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**EFFECT OF ENVIRONMENT AND MANAGEMENT ON
REPRODUCTIVE EFFICIENCY OF SOWS with special
emphasis on control of seasonal infertility**

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ACADEMIC DISSERTATION

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1. ABSTRACT

Seasonal infertility is well-defined phenomenon in modern swine production in the northern and southern hemispheres, where day length varies considerably between seasons. The outcomes mostly affected are age at puberty in gilts, weaning-to-oestrus interval (WOI) and farrowing rate in sows.

The European wild boar, the ancestor of our domestic pig, is a distinct short-day seasonal breeder. Photoperiod is thought to be the most important regulating factor in seasonal breeders. In addition to photoperiod, many environmental and management factors (e.g. social stress, feeding, boar contact, temperature) are known to adjust the manifestation of seasonal infertility. Finding solutions to the seasonal infertility problem by modifying the photoperiod and housing management of sows seems reasonable. The aim of this work was to obtain information about the effect of photoperiod on reproductive endocrinology, especially on the luteinizing hormone (LH) pattern, and on reproductive performance, measured by farrowing rate and WOI. In addition, the effect of re-modelling the piggery breeding unit on farrowing rate was studied.

In the first clinical trial (I), two light regimes were tested in experimental conditions. One group of ovariectomized gilts (both domestic pigs and European wild boars, altogether 20 animals) was kept under short daylight conditions (8 hours light, 16 hours dark) and the other group under long daylight conditions (16 hours light, 8 hours dark). After the treatment period, LH secretion patterns were determined by repeated blood sampling. In contrast to our expectations, LH pulse frequency remained unchanged in both light regimes. However, in the domestic pig, mean and basal LH concentrations were higher in the long-day group than in the short-day group.

To investigate the two light regimes under more practical conditions, two trials (II, III) were conducted in commercial piggeries. The outcomes were farrowing rate and WOI. In trial II, the long-day group was kept under a constant 16-h light, 8-h dark regime (16L:8D). The short daylight regime consisted a of light phase of 8-h and a dark phase of 16-h (8L:16D) in farrowing and breeding units. The length of the short-day treatment was 6 weeks before breeding. In the gestation unit, the short-day animals were also kept under a 16L:8D regime. The rationale for this arrangement was to hasten the natural seasonal breeding cycle such that sows would be fertile approximately twice a year, namely during the critical breeding period. However, the results of this trial revealed that the farrowing rate was 90% in both groups, and the two treatment groups also shared the same median WOI, i.e. 5 days.

In trial III, some methodological modifications of the light regimes were carried out. The long daylight regime consisted again of a constant long-day treatment. However, the photophase was 14L:10D. The short-day treatment was extended to 8 weeks and took place exclusively in the farrowing unit. The light regime was 10L:14D. The short-day group was also kept under a 14L:10D regime in the breeding and gestation units. Despite these modifications, the results were the same as in the previous trial. The farrowing rate was 90% and median WOI five days in both groups.

The last part (IV) of this thesis was an observational retrospective cohort study with a historical control. A cohort of farms with individual cages in their breeding unit was chosen. These farms either remodelled their breeding cages or switched to different group housing systems in the breeding unit between 1995 and 2002. The farrowing rate before and one year after the remodelling was then compared. The remodelling itself was shown to affect reproductive performance on these farms. The farrowing rate increased in farms that were classified as problematic based on initial reproductive performance. However, on the initially better farms, the farrowing rate decreased. If the herd's initial reproductive performance was not considered, the remodelling of the piggery breeding unit had no impact on farrowing rate.

In conclusion, the reproductive performance of sows is difficult to control by a single environmental (photoperiod) or management (housing strategy) factor.

2. LIST OF ORIGINAL PAPERS

This thesis is based on the following four original papers, referred to by their Roman numerals.

- I Hälli, O., Peltoniemi, O.A.T., Tast, A., Virolainen, J., Munsterhjelm, C., Valros, A, Heinonen, M. Photoperiod and luteinizing hormone secretion in domestic and wild pigs. *Anim. Reprod. Sci.* 2008, 103: 99-106.
doi: 10.1016/j.anireprosci.2006.11.019
- II Tast, A., Hälli, O., Virolainen, J.V., Oravainen, J., Heinonen, M., Peltoniemi, O.A.T. Investigation of simplified artificial lighting programme to improve the fertility of sows in commercial piggeries. *Vet. Rec.* 2005, 156: 702-705.
- III Hälli, O., Tast, A., Heinonen, M., Munsterhjelm, C., Valros, A., Peltoniemi, O.A.T. Simple light regime may not affect reproductive performance in a sow. *Reprod. Dom. Anim.*, in press.
- IV Hälli, O., Heinonen, M., Munsterhjelm, C., Valros, A., Peltoniemi, O.A.T. Re-modelling the piggery breeding unit may affect the farrowing rate. *Reprod. Dom. Anim.*, in press.

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3. ABBREVIATIONS

ACTH	adrenocorticotropic hormone
CV	coefficient of variation
FR	farrowing rate
GnRH	gonadotrophin-releasing hormone
HF	farms with initially high farrowing rate
HPA	hypothalamo-pituitary-adrenal
I ¹²⁵	radioactive iodine
LF	farms with initially low farrowing rate
LH	luteinizing hormone
rpm	rounds per minute
WOI	weaning-to-oestrus interval

4. INTRODUCTION AND REVIEW OF LITERATURE

4.1. Seasonal infertility

The European wild boar (*Sus scrofa*), the ancestor of our domestic pig, is a short-day breeder. The reason behind this phenomenon is quite simple – to create a suitable mechanism to adjust the fertile period of this species so that birth of offspring will occur during the optimal time of the year, namely spring. Thus, reproduction of wild boar is stimulated by the short daylength in autumn. Accordingly, long day length in the spring and early summer drives the European wild boar towards a sexually inactive period (Mauget, 1982). The impaired fertility of domestic pigs in the summer-autumn period is a vestige of ancestral seasonal breeding.

4.1.1. Manifestations of seasonal infertility

Seasonal infertility is an established problem in the swine industry (Love et al., 1993). In gilts and sows, seasonal infertility has three main manifestations. Firstly, farrowing rate (proportion of bred sows that farrow) decreases. Breedings completed during late summer and early autumn are more likely to spontaneously abort than breedings during the rest of the year. A significant proportion of bred gilts and sows return to oestrus, quite often with an irregular interval, during the seasonal infertility period, leading to a lower farrowing rate (Tast et al., 2002).

Secondly, the prolonged interval from weaning to oestrus could at least partly be caused by seasonal infertility. High temperatures may reduce feed intake during lactation. In addition, seasonality has a minor effect on postponing oestrus after weaning (review by Claus and Weiler, 1985). Parity-one sows are especially prone to suffer from delayed oestrus, probably because they cannot cope with the metabolic demands of lactation as well as older sows (Hurtgen et al., 1980; Peltoniemi et al., 1999).

Thirdly, seasonal infertility shows itself in delayed puberty of gilts (review by Hughes, 1982). In gilts expected to attain puberty between August and November, a more than five-day delay was observed (Peltoniemi et al., 1999). Paterson and Pearce (1990) claim that long days are inhibitory in gilts' in attainment of puberty. Nevertheless, appropriate boar contact around sexual maturation has been shown to weaken the innate effect of seasonality in gilts (Paterson et al., 1991).

4.1.2. Regulation of seasonality of reproduction

Photoperiod

Photoperiod is known to be the most important external regulating factor of reproduction in seasonal breeders. Already in the 1930's, the first studies demonstrated the importance of photoperiod in the regulation of seasonality. These studies dealt with photoperiodic reversals. When ewes were transported across the equator, their annual reproductive cycle was reversed to follow the photoperiod of

the new location; although that reversal took considerable amount of time, even years. Another cue of the deterministic role of photoperiod on seasonal reproduction is the possibility to accelerate the seasonal cycle with artificial light regimes. If short and long regimes are altered successively, ewes react to these changes by modifying their reproductive activity accordingly. Thus, the annual reproductive cycle can be shortened and one calendar year can contain two reproductively active periods (for reviews, see Karsch et al., 1984, sheep; Love et al., 1993, Peltoniemi and Virolainen, 2006, pig).

Feeding

Feeding has a potential modifying effect on seasonality. In wild boars, if there is an abundance of feed, the breeding season will commence earlier than with meagre fare (Mauget, 1982). Love et al. (1993) have shown that a high feeding level during the seasonal infertility period is advantageous over a low feeding level in terms of farrowing rate. Effect of feeding has been proposed to be mediated via luteinizing hormone (LH) secretion. Feed restriction can decrease mean LH concentration and LH pulse frequency. In addition, feed restriction causes diurnal variation in porcine LH secretion. During dark hours, mean LH concentration is higher than mean LH concentration during light hours. When feeding is returned to an *ad libitum* level, this diurnal variation vanishes (Cosgrove et al., 1993; Booth et al., 1996). However, in early pregnant gilts, feed restriction has been shown to alter LH pulse frequency only in the winter season, not in the summer-autumn period (Peltoniemi et al., 1997a, 1997b). Also, in most recent studies, LH pulse frequency remained unchanged with different feeding levels. However, mean and basal LH concentrations were elevated in gilts receiving a higher level of feeding (Virolainen et al., 2004). In conclusion, since both photoperiod and feeding are considered to have an effect on LH secretion, their combined impact on reproduction is of great importance.

Temperature

The implications of ambient temperature on seasonal reproduction are currently under debate. At least in Finland, the timing of seasonal infertility during late summer and early autumn does not coincide with the warmest period of the year – temperatures are already decreasing during this period. On the other hand, high temperature can have an undesirable effect on reproductive hormone levels in female pigs (Flowers and Day, 1990; Barb et al., 1991) and can also lower reproductive performance (Tantasuparuk et al., 2000; Almond and Bilkei, 2005; Suriyasomboon et al., 2006). These effects could be mediated via depressed voluntary feed intake at higher temperatures, leading to poorer reproductive performance as shown by Prunier et al. (1996) and Peltoniemi et al. (1999). The combined effect of ambient temperature and photoperiod on weaning-to-oestrus interval (WOI) was studied by Prunier et al. (1994). Their experiment revealed that both photoperiod and temperature could affect reproductive performance of gilts. However, the summary effect of these two environmental factors was the most relevant predictor of WOI. The best results were achieved under short photoperiod with moderate temperature and the worst under long photoperiod with high temperature. Under long photoperiod, a lower temperature was unable to save reproductive performance; this was also the case with short photoperiod and higher temperatures.

For the sake of clarity, it is essential to differentiate between seasonal infertility and the ‘autumn abortion syndrome’. Autumn abortion syndrome is similar to seasonal

infertility in terms of pregnancy losses – in both cases, the whole litter is typically lost. However, autumn abortion syndrome is related to major alterations in daily temperatures and poor coping possibilities provided to the sows. Sows kept in individual cages without bedding and fed only a moderate amount of feed are prone to react to sudden changes in ambient temperature (Almond et al., 1985).

Social factors and housing

Housing systems have been shown to affect both the welfare and the production of sows (McGlone et al., 2004). In the context of seasonal infertility, group housing in older studies has caused decreased reproductive performance compared with individual housing (Hurtgen and Leman, 1980; Love et al., 1995). In stalls, the weaning-to-insemination interval has been longer in autumn than at other times of the year (Peltoniemi et al., 1999). In group housing systems, early pregnancy losses are typical during the seasonal infertility period (Peltoniemi et al., 1999; Tast et al., 2002). In conclusion, social stress combined with an inhibitory photoperiod signal apparently compromises the reproductive performance of sows.

4.1.3. Endocrinology behind seasonal reproduction

Regulation of the seasonal reproduction relies on an innate circannual and circadian rhythm of animals. The term “circannual” refers to a cycle that has a length of approximately one year and repeats itself year after year. A circadian rhythm is a roughly 24-h cycle in the physiological processes of mammals. Both rhythms are endogenously generated, although they can be modulated by external cues – the photoperiod being the most important with regard to seasonal fertility and other factors acting as modulators as discussed above. To be able to entrain the innate rhythm to the prevailing photoperiodic conditions, a neuroendocrinological regulation mechanism is required.

Melatonin

In neuroendocrinological control of seasonality, melatonin is considered a chemical messenger that conveys information coded in a photoperiod to the reproductive functions of an animal (for review, see Karsch et al., 1984). Both wild boars (*Sus scrofa*) and domestic pigs react to changes in daylength by modified melatonin secretion (Tast et al., 2001a). The duration of nighttime melatonin secretion responds to photoperiod. Long duration of dark hours leads to the extended melatonin secretion. The melatonin secretion pattern also responds rapidly to changes in daylength in pigs (Tast et al., 2001b).

The primary target organ for melatonin action is the so-called ‘GnRH pulse generator’ in the hypothalamus. The effect of melatonin on GnRH is mediated by different neurotransmitters (e.g. dopamine, endogenous opioids). By changing the GnRH secretion, the effects of melatonin reach the whole hypothalamo – pituitary – gonadal axis. In short-day breeders, sufficiently long daily melatonin secretion triggers more frequent GnRH pulses, leading to increased pulsatile LH secretion. Frequency of the LH pulses is considered deterministic for the commencement of

reproductive functions –after either seasonally or lactationally induced anoestrus (Goodman and Karsch, 1981; Karsch et al., 1984).

Although short-day photoperiod and long duration of daily melatonin secretion coincide with commencement of breeding season, strong evidence exists that the entire seasonal reproduction cascade relies more on the endogenous circannual cycle of reproduction than on individual hormone concentrations. At least in sheep, the lengthening photoperiod after winter solstice entrains the innate reproductive rhythm, and the breeding season begins after a certain period of time has elapsed from the initial lengthening of day (Malpaux et al., 1989; Wayne et al., 1990). Shortening daylength in turn, has an important role in maintaining the normal duration of the breeding season (Malpaux et al., 1988a; Malpaux and Karsch, 1990). The end of the breeding season can be controlled in at least two different ways. In sheep, photorefractoriness to short days or manifestation of an endogenous reproductive rhythm is proposed to terminate the breeding season (Malpaux et al., 1988b). Thus, there is an obligatory cessation in reproductive functions. On the other hand, red deer seem to react to the inhibitory signal of long daylength. Thus, breeding season ends when the day is sufficiently long (Adam et al., 1989).

The effect of circannual and circadian melatonin rhythms and their implications and modes of action in regulation of reproduction nevertheless remain partly unknown in pigs. We do not know how the pig interprets or employs the circadian rhythm of melatonin secretion to entrain the innate circannual reproductive cycle. Basset et al. (2001) reported that melatonin implants inserted around the spring solstice or *per os* treatment prohibited the seasonal anoestrus in sows with a confirmed history of reproductive failure, but not so strongly in more fertile sows with more recent boar contact. Melatonin treatment had showed no influence on the seasonally oscillating LH pattern during melatonin treatment. However, this is not unexpected since sheep LH secretion has been demonstrated to increase at the resumption of oestrous cycles, not earlier (Robinson et al., 1991). In gilts, melatonin treatment *per os*, but not as an implant, proved efficient in preventing seasonal delay in puberty (Paterson et al., 1992).

In a trial by Basset et al. (2001), melatonin implants were used to block perception of increasing daylength in a group of cyclic sows. Thus, the aim was to prevent sows from becoming anoestrous. Interestingly, in sheep, prevention of anoestrus by using melatonin implants shortly before the end of the breeding season seems not to be possible (Malpaux et al., 1988b; Jordan et al., 1990). These observations suggest that the pig is more like red deer in terms of endocrinological control of breeding season termination.

Again, in sheep, it is known that melatonin implants or melatonin given *per os* as well as artificial light regimes can advance the beginning of the breeding season after anoestrus (English et al., 1986). Based on results from sheep, red deer and pigs, the effect of melatonin implants depends at least on the species involved and the reproductive state of animals. The mode of action of the continuous elevation of melatonin achieved with implants has been studied only in sheep. Implants can act as a short-day signal instead of turning ewes nonphotoperiodic, and thus, unable to recognize the inhibitory long-day signal. This mode of action is limited to certain reproductive situations and may not cover practical applications of melatonin implants (O'Callaghan et al., 1991).

Luteinizing hormone

The sheep is considered a model species of short-day seasonal breeders (Karsch et al., 1984). The pulsatile LH secretion changes throughout the different seasons in sheep. During seasonal anoestrus, LH pulses occur at a low frequency, in contrast to more frequent pulses during the breeding season (Yuthasastrakosol et al., 1975; Scaramuzzi and Baird, 1977). Infrequent LH pulses seem to be inadequate for stimulating follicle growth, and thus, no ovulation occurs during anoestrus (Baird and McNeilly, 1981; Goodman and Karsch, 1981).

As stated above, photoperiod is the most important external clue for seasonal breeders to distinguish between anoestrus and the breeding season. Robinson et al. (1985) were able to demonstrate the stimulatory effect of shortening daylength on LH pulse frequency using an artificial light regime. Ovariectomized, anoestrous ewes were first reared in a long-day light-dark (L:D) cycle. After the L:D cycle was changed to a shorter day treatment, LH pulses occurred more frequently. Photoperiod itself seemed to have a direct effect on pulsatile LH secretion.

Steroids secreted from ovaries, especially oestrogen, have an important role in the regulation of LH pattern. The LH pulse frequency increases markedly following ovariectomy in anoestrus (Diekman and Malven, 1973). However, oestradiol supplementation after ovariectomy can inhibit the increase in LH pulse frequency. Interestingly, this suppression occurs only in anoestrous ewes. During the breeding season, oestradiol supplementation after ovariectomy was able to suppress only the LH pulse amplitude, without decreasing the pulse frequency (Goodman et al., 1982). Thus, strong evidence exists to support seasonal variation in oestradiol's ability to suppress pulsatile LH secretion in sheep. The seasonally changing ability of oestradiol to suppress LH pulse frequency is very likely connected to photoperiod. It is known to be a steroid-dependent effect of photoperiod on LH secretion.

To determine whether season and reproductive cycle have an impact on porcine LH secretion, a few trials have been carried out. Almond and Dial (1990a) found that LH pulse frequency tended to be higher in dioestrous, cyclic sows than in anoestrous ones. In pregnant gilts, the LH pulse frequency was higher during winter than during autumn (Smith and Almond, 1991). When gilts that are about to attain puberty are reared under artificial long or short days, LH pulses are more frequent in long-day gilts than in short-day gilts. The author explains these results with the light regime in which the gilts are reared before sampling. Short-day gilts appear to reach puberty earlier than long-day gilts, and therefore, ovarian steroids inhibit the LH pulse frequency, to which the hypothalamus is sensitive after puberty (Paterson et al., 1992). A trial that focused mainly on the effect of different energy feeding levels during early pregnancy revealed that season tended to influence the LH pulse frequency. During winter, LH pulses seemed to be of a more regular shape and definitely had a higher amplitude. Summertime basal LH level appeared to be irregular, thus making detection of LH pulses difficult (Peltoniemi et al., 1997a). In conclusion, whether true differences exist in the pulsatile LH secretion of pigs during different times of the year remains somewhat unclear.

Regarding the steroid-independent effect of photoperiod on LH secretion in pigs, results again are quite confusing. In ovariectomized pigs held in an artificially controlled short photoperiod, LH pulse frequency stayed unchanged compared with

pigs maintained under a long photoperiod. However, in a long photoperiod, basal LH concentration was higher than in a short photoperiod (Peacock, 1991).

Similar to sheep, ovaries and oestradiol contribute to the regulation of LH secretion in pigs. After ovariectomy, LH pulse frequency increases considerably in sows that were either anoestrous or cyclic before ovariectomy. The increase in pulse frequency in anoestrous sows was even higher than in cyclic sows. This might be due to the greater inhibition of oestradiol on LH release in anoestrous sows before ovariectomy (Almond and Dial, 1990b). To further study the impact of oestradiol on LH secretion in different types of sows, a trial was conducted. In the trial, anoestrous and cyclic sows were treated with an oestradiol implant after ovariectomy. Sham-treated anoestrous sows had higher LH pulse frequency than oestradiol-supplemented anoestrous sows. No differences in terms of LH secretion were detected in sham-treated cyclic sows as compared with oestradiol-treated cyclic sows. Oestradiol also suppressed the LH pulse frequency more in anoestrous sows than in cyclic sows: pulse frequency was lower in anoestrous animals (Almond and Dial, 1990c). Thus, the regulation mechanism of LH secretion seems to be more sensitive to the negative feedback of oestradiol in anoestrous than in cyclic sows.

When trying to connect the effect of both photoperiod and oestradiol on LH secretion, the pig is not as easy to understand as the sheep. Natural photoperiod affected oestradiol benzoate-induced oestrus behaviour and some LH secretion patterns in ovariectomized primiparous sows. Oestradiol benzoate-induced inhibition of LH secretion occurred more slowly in autumn than in summer and winter. Most importantly, this inhibition lasted longer in autumn, especially in sows that failed to show oestrus behaviour. However, no difference was present in LH pulse frequency between different seasons. Amplitude and basal level were greater during the summer than during other seasons (Cox et al., 1987). When monthly variation of LH profiles is compared in ovariectomized and oestradiol-implanted sows throughout the year, LH pulse frequency is higher in December than in July. Moreover, pulses tended to be higher throughout the winter as opposed to the summer months (Smith et al., 1991). In another experiment that also employed ovariectomized and oestradiol-implanted pigs, LH pulse frequency was similar in both short- and long-day animals (Peacock, 1991). These results indicate that at least to some extent photoperiod can modulate LH secretion pattern through oestradiol in pigs.

4.1.4. Control of seasonal infertility

Seasonal infertility seems to be regulated by various external and management factors. At the same time, impaired fertility during the summer-autumn period can cause serious economic losses in the swine production industry. Against this background, it is quite logical to try to find management solutions to control the costs caused by seasonal infertility.

Our domestic pigs are, at least to some extent, considered seasonal breeders and their endocrinology has been shown to react to changes in photoperiod. Artificially controlled light regimes seem a viable option to control seasonal infertility. The main idea is to be able to time the innate circadian rhythm of the animal to ensure that the endocrinological state of the animal suits the needs of commercial pig production.

Nowadays, sows are demanded to farrow over two times per calendar year. By controlled light regimes, it could be possible to hasten the endogenous reproductive rhythm, namely alterations between anoestrus and breeding seasons, so that they coincide with the production cycle requirements in the modern piggery.

The photoperiodic control of reproduction in the pig has not been shown to be as strong and deterministic as in the sheep, a distinct seasonal breeder. Thus, photoperiodic control alone probably is insufficient to produce the best possible outcome in terms of reproductive performance of the sow. Appropriate feeding strategies, boar contact, housing and prevention of social stress are important components in successful reproductive management.

4.2. Housing systems and reproductive performance

The European wild boar lives in small groups of four to six animals (Mauget, 1982). Housing systems for domestic pigs vary from single housing in crates to dynamic group housing with tens of animals, with flooring ranging from fully slatted to deep-litter. Housing systems have been shown to affect both the welfare and production results of sows (McGlone et al., 2004). More knowledge about fertility and production with regard to housing systems of sows is needed.

4.2.1. Effect of stress on reproductive functions

Dobson and Smith (2000) offered a definition of stress, which is suitable for production animal studies: “the inability of an animal to cope with its environment, a phenomenon that is revealed by a failure to achieve genetic potential, e.g. for growth rate, milk yield, disease resistance, or fertility”. Stressful situations can alter an animal’s behaviour and health status as well as production and reproductive parameters. The endocrine system especially, the hypothalamo-pituitary-adrenal (HPA) axis, plays a major role in regulation of animals’ responses to stressors (Buckingham et al., 1997).

Stress and cortisol can affect reproductive hormone concentrations negatively. Interference with the pulsatile gonadotrophin-releasing-hormone (GnRH) and LH secretion has been proposed to be the main control pathway involved in stress-induced subfertility (for review, see Dobson & Smith, 2000). Basic laboratory studies have shown that cortisol down-regulates the pituitary LH secretion stimulated by GnRH administration (Li, 1987). In sows, similar results have been obtained. Simultaneous cortisol and GnRH infusions lead to diminished LH release (Pearce et al., 1988). When cortisol or adrenocorticotrophic hormone (ACTH) was injected repeatedly into sows, the LH surge required for ovulation was prevented (Barb et al., 1982). ACTH injections for 48 h during oestrus could also disturb oestrus behaviour by shortening the duration of standing oestrus (Brandt et al., 2007).

A short-lasting increase in cortisol concentration does not have an impact on LH secretion. Cortisol levels should be elevated for at least four days in order to see the

decrease in mean LH level (Turner et al., 1999). Razdan mimicked the short-lasting stress by ACTH injections immediately after ovulation and on days 13–15 of pregnancy. ACTH treatment after ovulation led to a decreased embryonic cleavage rate and a lower number of spermatozoa attached to the ovas. Authors explain these changes by an altered oviduct environment (Razdan et al., 2002). During the time of maternal recognition of pregnancy (days 13–15 of pregnancy), induced stress did not affect embryonic survival. However, the rise in plasma oestrone sulphate concentration was delayed by two days during the second signal from embryos to the pregnant sow (Razdan et al., 2004). In conclusion, even short-lasting stress and increased cortisol concentrations can affect reproductive functions of the sow. In all of these studies, the animals used were multiparous sows, which seem to be able to cope with these changes (Razdan et al., 2002, 2004).

Even repeated acute stress treatment has been unable to alter reproductive performance of gilts. A six-week treatment period (five weeks before and one week after insemination) consisting of weekly regroupings and twice weekly feed competitions produced more fighting in stressed groups than in the non-stressed control group. However, treatments did not affect the ovulation or pregnancy rate (Soede et al., 2006). In individually housed gilts subjected repeatedly to stressful handling during the follicular phase and in early pregnancy, reproductive parameters were unaltered by treatment (Soede et al., 2007). Similar results were obtained earlier in the trial, where repeated stress consisted of re-grouping of primiparous gilts during early pregnancy. Re-grouping did not modify reproductive hormone concentrations or embryonic survival (Tsuma et al., 1996). Gilts and sows were apparently able to recover from these stressful situations quickly enough, and repeated acute stress did not lead to a chronic stress reaction. Nevertheless, the reproductive success of female pigs is thought to be compromised by chronic stress (Turner and Tillbrook, 2006).

4.2.2. Housing systems and stress

Housing systems can cause prolonged stress in female pigs (for review, see Turner and Tillbrook, 2006). Restricted resources are the major disadvantage of living in groups in the modern production environment. Competition over unevenly distributed resources leads to aggressive behaviour and social stress (McGlone, 1985; Mendl et al., 1992). In addition, a novel and unstable social environment (e.g. repeated re-grouping) can lead to social instability (Archer, 1987). Most adverse effects of group housing systems are proposed to be related to suboptimal group size or space allowance (review by Hemsworth and Barnett, 1990). Optimal group size and space allowance are yet to be defined – thus far studies have given contradictory results (for review see, Arey and Edwards, 1998). In a more recent review, new aspects of group housing are brought into the discussion. Social relationships of farm animals are not restricted solely to hierarchy constitution, but are more flexible in terms of avoidance of costly adverse interactions between animals (Estevez et al., 2007).

In individual housing, close confinement has been hypothesized to cause stress for sows during gestation. Pigs in tether-stalls have shown a chronic stress response. On the other hand, individual cages caused only slightly increased cortisol concentration compared with group housing (Barnett et al., 1985, 1989). A more recent study

comparing pen and crate housing systems during gestation did not reveal significant stress responses in either of the housing types (Hulbert and McGlone, 2006). However, Munsterhjelm et al. (in press) found that stall-housed sows during early gestation performed more passive sitting and standing behaviours than group-housed sows. The authors concluded that stall housing could be associated with stress caused by a more restricted environment. In late gestation, no differences were recognized in acute phase response between gilts housed in pens or in individual gestation stalls (Sorrels et al., 2007). Based on these results, individual stall housing (except tethering) seems not to be as stressful for sows as group housing.

4.2.3. Effect of housing systems on reproductive performance

The most striking difficulty in comparing different housing systems in terms of reproductive performance of sows is the inconsistent description of housing systems. While great variability is present among group housing systems, they are usually handled as a single entity. When ignoring the effect of size, space allowance and stability of the groups, existing differences between housing systems could be challenging to detect.

Quite recently, a good effort has been made to overcome the heterogeneity of housing systems. In this meta-analysis, farrowing rate was found to be similar in sows and gilts kept in pens and individual stalls (McGlone et al., 2004). However, the farrowing rate tended to be higher in individually housed pigs. This finding is supported by a clinical trial carried out in Australia. In this trial, a deep litter group housing system was compared with an individual stall housing. Group housing consisted of batches of 85 sows in stable groups with a 2.3 m² space allowance. Sows were group-housed right after insemination until one week prior to farrowing. The authors describe advantages and disadvantages for both housing systems. In group-housed sows, farrowing rate was significantly lower (66%) than in stall-housed sows (77%). Moreover, the re-breeding rate tended to be higher in group-housed animals (13%) than in stalled sows (7%). However, individually housed sows clearly showed more lameness during gestation than group-housed sows (13% vs. 1%) respectively (Karlen et al., 2007). A drawback of this trial is that it was carried out in two units of a single commercial piggery. Thus, management factors of this particular farm could have affected the results considerably. In another study, where group housing was used within the first four weeks of pregnancy, group-housed sows had a greater risk of not being pregnant 28 days after service than their individually housed farm-mates (Munsterhjelm et al., 2007). According to Oravainen et al. (2006), confinement in an individual stall after mating (from a few days up to one month) provides a sow with a greater likelihood of farrowing afterwards. Farm surveys carried out in the UK revealed no a clear difference in the farrowing rate, although group housing seemed to have a slight advantage over stalls (Arey and Edwards, 1998). However, in these farm surveys, a definition of group housing is lacking.

In group housing, whether sows are kept in stable or dynamic groups during early pregnancy is worth considering. Dynamic groups (compared with stable groups) have had a higher conception rate (0.85 vs. 0.78) (Simmins, 1993). In addition, the timing of social instability seems to be important. Social stress during early

pregnancy is thought to interfere with maternal recognition of pregnancy. Very delicate hormonal messaging between developing embryos and the sow is required during the second and third weeks of pregnancy. Stress might hamper the development of embryos and their ability to send a sufficiently strong message to the sow (for review, see Tast, 2002). Mixing sows soon after mating has resulted in a greater number of returns to service than mixing of sows four weeks after mating (Bokma, 1990; Te Brake and Bressers, 1990). This finding is somewhat contradictory to more recent studies, where the effect of induced stress or repeated acute stress was investigated (Razdan et al., 2002 and 2004; Soede et al., 2006). In these studies, mixing of early pregnant pigs did not have a clear impact on reproductive performance. The main difference between these studies was probably the duration and intensity of the stress. In more practical situations, the stress experienced by sows might be more severe and continuous than in experimental situations, where sows had peaceful time periods between acute stress treatments.

In the meta-analysis carried out by McGlone et al. (2004), housing system did not have an effect on litter size of the sow. This was also the case in a more recent study, where the impact of repeated regrouping during a 6-week period around insemination was evaluated (Soede et al., 2006). No effect on litter size was found in a trial in which mixing of sows during the first week of pregnancy was compared with mixing during the third week of pregnancy (Bokma, 1990). Dynamic groups have resulted in a lower proportion of litters containing over 10 piglets than stable groups after mating (Simmins, 1993). In within-farm comparison in The Netherlands, stall and group housing resulted in similar numbers of live-born piglets (Den Hartog et al., 1993). In contrast to this result, in a farm trial carried out in USA, group-housed sows had more live-born piglets than individually housed sows. However, the total born piglets only tended to be higher in the group-housed group (Lammers et al., 2007).

5. AIMS OF THE STUDY

The primary aim of this work was to investigate the effect of the production environment on reproduction of the sow, especially on the farrowing rate. Based on the knowledge attained, we aimed to develop practical management protocols concerning light regimes and sow housing. Specific aims are as follows:

I)

To determine whether the LH secretion profile in the domestic pig and wild boar could be altered by changes in photoperiod. This study was intended to form the basis for the subsequent two light regime trials.

II and III)

In the two light regime trials, the purpose was to develop a practical light regime that could be applied in commercial piggeries to enhance the reproductive performance of sows.

IV)

The aim of the fourth study was to clarify the effect of the second environmental factor, namely sow housing, on the reproductive success of sows.

6. MATERIALS AND METHODS

6.1. Experimental and clinical trials (I, II, III)

One study in this work is experimental trial and two studies are clinical trials. The first (I) was carried out in a controlled experimental environment and the two (II, III) in commercial piggeries following common guidelines for animal management. In all of these trials, two different light regimes were applied. In trial I, the effect of the light regime on LH secretion pattern, especially LH pulse frequency, in gilts was examined. Trials II and III concentrated on the implications of the light regime on sows' reproductive performance, particularly on the farrowing rate. Details of each trial are presented in Table 1. We assumed that the short day light regime would prove to be beneficial in all three trials (I, II, III). In trial I, we hypothesized that short day light regime would lead to higher LH pulse frequency compared to long days. In trials II and III, farrowing rate was presumed to be higher under short day regime compared to long days.

Table 1.
Details of the experimental trial and two clinical trials.

Study	Number of animals	Main effect	Type	Duration (months)	Status of pigs
I	20	LH	Experimental trial	6	Ovariectomized
II	1100	FR	Clinical trial	8	Intact
III	1300	FR	Clinical trial	18	Intact

6.1.1. Animals

The domestic pigs used were Finnish Landrace, Yorkshire or crosses of these two (I, II, III). In the first trial (I), we also used European wild boars. These wild boars originated from a farm where animals lived in a semi-natural environment. To expose the animals to handling by humans, the wild boar piglets were transferred at the age of a few days from their own dam to be fostered by a domestic sow in confinement.

In the trial where LH secretion was investigated (I), all animals were ovariectomized and oestradiol-implanted (Compudose[®] 24 mg, Elanco, 8 mg per animal) six months old gilts. In lighting regime trials (II, III), animals consisted of the population of a commercial pig farm. Due to the experimental design, animals had a parity of two or more.

6.1.2. Sample sizes

To detect one pulse per 12-h window difference between treatments with standard deviations of 0.7, 95% confidence level and power of 0.8, the required group size was calculated to be eight animals. In the LH trial (I), altogether 20 animals were included, four of them wild boars. These animals were divided into two groups of 10 (eight domestic pig, two wild boars).

In light regime trials (II, III), the required sample size was also calculated. To detect a five percentage unit difference between treatments (*e.g.* farrowing rate 85% vs. 90%) with a power of 0.9 and a 95% confidence level, we estimated that we needed to collect information from 1000 inseminations per treatment group. To take into account the clustered structure and the light regime not being the only factor affecting the parameters measured, we increased the number of inseminations taken into the study. Altogether 1106 and 3400 inseminations were included in the first and second light regime trials, respectively.

6.1.3. Blood collection (I)

Repeated blood collection took place in trial I. All animals were fitted non-surgically with indwelling jugular vein catheters via an ear vein one day before the sampling as described by Peacock (1991). Domestic gilts were restrained using a soft rope tightened around the upper jaw to allow the catheter placing. Wild boars were sedated for the catheterization using medetomidin (Domitor[®] 1 mg/ml, Orion-Farmos, Finland) and zolazepam + tiletamine combination (Zoletil[®] forte 50 mg/ml + 50 mg/ml, Virbac Laboratories, France). Doses were 0.025 mg/kg and 5 mg/kg, respectively.

Blood samples (10 ml, Vacuette[®] serum tubes, Greiner Bio-One, Austria) were taken at 20-min intervals starting at 9:00 and concluding at 21:00. During the whole sampling procedure, the lights were turned off. This intensive sampling took place twice following a six-week entrainment period. Samples were taken in the pens while the animals were moving freely. Before each sampling, approximately 2 ml of blood was drawn and discarded and a 10 ml sample was taken. After each sampling, catheters were flushed with diluted heparin (Heparin 5000 IE/ml, Lövens, Denmark) to prevent coagulation. Samples were stored at 10°C and centrifuged (3000 rpm, 15 min) within 3 h of sampling. The serum was then stored frozen in duplicates at –20°C until analysed.

6.1.4. Hormone assays (I)

LH concentration was determined using a previously validated direct homologous double-antibody radioimmunoassay (Niswender, 1970) modified by Peacock (1991). Purified porcine LH (LER-786-3) supplied by Professor L.E. Reichert Jr. was used and labelled with I¹²⁵ (Amersham Australia Pty Ltd., Baulkham Hills, NSW, Australia). The antibody used was anti-porcine Niswender No. 566, donated by Professor G. Niswender. A solid-phased second antibody-coated cellulose

suspension raised in donkeys against rabbit serum (Sac-Cel, A-SAC1, Abacus Diagnostics, Brisbane, Australia) was used to separate bound and unbound label. Sensitivity of the assay was 0.14 ng/ml. Average intra- and interassay CVs were <10% (six assays performed).

6.1.5. Luteinizing hormone pulse identification (I)

The LH pulse identification procedure used was a modification of the method described by Shaw et al. (1985). An LH pulse was defined as any increase in the concentration of LH exceeding the basal line (basal LH) by more than three standard deviations and remaining at this level for at least two consecutive samples, thereafter declining to basal level or below. A minimum interval of 30 min was required between LH pulses. The number of LH pulses was counted for each individual over each 12-h window. The LH pulse amplitude was calculated as the difference between the peak pulse value and the baseline. Mean LH was calculated as a mean of all samples from one animal for each 12-h window.

6.1.6. Light regimes (I, II, III)

In experimental conditions, the first group was kept under a short daylight regime of 8 h of light and 16 h of dark (8L:16D), and the second group under a long daylight regime of 16L:8D. Lights were turned on every day at 7:00. For the short-day group, lights were turned off every day at 15:00, and for the long day group at 23:00. After a six-week treatment period, the first intensive blood sampling was accomplished. Following sampling, the light regimes of the two study groups were reversed, and the treatment period and intensive blood sampling were repeated (criss-cross study design). The light regime in trial I is illustrated in Figure 1. The duration of treatment period was chosen based on the observation that domestic pigs are able to react rapidly to the changing light regime in terms of their melatonin secretion (Tast et al. 2001b). On the other hand, six-week treatment period would be possible to apply in commercial piggery environment in the future.

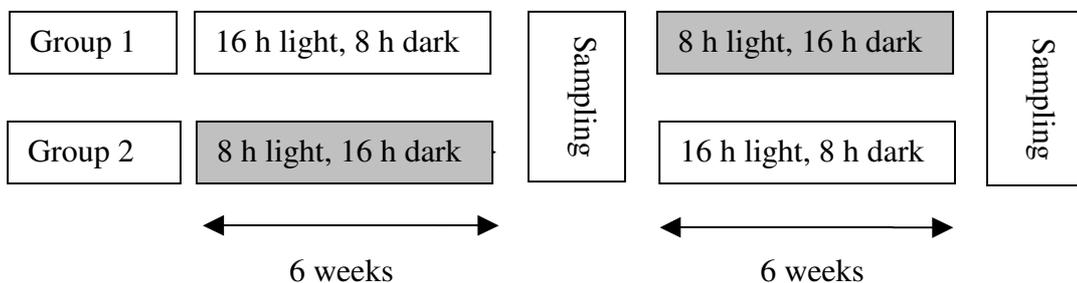


Figure 1.
Light regime employed in trial I

Also in clinical trials carried out on commercial farms, two different light regimes were used. In these trials, the light regimes were fitted in the commercial piggery environment and the duration of treatment periods were partly determined by

production cycle and sectioning of the piggery. The first light regime (II) consisted of short- and long-day treatments in farrowing and mating units. In the short-day treatment, the light phase was 8 h and dark phase 16 h. In the long-day treatment, the light phase was 16 h and dark phase was 8 h. In both short-, and long-day treatments, the photoperiod was 16 h of light and 8 h of dark in the gestation unit. The short-day treatment in farrowing and mating units lasted six weeks before mating took place. After mating, sows spent an additional three weeks under a short-day regime before they were moved to the gestation unit. This light regime is illustrated in Figure 2.

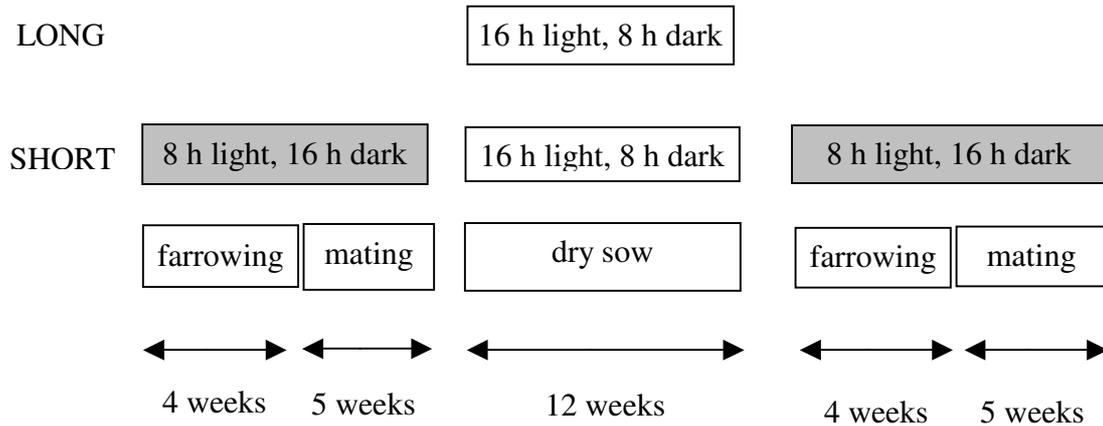


Figure 2.
Light regime employed in trial II.

Similarly, the second light regime (III) was composed of short- and long-day treatments. In the short-day treatment, sows were maintained under 10 h of dark and 14 h of light in the farrowing unit. In the long-day treatment, there was a light phase of 14 h and dark phase of 10 h. In both treatments, the photoperiod was 14 h light and 10 h dark in the mating and gestation units. The short-day treatment in the farrowing unit lasted eight weeks and continued until one week before mating. The light regime is illustrated in Figure 3.

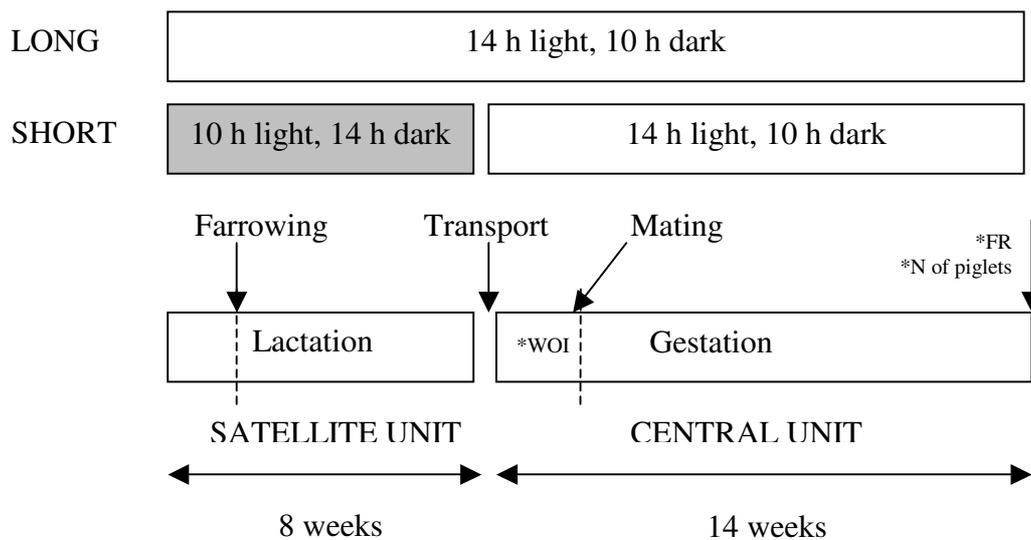


Figure 3.
Light regime employed in trial III. WOI=weaning to oestrus interval, FR=farrowing rate.

The light intensity during the light phase was over 100 lx in all three trials. During the dark phase, light intensity was under 10 lx. Light intensity was measured at sows' eye level (Gossen Mavolux digital®, Gossen, Germany).

6.1.7. Data collection (II, III)

Winpig (Agrosoft Ltd.) software was used for production data collection. The parameters included were breed, batch, light regime, parity, breeding season, weaning-to-oestrus interval, number of rematings, number of live-born piglets and culling reasons for the sows in light regime trial II. In trial III, information was gathered about parity, weaning-to-oestrus interval, type of breeding (insemination, mating, combined), possible culling due to failure to attain oestrus and light regime. In both trials, the effect of the light regime means the effect of the specific light regime in the farrowing unit preceding each breeding for the production parameter of interest (*e.g.* farrowing rate, weaning to oestrus interval).

6.2. Observational study (IV)

The fourth study was a retrospective cohort study of the effect of remodelling the piggy breeding unit on farrowing rate, employing a historical control.

6.2.1. Sample size

To be able to detect a 10 percentage unit difference between treatments with standard deviations of 10%, power 0.8 and 95% confidence level, we estimated that we needed to collect information from a minimum of 15 study herds for each of the four remodelling types, therefore requiring a minimum of 60 herds.

6.2.2. Data collection

The sampling frame for study herds was a list of herds belonging to the Finnish herd surveillance system, which included 787 herds in 2004. From this list, all herds fulfilling inclusion criteria (individual cages in the breeding unit before remodelling, remodelling of the breeding unit between 1995 and 2002 and participation in the Finnish herd surveillance system covering at least the period from 1990 to 2004) were asked to participate in the study.

A visit was made to every farm that agreed to participate. The visit took place after the constructional work of the breeding unit on each farm had been completed. During the visit, detailed information about management practices and the housing system before and one year after the remodelling was gathered. The main treatment effect studied was the remodelling type of breeding unit. This remodelling was divided into four categories: from cage to cage, from cage to deep-litter, from cage to solid floor or from cage to partly or totally slatted floor. A more detailed description of data gathered from herds can be found in the study IV.

For all participating herds, production records were obtained from the Finnish herd surveillance system database. Data collected included average herd size and parity, farrowing rate after the first insemination or breeding, and proportion of sows culled due to fertility or leg problems, the two main reasons for culling in Finland. The farrowing rate was the outcome of the study and other factors served as covariants in the statistical modelling. Data for every farm were checked manually. Any farm for which reliable or complete data were unavailable was excluded from the study.

Of the original 63 study herds, three herds refused to participate and a further 13 herds had incomplete data. Thus, 47 herds (75% of the study population) were included.

6.3. Statistical analyses

Statistical analyses were carried out with STATA 9.1 or 9.2 computer software packages (Stata Corporation, Texas, USA).

The random effect Poisson regression model with individual as a clustering variable was used to compare LH pulse counts of the two treatment groups in trial I. For mean and basal LH concentration and LH amplitude comparisons, the Wilcoxon rank-sum test was applied. All analyses were conducted with data containing all pigs as well as with data from which the wild boars were omitted and data containing only wild boars.

In trials II and III, to estimate the effect of light regimes on reproductive performance, we fitted linear, logistic or poisson regression models depending on the nature of the outcome at hand.

The effect of remodelling types on farrowing rate in trial IV was tested using a linear regression model. Herd identity was included in the model as a random effect to account for the lack of independence between observations in the same herd. Data were analysed first as a whole data set. For further evaluations, data set was divided into two subsets, namely 'farms with initially high farrowing rate' (HF) and 'farms with initially low farrowing rate' (LF). The mean from the full data set was used as a cut-off point.

7. RESULTS

7.1. Effect of light regime on luteinizing hormone secretion

No differences existent between short and long daylight regimes in terms of LH pulse frequency in either the domestic pig or the European wild boar. Mean and basal LH levels were significantly higher in the long-day treatment group when only data for domestic pig were taken into account. In wild boars, mean and basal LH levels were also similar across treatment groups. Numerical results can be found in Tables 2 and 3.

Table 2.

LH secretion patterns in short- (8 h light, 16 h dark) and long-day (16 h light, 8 h dark) groups. Group mean and standard deviation (in parentheses) of all animals (16 domestic pigs, 4 European wild boars) in a cross-over study design are shown.

	No. of LH pulses in 12 h	Basal LH (ng/ml)	Mean LH (ng/ml)	LH amplitude (ng/ml)
Short day (8L:16D)	2.3 ^a (1.7)	0.7 ^a (0.4)	0.9 ^a (0.4)	0.5 ^a (0.4)
Long day (16L:8D)	2.3 ^a (2.0)	1.0 ^b (0.5)	1.3 ^b (0.6)	0.6 ^a (0.5)

^{a,b} Results in the same column with different superscripts are significantly different ($p < 0.05$).

Table 3.

Luteinizing hormone secretion patterns in short- (8 h light, 16 h dark) and long-day (16 h light, 8 h dark) groups. Group mean and standard deviation (in parentheses) of domestic pigs ($n=16$) and European wild boar ($n=4$) in a cross-over study design are provided.

	No. of LH pulses in 12 h		Basal LH (ng/ml)	Mean LH (ng/ml)		LH amplitude (ng/ml)		
	domestic	wild	domestic wild	domestic	wild	domestic	wild	
Short day (8L:16D)	2.6 ^a (1.7)	1.3 ^a (1.9)	0.7 ^a (0.4)	0.7 ^a (0.4)	0.9 ^a (0.5)	0.9 ^a (0.6)	0.5 ^a (0.4)	0.4 ^a (0.6)
Long day (16L:8D)	2.6 ^a (2.1)	1.5 ^a (0.7)	1.1 ^b (0.4)	0.3 ^a (0.1)	1.4 ^b (0.5)	0.3 ^a (0.1)	0.6 ^a (0.5)	0.2 ^a (0.1)

^{a,b} Results in the same column with different superscripts are significantly different ($p < 0.05$).

7.2. Effect of light regime on reproductive performance

In both light regime trials (II, III), farrowing rate was 90% in both short- and long-day treatment groups. Thus, there was no treatment effect on the farrowing rate of sows. Moreover, all treatment groups in both trials shared the same median weaning-to-oestrus interval (WOI) of five days. Slight differences were present in the range of WOI across different treatments. Unfortunately, the results were inconsistent; in trial II, WOI had wider range in the short-day group, while in the trial III, WOI showed a greater variation in the long-day group. In trial II, the culling rates due to fertility problems were 2.4% and 3.2% in the short- and long-day treatments, respectively. The total number of sows culled due to fertility problems in trial III was 31 sows representing only 1% of all weaned sows. A summary of the reproduction results in trial III is provided in Table 4.

Table 4.

Reproductive results of 3391 weanings in trial III shown separately for each season. Where appropriate, standard error (SD) appears in parentheses. WOI=weaning to oestrus interval.

Reproduction parameter	Winter	Spring	Summer	Autumn
Farrowing rate, %	90.3	90.8	85.3	90.1
WOI, days	7.3 (6.3)	7.2 (6.5)	7.7 (7.2)	7.6 (7.9)
WOI <10 days, %	90.5	90.4	88.7	89.2
Total born piglets	12.2 (3.0)	12.7 (3.2)	12.3 (3.2)	12.5 (3.3)

7.3. Effect of re-modelling of breeding unit on farrowing rate

Great variation was present in farrowing rate among the 47 study herds. Farrowing rate varied between 46.4% and 98.2%, with an average of 72.8% (SD 9.5). Leg problems were the cause of culling in less than 10% of sows in 56% of herds. Farrowing rate was 71.1% (SD 9.5) for herds that culled less than 10% of sows and 75.4% (SD 9.1) for herds that culled more than 10% of sows.

Remodelling breeding unit had no significant effect on farrowing rate when the initial reproductive performance of the herd was neglected. However, remodelling 'from cage to deep litter' seemed to have the most consistent negative effect on farrowing rate ($p=0.05$). After dividing study herds into two subpopulations, *i.e.* HF and LF herds, the farrowing rate was affected by the remodelling; farrowing rate decreased in HF herds and increased in LF herds. The distribution of herds according to different remodelling types of breeding unit and their farrowing rates is displayed in Tables 5 (complete data set), 6 (HF herds) and 7 (LF herds)

Table 5.

Distribution of observations according to remodelled breeding unit types and farrowing rates of 94 observations in 47 study herds. SD=standard deviation.

Remodelling of breeding unit	No of observations (n)	Farrowing rate, % (SD) before	Farrowing rate, % (SD) after
Observations before remodelling	47	74 (11.0) ^a	-
From cage to cage	5	71.5 (16.2)	67.6 (12.6) ^a
From cage to deep litter	15	72.3 (10.6)	69.2 (8.07) ^a
From cage to solid floor	12	77.9 (9.3)	75.4 (6.5) ^a
From cage to slatted floor	15	73.6 (8.9)	72.0 (5.5) ^a

^a Results in the columns with different superscripts are significantly different ($p < 0.05$).

Table 6.

Distribution of observations according to remodelled breeding unit types and farrowing rates of 54 observations in 27 study herds with an initial high farrowing rate (HF data set). SD=standard deviation.

Remodelling of breeding unit	No of observations (n)	Farrowing rate, % (SD) before	Farrowing rate, % (SD) after
Observations before remodelling	27	81 (7.12) ^a	-
From cage to cage	2	88.8 (4.1)	62.95 (23.41) ^b
From cage to deep litter	7	83.24 (7.92)	70.81 (7.90) ^b
From cage to solid floor	9	82 (6.24)	76.83 (6.92) ^b
From cage to slatted floor	9	78.64 (7.17)	73.97 (4.70) ^b

^{a,b} Results in the columns with different superscripts are significantly different ($p < 0.05$).

Table 7.

Distribution of observations according to remodelled breeding unit types and farrowing rates of 40 observations in 20 study herds with an initial low farrowing rate (LF data set). SD=standard deviation.

Remodelling of breeding unit	No of observations (n)	Farrowing rate, % (SD) before	Farrowing rate, % (SD) after
Observations before remodelling	20	63.75 (5.21) ^a	-
From cage to cage	3	59.93 (4.24)	70.63 (2.90) ^b
From cage to deep litter	8	62.71 (5.50)	67.86 (8.49) ^a
From cage to solid floor	3	65.57 (4.74)	71.2 (2.79) ^b
From cage to slatted floor	6	66.13 (5.02)	69.1 (5.60) ^b

^{a,b} Results in the columns with different superscripts are significantly different ($p < 0.05$).

The mean parity of sows and the proportion of sows culled due to leg problems influenced farrowing rate. Farrowing rate increased by five percentage units one unit increase in parity ($p=0.01$). If more than 10% of sows in the herd were culled due to leg problems, farrowing rate increased by five percentage units compared with herds in which the culling rate due to leg problems was less than 10% ($p=0.01$).

8. DISCUSSION

Based on our results, the reproduction of the sow appears to be difficult to control by a single environmental or management factor. In contrast to our expectations, short or long daylight regimes did not have a clear effect on either LH secretion patterns of prepubertal ovariectomized gilts or reproductive performance of sows, as measured by farrowing rate and weaning-to-oestrus interval. In previous studies of LH pulsatility in the pig, results have been somewhat confusing. Although season and photophase have affected LH secretion patterns, the LH pulse frequency has remained unchanged (Cox et al., 1987; Peacock, 1991; Smith et al., 1991; Smith and Almond, 1991). In our LH study (I) as well as, in the first light regime study (II), we used an entrainment period of approximately six weeks to adapt the light regime to a commercial setting. It is noteworthy that in sheep a minimum period of 40–50 days for entrainment was required (Kennaway, 1988), and in many seasonality studies lighting has been altered in periods of 16 weeks (Lincoln, 2002). Thus, the adaptation period might have been too short for even wild boars to change their LH secretion and subsequently their other reproductive functions. In addition, in our LH study (I), the LH baselines and LH pulses were somewhat unclear compared with previous work LH profiles (Peltoniemi et al., 1997a; Virolainen et al., 2004). This may have made recognition of pulses difficult and masked the true pulse frequency. Difficulties in pulse recognition were probably caused by the 20-min intervals used for the sampling. This sampling interval seems to be too long based on the knowledge obtained from the sheep. In sheep during the breeding season, samples must be taken at 4-min intervals to identify very frequent pulses.

In the second light regime trial (III), we aimed at correcting methodological shortcoming in the duration of light regime. We now used an adaptation period of eight weeks. However, even with a longer entrainment period, the artificial lighting regimen that changed between short- and long-day lighting according to sows' production cycle failed to stimulate reproduction performance of sows compared with a long-day regimen.

The second environmental factor investigated, the remodelling of the breeding unit, revealed mainly the effect of the alteration itself. Equal reproductive success was achieved in traditional individual cages and in various types of group housing. This result is in agreement with most previous studies (*e.g.* McGlone et al., 2004).

Reproduction is given a high priority in the life of animals. This can also be seen in the sow, as short-lasting disturbances do not affect even the most sensitive phases of reproduction (for review see, Radzan, 2003). Against this background, it is unsurprising that alterations in a single environmental or management factor are not highly deterministic for the fate of the whole reproductive cascade. The price would be too high if the production of offspring were endangered by every disturbance in the environment. On the other hand, chronic stress can compromise reproductive success (Turner and Tillbrook, 2006). In addition, seasonal fertility is a well-known phenomenon in swine production (Love et al., 1993; Peltoniemi et al., 1999; Peltoniemi and Virolainen, 2006).

Photophase has been shown to have a clear impact on melatonin secretion in domestic pigs and in the European wild boar. The pig has a circadian rhythm in

melatonin secretion. The duration of increased melatonin levels coincides with the duration of dark hours within the 24-h period (Tast et al., 2001a). Also, melatonin secretion can be altered by rapid changes in daylength (Tast et al., 2001b). However, the effect of this melatonin output remains at least partly unclear. Basset et al. (2001) reported that melatonin implants inserted around the spring solstice or *per os* treatment significantly affected the appearance of seasonal anoestrus mainly in sows with a confirmed history of reproductive failure, but not in more fertile sows with more recent boar contact. However, in the fertile sow group, only two non-implanted control sows became anoestrous and thus, there was no real possibility to see the difference between treatment groups. Melatonin treatment had shown no effect on the seasonally oscillating LH pattern. In gilts, melatonin treatment *per os*, but not as an implant, proved efficient in preventing seasonal delay in puberty (Paterson et al., 1992). The melatonin signal may have only a partial effect on reproduction in modern pigs kept as production animals. If the effect of melatonin on the hypothalamus and the GnRH pulse generator is partial, understandably also the implications on the LH secretion pattern are diminished. Based on this hypothesis, photoperiod alone cannot affect LH secretion dramatically in the domestic pig. If LH secretion is not severely affected, the reproductive performance of the sow is not inevitably harmed.

On the other hand, reproductive failures are most common during the so-called seasonal infertility period. This period coincides with long photoperiods after a required adaptation phase. One typical feature of seasonal infertility, at least in Finland, is the varying severity of fertility problems between different years. Photoperiod may hinder the reproductive functions of the pig, although it cannot compromise the whole cascade. Other regulating factors (e.g. social stress, temperature, feeding, boar contact) superimposed on the impact of the photoperiod can then modulate the final outcome quite drastically. Thus, the summary effect of all environmental and management factors should be considered the main effector in seasonal infertility problems.

Concerning different housing systems, the net effect of the housing system has been proposed to be influenced by the overall quality of management (Arey and Edwards, 1998). Important factors that should be taken into consideration when trying to evaluate overall success of particular housing system are space allowance, group size, social stability and feeding arrangements and, of course, the professional skills and motivation of the caretaker of the animals (Simmins, 1993; Tsuma et al., 1996; Virolainen et al., 2004; Estevez et al., 2007). In addition, in our study, an effective culling strategy to ensure the good locomotor health of breeding sows, one component of successful herd management, resulted in better reproductive performance. Also results warrant comments on the implications of space allowance in group housing systems. Generous space allowance seems to be especially important in deep litter housing systems in Finland, because the factor 'space allowance' intervened a nearly significant effect of the remodelling type 'deep litter'. At least in Finland, deep litter housing systems tended to have bigger group sizes than other group housing types. The role of space allowance may be emphasized with increasing group size. Overall, many management factors included in our study were revealed to be non-significant. This result might have been caused by great variation in management factors and our relatively small sample size.

In the future, one step backwards might be necessary in studies concerning the effect of photoperiod and melatonin on LH secretion. First of all, we need to find out that the photoperiod really has steroid-independent and steroid-dependent effects on LH secretion in pig. In practice, this requires the repetition of older studies carried out in Australia by Peacock et al. (1991) and also the first study in this dissertation. In order to be able to be successful in revealing the true effect of photoperiod, a few methodological arrangements need to be carefully taken into account. Firstly, the innate circannual rhythm needs to be entrained by using long enough (preferably several months, even years) long day light regime. After the adaptation period, the actual trial employing short and long day light regimes could begin. These regimes are also required to continue over several months before intensive sampling take place. During sampling, the sampling interval has to be set as short as five minutes at least for part of the sampling time. After revealing the true effect (or lack of consistent effect) of photoperiod on LH secretion, further studies could be planned on a more solid base.

The next practical studies on light regimes should focus on situations and farms where a distinct seasonal infertility problem in terms of lowered farrowing rate is clearly visible. On farms like the ones in our clinical trials, fertility was at a very high level, although some seasonal fluctuations were evident. In situations where farrowing rate is almost 90%, it is very challenging, perhaps even impossible, to find ways of further enhancing reproductive performance.

9. CONCLUSIONS

- The LH secretion pattern, especially the LH pulse frequency, remained unchanged with the two different light regimes. However, the result might have been confounded by methodological shortcomings.
- Using short or long daylight regimes to enhance already high level of reproductive performance appears to be difficult.
- The effect of a remodelled piggery breeding unit on farrowing rate depends on the initial reproductive performance of the herd. The remodelling improved reproductive performance in problematic herds and decreased reproductive performance in better herds.
- Equal reproductive performance can be obtained both with traditional individual cages and with different kinds of group housing systems.
- Overall, the effect of single factor (either light program or housing) seems to be difficult to isolate from the complex interactions of reproduction and environment.

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