha and cloprostenol. Biol. Reprod. 43, 290–297.