

Seasonality of reproduction in gilts and sows

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In the wild, the pig adapts her reproductive functions according to the seasonal changes in the environment, such as the ambient temperature and availability of food. Like in other short day seasonal breeders, breeding season is favoured in the mid winter in order to provide the offspring with the best chances to survive four months later. Seasonal changes in environment are perceived mainly by the ability of the pig to recognise seasonal changes in photoperiod. This information is mediated through changes in the activity of the pineal gland to secrete melatonin, essentially by the same mechanism as reported for other mammals. Stimulation of melatonin receptors located in the hypothalamus has a significant role for the release of GnRH and subsequent gonadotrophin release from the pituitary. Management and nutrition related factors determine the degree of seasonal effects on reproduction in the commercial piggery environment. Significant improvements in fertility in herds suffering from seasonal infertility are achievable by providing gilts and sows with abundant feed after mating. Attempts to alleviate the seasonal effects on fertility by applying light programs are underway and may lead to significant improvements in productivity of the domestic pig in the long run. Hormonal treatments may be somewhat effective, but not a sustainable solution to seasonal infertility. In conclusion, seasonal infertility is a photoperiod induced phenomenon that can be manipulated by changes in photoperiod and by accounting for season as a significant factor when feeding strategies are applied in commercial piggeries.

Introduction

The European wild boar is a distinctive short day seasonal breeder with the breeding season commonly occurring in November and December in the Northern hemisphere (Mauget, 1982). Autumn is a season of sexual arrest and building up of energy reserves for the forthcoming winter and pregnancy. Endocrine characteristics include down regulation of gonads and high growth hormone activity. Metabolically speaking, an anabolic autumn with no sexual activity is followed by a catabolic winter and spring, when energy reserves are consumed for growth of foetuses and subsequent lactation. In the wild pig, losing body weight in lactation may be considered as a quite natural phenomenon.

The domestic pig may breed throughout the year; however a tendency for seasonal breeding remains, with the lowest farrowing rate in autumn. This reduction in farrowing rate is evidence for seasonal effects (Peltoniemi *et al.*, 1999a; Tummaruk *et al.*, 2000). Delayed puberty in gilts is a

frequently reported seasonal effect on reproduction in the pig (Paterson *et al.*, 1991). Furthermore, a prolonged weaning to oestrus interval clearly is a major seasonal effect, especially if sows are confined in an individual pen after weaning (Hurtgen and Leman, 1980; Hurtgen *et al.*, 1980; Peltoniemi *et al.*, 1999b). As the seasonal infertility problem was discovered, high ambient temperature was considered as a causative factor (Love *et al.*, 1978). Ever since, a number of studies with a variety of mammalian species demonstrated the central role of natural photoperiod in controlling seasonal breeding (for review see Lincoln *et al.*, 2003; Malpaux *et al.*, 1999). Documentation of the effects of photoperiod on fertility of the domestic pig is not conclusive. Some reports, however, imply that the domestic pig is able to recognise and respond to changes in photoperiod (Paterson and Pearce 1990; Andersson *et al.*, 1998). Furthermore, the earlier confusion about melatonin rhythms of pigs has been clarified and it was also demonstrated that the domestic pig responds to changes in photoperiod in a way similar to other mammalian species in terms of melatonin secretion (Klupiec *et al.*, 1997; Andersson *et al.*, 1998; Tast *et al.*, 2001a, b; Peltoniemi *et al.*, 2005). We also demonstrated that the circadian melatonin profile of the domestic pig is identical to the profile of the European wild boar, and that domestic pigs recognise and respond to changes in natural photoperiod under a conventional piggery environment, which uses the light coming through the windows (Tast *et al.*, 2001a). In sheep, abrupt changes to extremes of photoperiod, a short and a long day, caused the same physiological changes in reproduction as a natural step-wise change in photoperiod (Bittman *et al.*, 1983; Karsch *et al.*, 1984). Because this appears to be the case with the domestic pig as well (Tast *et al.*, 2001b), it should be possible to develop a simplified artificial lighting program to control seasonal variation in reproduction in commercial piggeries.

Seasonal effects on reproductive performance

Major manifestations of seasonal infertility in gilts and sows are illustrated in Fig. 1. Reduction in the farrowing rate is the most compelling evidence for seasonal effects (Peltoniemi *et al.*, 1999a). Much of the reduction in farrowing rate in summer-autumn has been attributed to a disruption of early pregnancy rather than to conception failure (Love *et al.*, 1993; Peltoniemi *et al.*, 2000a). These sows were mated, they conceived apparently well, and pregnancy was established. The embryos were present for some time, but quite early on, pregnancy was interrupted and the sows returned to oestrus after a prolonged oestrus to oestrus interval (Tast *et al.*, 2002).

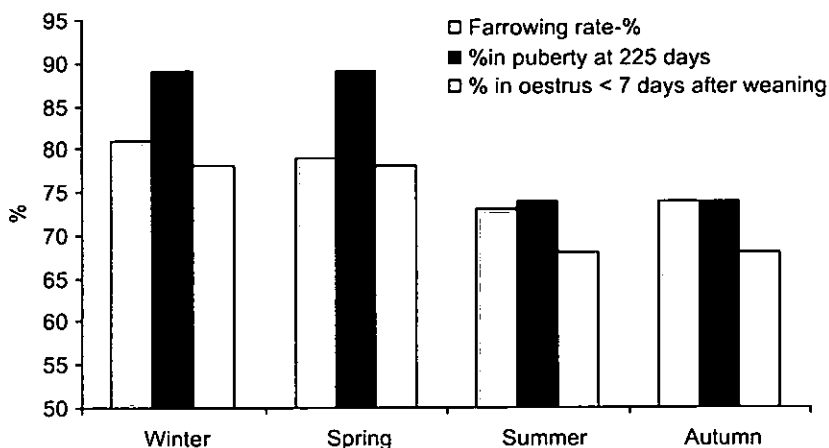


Fig. 1 Major manifestations of seasonal infertility in the pig presented as a percentage for each reproductive parameter. Data pooled from Peltoniemi *et al.*, 1999, Paterson *et al.*, 1991, Hurtgen *et al.* 1980.

Among European wild boars, gilts reach puberty only in autumn, as demonstrated by the study of Pepin and Mauget (1989). In the domestic pig, delayed puberty in gilts is a frequently reported seasonal effect on reproduction (Paterson *et al.*, 1991; Love *et al.*, 1993; Gaustad Aas *et al.*, 2004). In a retrospective study of 1081 herds, puberty was delayed by more than 5 days in gilts born between December and April, and therefore, were expected to attain puberty between August and November, (Peltoniemi *et al.* 1999b). Long days (> 12 h) delayed puberty under standardised field conditions, but the delay was alleviated by boar exposure (Paterson *et al.*, 1991).

A prolonged weaning to oestrus interval clearly is a major seasonal effect, especially if sows are confined in individual pens after weaning (Hurtgen and Leman, 1980; Hurtgen *et al.*, 1980; Peltoniemi *et al.*, 1999b). High ambient temperature reduced voluntary feed intake during lactation in summer-autumn, thereby postponing oestrus after weaning (Prunier *et al.*, 1996, 1997). The prolonged weaning to oestrus interval in summer-autumn, which clearly affects primiparous sows more than older sows (Peltoniemi *et al.*, 1999b), may allow these sows to recover from the metabolic stress imposed by lactation.

The majority of studies indicate that season has no effect on litter size (Love, 1978; Paterson *et al.*, 1978; Mattioli *et al.*, 1987; Reilly and Roberts, 1991; Peltoniemi *et al.*, 1999a), but some other studies suggest a clear seasonal effect, in that litter size was reduced by about one piglet after summer matings (reviewed by Claus and Weiler, 1985). This inconsistency may be due to several conflicting factors, such as an increase in number of return matings in summer-autumn, which would result in larger litters, an increase in number of gilt matings producing smaller litters and an increase in the culling rate, which reduces the number of older less fertile sows, and thus, increases the percentage of successful matings. We found that, although litter size at birth was neither reduced nor increased by season, there was a clear tendency for litters to be larger at weaning during the first half of the year, suggesting a seasonal impact on lactation performance (Peltoniemi *et al.*, 1997b). Such a seasonal effect on lactation performance may be explained by seasonal effects on prolactin secretion (Basset *et al.*, 2001). Reduced litter size is, therefore, a potential manifestation of seasonal infertility and this seasonal effect may be present at birth and at weaning.

Factors underlying seasonal infertility

Seasonal infertility is generally accepted to be a photoperiod driven phenomenon, however a set of other factors contribute to the annual pattern of seasonality (Figure 2.). These factors include ambient temperature, social interaction between males and females, social interaction between females, housing, feeding strategy, components of feed and genetics.

Photoperiod

In essence, the pig is considered to be a short day seasonal breeder (Love *et al.*, 1993; Peltoniemi *et al.*, 2000). Sexual activity in autumn is down regulated in anticipation of an unfavourable farrowing season the following winter.

Much of the present understanding about seasonal infertility is still based on the extensive research work carried out with the model short day seasonal breeder, the sheep. In this species, both photoperiodism and circannual rhythm generation participate in regulation of the breeding season (Malpoux *et al.*, 1995, 1998, 1999; Lincoln *et al.*, 2003). Photoperiodism depends on transduction of photoperiod into a nocturnal melatonin signal by the pineal gland that reflects the length of night. Photoperiodic stimuli every 24 h act to entrain the circadian clockwork of the suprachiasmatic nuclei (SCN). Generation of the circannual rhythm is considered intrinsic

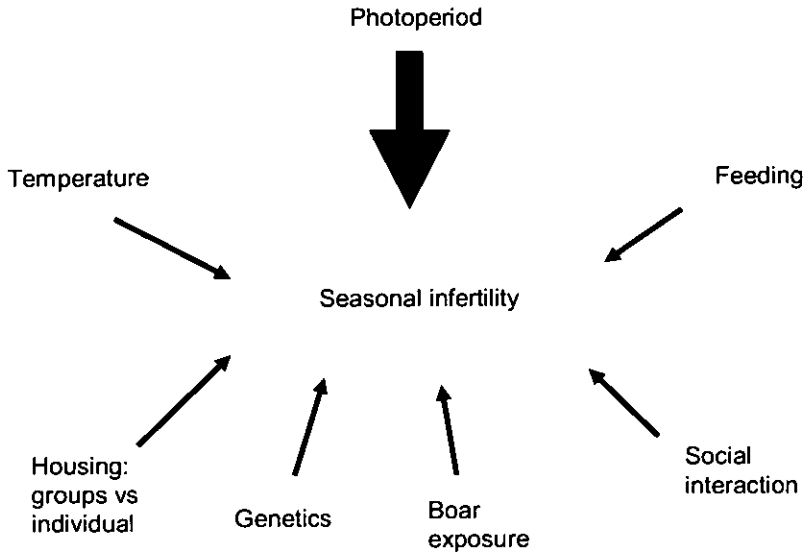


Fig. 2 Factors involved in seasonal infertility. The ambient photoperiod synchronises the intrinsic biological clock controlling seasonality of breeding activities. A number of other factors determine the degree of seasonality of breeding expressed by the domestic pig.

and functions independently in some mammals (Woodfill *et al.*, 1994; Lincoln *et al.*, 2003), but in the sheep ambient photoperiod may dictate whether or not the long term seasonal activity in reproduction is expressed. Work is currently underway to locate the calendar cells, which control seasonal changes in the gonadotrophin/gonadal axis, however, present evidence implies that these cells are located in the mediobasal area of the hypothalamus (Malpoux *et al.*, 1995, 1998; Lincoln *et al.*, 2002; Lincoln *et al.*, 2003).

There is little evidence to suggest that pigs are different from sheep in the essential mechanism by which season affects reproductive function. Although some confusion exists regarding the existence of a circadian melatonin pattern in the pig (Diekman *et al.*, 1997; Bollinger *et al.*, 1997), recent evidence firmly established that pigs have this pattern (Klupiec *et al.*, 1997; Andersson *et al.*, 1998; Tast *et al.*, 2001a, b; Peltoniemi *et al.*, 2005).

Therefore, it appears likely that the pig is similar to its fellow short day breeder, ungulate sheep, in terms of mechanisms controlling seasonality of reproduction. An intrinsic circannual rhythm, which affects the GnRH pulse generator, is likely to exist and is subject to seasonal changes in photoperiod. Both the intrinsic clock (intrinsic circannual rhythm generation) and photoperiodism are likely to affect the degree of seasonality of reproductive function that is expressed in the pig.

Ambient temperature

If high ambient temperature was the main factor causing seasonal infertility, one would expect the major effect of season to be a reduction in litter size rather than loss of the whole litter. However, this is not the case because early disruption of pregnancy and subsequent reduction in farrowing rate is clearly the major manifestation of seasonal infertility, and high ambient temperatures in mid summer do not correlate with the major seasonal effect on reproduction. Furthermore, seasonal disruption of pregnancy and reduced farrowing rate is commonly seen at the end of summer and during autumn, when temperatures are not high any more.

Prunier *et al.* (1996) demonstrated that high ambient temperature has an impact on voluntary feed intake during long days resulting in negative energy imbalance and prolonged weaning to oestrus intervals in autumn. The same mechanism may cause delayed puberty in gilts in autumn. High ambient temperatures in summer may depress voluntary feed intake of prepubertal gilts, and therefore, delay onset of puberty in autumn (Peltoniemi, 1999). Autumn abortion syndrome appears to be related to low temperatures and individual housing in late autumn or early winter (Almond *et al.*, 1985). This phenomenon was related to high variation in the daily ambient temperature over 24 hours. Affected animals could not compensate for the sudden drop in ambient temperature because their movement was restricted and no bedding material was provided. Sows respond to this situation by aborting the whole litter at any stage of pregnancy.

Feeding

Availability of feed significantly affects onset of the breeding season in the European wild boar (Mauget, 1982). If feed is readily available and plentiful, the breeding season commences substantially earlier than under adverse nutritional circumstances.

In the domestic pig, the type of housing (individual stalls vs. group housing) and feeding level had a profound effect on fertility of the sow in summer-autumn in two large piggeries in Australia (Love *et al.*, 1995). In the group housing system, restricted feeding increased the weaning to oestrus interval and decreased the farrowing rate by 50 % during summer and autumn (Table 1.). In the winter and spring, the same level of feeding did not adversely affect the weaning to oestrus interval and the farrowing rate remained high (> 85 %). In contrast, high feeding level had a positive effect on the farrowing rate in summer and autumn. Seasonal infertility was not detected when sows were kept in individual stalls and fed moderately. This appears to be a valid study, because the comparison between groups was carried out under constant management, whereas many other studies have compared housing systems and feeding levels between piggeries, thereby confounding the data. Our recent experiments with early pregnant gilts (Virolainen *et al.*, 2004a,b) and sows (Virolainen *et al.*, 2005b) support the beneficial effect of an abundant feeding level after mating in summer autumn.

Table 1. Effect of type of housing and feeding* level on farrowing rates (Love *et al.*, 1995).

Season	Farrowing rate				
	Feeding	Group housing		Individ. stalls	
		Low	Moderate	High	Moderate
Summer-Autumn		50.0	69.0	74.1	84.0
Winter-Spring		87.0	-	87.5	87.6

*Level of feeding; low = 1.6-2.0 kg/day, moderate = 2.5 kg/day, high > 3.6 kg/day (13 MJ/kg). These feeding levels were applied for the first four weeks of pregnancy. Thereafter, the feeding level was 2.5-3.2 kg/day for the remainder of pregnancy.

Genetics

Differences among sheep breeds in timing and duration of seasonal anoestrus are well documented. Breeds of Merino ancestry (Rambouillet, Dorset) and North European breeds (Finnish Landrace, Romanov) have long breeding seasons, are responsive to ram introduction in spring and perform well outside their natural breeding season (Notter *et al.*, 1985; Thomas *et al.*, 1988; Nugent *et al.*, 1988; Casas *et al.*, 2004). However, selection for less-seasonal lines of sheep has

not improved reproductive performance. Heritability for spring matings appears to be low. The trait is not expressed until late in life, data records are usually available for females only and the spring breeding trait may only be expressed in particular lambing seasons and management systems (Notter and Cockett, 2005). Therefore, genetic improvement through traditional means seems particularly challenging in the sheep.

The situation is, if possible, even more complicated in the domestic pig. The majority of pig breeds reproduce throughout the year with only a portion of females displaying a tendency for short day seasonal breeding. Seasonal effects on reproduction change from year to year, from one piggery to another, and even, from pen to pen (Love *et al.*, 1993). In the European wild boar, a second breeding season in late spring or early summer may be possible, but is rare.

We compared the genetic background of two wild pig subpopulations on two farms in Finland (Gongora *et al.*, 2003). Both of these farm organizations argued that their animals originate from genuine Wild Boar. The glucose phosphate isomerase pseudogene (GPIP) allele frequency indicated that there was contribution from Asian breeds in subpopulation A, which implies crossbreeding with the domestic pig. More conclusively, the same subpopulation also had melanocortin 1 receptor*3 (MC1R*3) allele present, indicating distant crossbreeding with the domestic pig. The DNA sequencing technique implied, however, that subpopulation B had only European wild boar related alleles indicating a genuine origin (Gongora *et al.*, 2003).

In terms of seasonality of reproduction, the small genetic difference between subpopulations A and B appears to have a significant impact. Individuals in subpopulation A frequently had a second breeding season in spring with a second litter in summer and sows in subpopulation A were not quite as demanding from the management point of view. In contrast, subpopulation B sows were distinct short day seasonal breeders without any sign of oestrous activity after the spring litter until the next breeding season during the subsequent winter. If farms represented by subpopulation B were given the relatively limited space usually allotted on farms of population A, it is highly unlikely that they would successfully reproduce at all (Gongora *et al.*, 2003).

In domestic breeds, clear breed differences in reproductive performance have been noted (Yong, 1992; Yong, 1995), but the seasonal distribution of these differences were rarely reported. In one of our studies (Peltoniemi *et al.*, 1999b), Yorkshire sows had 1.20 times higher risk of rebreeding and Landrace sows had 1.12 times higher risk of rebreeding than crossbred sows. However, the Yorkshire breed performed better than the Landrace and Landrace x Yorkshire crossbred regarding the weaning to oestrus interval (Peltoniemi *et al.*, 1999b; Tummaruk, 2000). Furthermore, the Yorkshire breed appeared to be more susceptible to seasonal variation in reproduction than the Landrace breed (Tummaruk *et al.*, 2000).

Social interaction and boar exposure

The olfactory system is used for communication between pigs. Pheromones secreted by the boar have a strong positive effect on oestrous signs in sows. In a study by Pearce and Pearce (1992) sows, which were in oestrus had a stimulating effect on other sows in the same group so that oestrous symptoms within the group became synchronized. Similar synchronization of oestrous symptoms were reported in European wild boar sows by Delcroix *et al.* (1990). However, pheromones from older sows may have a negative effect on oestrus in younger sows or gilts (Eliasson-Selling *et al.*, 2000). In the summer and autumn, when sows appear more sensitive to a number of adverse effects on fertility, certain pheromones may prevent oestrus and disrupt pregnancy. Pregnancy may terminate in sows or gilts that are of a lower social ranking when too many animals are stocked in a pen. In one of the earlier studies, older pregnant sows caused lower fertility in younger sows housed in the same pen (Wilson and Love, 1990).

Housing

Group housing led to lower fertility compared to individual stalls or pens in summer-autumn (Hurtgen and Leman, 1980; Love *et al.*, 1995). This was explained by social stress due to competition for feed and a need to defend the social rank in a group housing situation. However, in one of our studies (Peltoniemi *et al.* 1999a), where management and seasonal effects on fertility were examined on 1,298 pig farms over the period of 1992-1996, a clear reduction in farrowing rate was evident during late summer and early autumn despite the great majority of the sows being housed in individual stalls. This study did not support the earlier studies, in which individual stalls alleviated the reduced farrowing rate in summer-autumn. The management strategies that are essential for achieving good fertility in a loose housing system differ from those followed in piggeries where animals are individually housed. However, if these differences in management, especially in the feeding strategies during early pregnancy, were accounted for, there was no evidence that individual housing per se provided better fertility.

A common strategy recommended and used to compensate for adverse seasonal effects on fertility in the pig industry is to increase the number of females mated. However, as discussed earlier, increasing the stocking density is likely to increase the stress level within the herd, thereby amplifying the seasonal effects on reproduction. In addition, the chances of good fertility results are likely to be compromised, if sows that should be culled from the herd in summer-autumn are saved in order to keep the number of animals as high as possible.

Stress

Wan *et al.* (1994) proposed the hypothesis that pigs with greater adrenal responsiveness to ACTH are more susceptible to seasonal effects on fertility. The relationship between adrenal responsiveness and seasonal infertility was especially true for gilts, which are known to be more easily affected by season than older sows. This hypothesis implies that environmental factors associated with stress are likely to be important risk factors for seasonal infertility. However, it was shown recently that an acute stress lasting 48 h, and induced during early pregnancy, did not significantly affect embryonic survival and maintenance of pregnancy (Radzan, 2003).

Endocrine basis of seasonal breeding in the pig

A simplified theory of how short days support and long days tend to depress fertility is presented in Fig. 3. Under long days, photoperiod up regulates the melatonin mediated negative steroid feedback mechanism controlling the GnRH pulse generator. Therefore, the pituitary LH secretory response is weak, which results in decreased progesterone secretion by the corpora lutea and depressed fertility. On the contrary, short days stimulate pineal gland secretion of melatonin and down regulate the negative steroid feedback mechanism, thus fertility is supported.

Melatonin

The basis for lighting – melatonin transduction in the pig is thought to be similar to that of other mammals (Tast, 2002). Melatonin affects the GnRH pulse generator by a mechanism yet to be confirmed for the pig. However, some characteristics of the melatonin response to varying photoperiod related factors were studied in the pig. Light intensity of 40 lx triggered a similar nocturnal melatonin response as a 10,000 lx environment during the day time (Tast *et al.*, 2001c), suggesting that light intensity may not play a major role in the mechanism by which

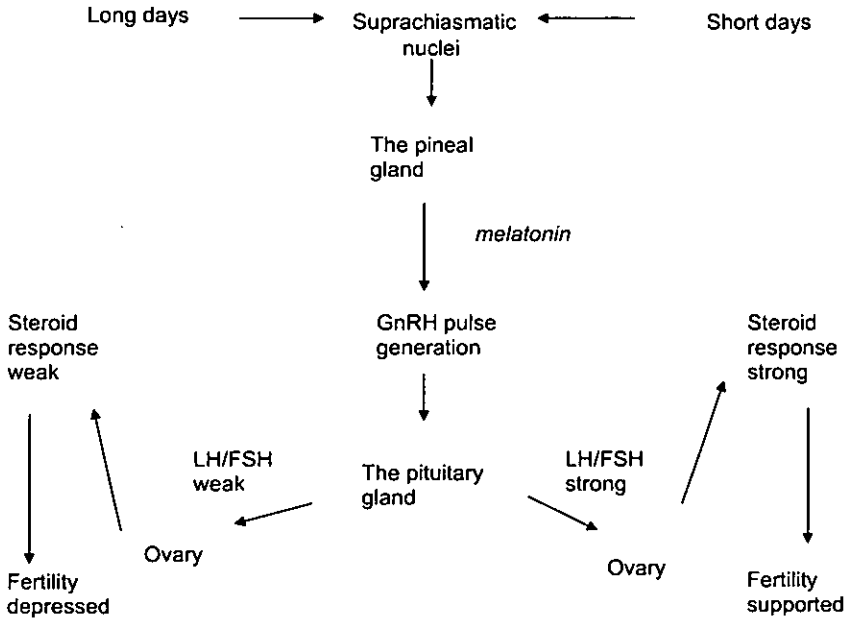


Fig. 3 A schematic presentation of how short days support and long days tend to depress fertility in the domestic pig.

seasonal breeding activities are controlled. Furthermore, a change from one photoperiod to another entrained a corresponding change in the melatonin profile within two weeks in the domestic pig (Tast *et al.*, 2001c). Therefore, it was concluded that it should be possible to develop a lighting program, which supports fertility in the pig, similar to the lighting programs developed to enhance fertility of the other short day seasonal breeder, the sheep (Karsch *et al.*, 1984; Tast, 2002).

Luteinising hormone (LH)

It was shown earlier, that season affects pulsatile LH secretion during early pregnancy in the domestic gilt (Peltoniemi *et al.*, 1997a). These seasonal changes were similar to those during the oestrus cycle. In winter, pulsatile LH secretion was like that in the mid luteal phase of the oestrus cycle; pulse amplitude was high and the baseline appeared stable. However, in summer-autumn, amplitude of pulsatile LH secretion and the baseline appeared unstable, like in a sow approaching the follicular phase of the oestrus cycle. Definition of a LH pulse was difficult with the unstable baseline (Peltoniemi *et al.*, 2000b).

Seasonal variation in pulsatile LH secretion may not be the cause of early loss of embryos in summer-autumn. Manipulation of pulsatile LH secretion disrupted pregnancy if pulsatile LH secretion was suppressed for more than a week rather than for two days only (Peltoniemi *et al.*, 1995, Tast *et al.*, 2000, Virolainen *et al.*, 2004a). Therefore, it appears that a more local component of the effector mechanism disrupting pregnancy at the conceptus-uterine level may play the key role in seasonal infertility.

Progesterone

The role of pulsatile progesterone secretion during early pregnancy (Virolainen *et al.*, 2005a; Fig. 4.) may be a key element in the mechanism by which season affects pregnancy rate in

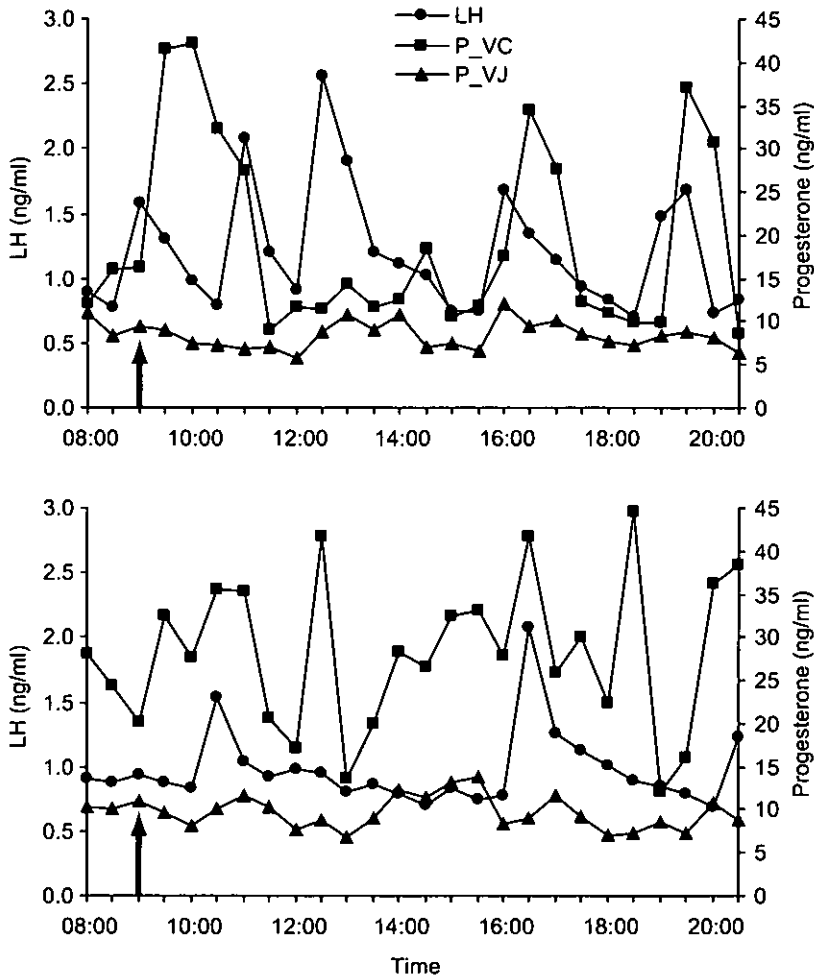


Fig. 4 Plasma progesterone profiles sampled from the caudal vena cava (P_VC, ■) and the jugular vein (P_VJ, ▲) and plasma luteinising hormone (LH) profiles (●) during a 12 h bleeding window at 30-min intervals on day 22 of pregnancy for two gilts. Gilt A received a low level of feed starting on day 11 of pregnancy and gilt B received a high level of feed starting on day 20 of pregnancy. Animals were fed once daily after bleeding (shown with arrow) at 0900 h. All of the feed offered was consumed within 10 min by gilt A, but not until late afternoon by gilt B. Data from Virolainen *et al.*, 2005.

summer-autumn. Changes in LH secretion probably influence the local progesterone milieu within the uterus. During early pregnancy, there was no obvious effect of season on baseline progesterone concentration measured in jugular vein blood (Tast *et al.*, 2002). However, the picture became much more complicated if pulsatility of progesterone concentration within the utero-ovarian circulation was accounted for.

An integral of the local progesterone curve may be a much more reliable indication of the progesterone milieu affecting maternal recognition of pregnancy than that provided by a daily measurement of peripheral progesterone. If the local progesterone milieu, as measured by the integral, is inadequate to support the early embryos sufficiently, they may fail to produce the

second embryonic oestradiol signal required for continuation of pregnancy. Failure of the second oestradiol signal from the embryos caused pregnancy failure and return to oestrus on day 25-35 after mating (Pusateri *et al.*, 1996). Irregular return to oestrus was frequently observed in sows affected by seasonal infertility (Love *et al.*, 1993, Peltoniemi *et al.*, 1999a; Peltoniemi *et al.*, 1999b).

Generally, when progesterone has been a topic in the literature, progesterone in its metabolised form was measured in jugular vein blood or blood from one of the veins in the limbs. However, evidence that metabolised progesterone may not reflect the true progesterone status of the experimental pig is presented in Figure 4. We sampled gilts from the vena cava caudalis, where progesterone was yet to be subjected to metabolism by the liver.

Keys to avoid the seasonal effects on reproduction in the domestic pig

Photoperiod is the only factor in common in all reports about seasonal infertility. Whether in the Northern or Southern hemisphere, seasonal infertility appears to be driven by photoperiod. Therefore, there is little doubt that manipulation of photoperiod will eventually be the most effective way of alleviating the detrimental effects of season on reproduction in the domestic pig breeds. Furthermore, consideration of season is important when planning and applying feeding strategies which affect reproduction. In addition, social environment and stocking density are clearly factors of significance. The clear difference in seasonal breeding characteristics between the genuine European wild boar and its crossbred progeny implies that there is a genetic contribution to seasonal infertility. Whether or not the tendency toward seasonal breeding can be avoided by selecting for genes resistant to seasonal effects remains to be explored. Ambient temperatures exceeding the thermal comfort zone are frequently reported to be the cause of seasonal infertility. Thus, cooling devices may prove to be effective. Hormonal treatments may be effective, but are not a sustainable way to control the tendency of the domestic pig towards seasonal reproduction.

We attempted to improve fertility and seasonality of reproduction of the domestic gilt and sow by applying various lighting programs under experimental and field conditions (Tast *et al.*, 2005). Our goal was to build up two "photoperiodic years" within one calendar year; the idea being that short day seasonal breeders may not benefit from being under a constant photoperiod, whether the photoperiod is short or long. In sheep, a constant photoperiod essentially induced refractoriness to the unchanged photoperiod applied (Lincoln *et al.*, 2003).

The attempted lighting program included long days (16 h of light) in the breeding and gestation units and short days (8 h of light) in the farrowing unit to stimulate oestrus after weaning (Tast *et al.*, 2005). In terms of reproductive performance and seasonal infertility, this program was better than the uncontrolled lighting program previously used, but not as effective as a constant long day lighting program. It was postulated that 35 – 42 days under short days prior to moving to the breeding unit was slightly insufficient for a complete reproductive response (Tast *et al.*, 2005), which was based on the assumption that the time needed in the pig is similar to that in the sheep. It is worth noting that 40 – 50 days is the minimum period necessary for a photoperiod response in the sheep, and in many seasonality studies, altered lighting was applied for periods of 16 weeks (Lincoln *et al.*, 2002). Another version of the lighting program is therefore currently being explored. In this latest version, an adaptation period of 56 days was applied to sows before moving them into the breeding unit. In this study (Hälli *et al.*, unpublished data), sows kept under short days prior to mating had the best fertility results. Altogether, these studies suggest that fertility of the domestic pig, and especially seasonal variation of fertility can be improved by lighting programs.

A number of studies demonstrated that seasonal infertility may be avoided by providing gilts and sows with abundant feeding after mating (Love *et al.*, 1995; Virolainen *et al.*, 2004b, Virolainen *et al.*, 2005a, b). The higher pregnancy rates achieved by abundant feeding may well out-weigh the possible disadvantages of reduced embryonic survival following a high plane of feeding after mating as reported by Foxcroft *et al.* (1997). In any case, providing newly mated or inseminated gilts and sows with roughage feed (hay or straw), to some extent, prevented seasonal effects on reproduction (Peltoniemi *et al.*, 1999a).

The prolonged weaning to oestrus interval due to season may be avoided by group housing sows after weaning instead of keeping them in individual pens. Social interaction between sows and adequate boar exposure are thought to be key elements stimulating oestrus after weaning (Eliasson-Selling *et al.*, 2000). It is true that, under intensive pig production, loose housing may, to some extent, increase the repeat breeding rate (Peltoniemi *et al.*, 1999a). However, this is likely due to limited possibilities for the pig to express species specific behaviour rather than a true negative effect of social interaction on maintenance of pregnancy. If loosely housed sows are given appropriate chances to move around freely and avoid conflicts, they are likely to perform, at least, as well as individually housed sows. Homogenous grouping according to size and age and appropriate use of boars is of fundamental importance to avoid seasonal reduction in reproductive parameters under loose housing conditions (Eliasson-Selling *et al.*, 2000). In addition, if extra females are to be maintained in preparation of forthcoming autumn, extra care should be taken to avoid too high of a stocking density. In other words, extra animals will require extra space that may require building additional production capacity.

The fact that the ancestor of the present domestic pig breeds is a true seasonal breeder, while her progeny has been domesticated away from distinct seasonal breeding, suggests that further selection may be used to negate seasonal effects on reproduction. As discussed above, cross-breeding of the European wild boar with the domestic pig quickly reduced the distinct tendency for seasonal breeding. In addition, Yorkshire sows are more susceptible to the seasonal reduction in farrowing rate than Landrace sows (Tummaruk *et al.*, 2000). Therefore, it appears feasible that selection against seasonal breeding will be used to improve the reproductive performance of the domestic pig in the future.

Cooling systems designed to decrease either the ambient temperature or skin temperature may prove effective in cases when delayed puberty or prolonged weaning to oestrus interval is the major seasonal effect on fertility on a given farm under a hot climate (Prunier *et al.*, 1996; Peltoniemi, 1999). However, if a reduction in the farrowing rate is the major problem, cooling systems may not be effective (Love *et al.*, 1993; Peltoniemi *et al.*, 2000a). Undernutrition due to heat-induced loss of appetite could retard embryonic growth at early stages of embryonic development, which would negatively affect the embryonic signals required for maternal recognition of pregnancy, thereby interrupting establishment of pregnancy (Findlay, 1993). However, as discussed above, a reduction in farrowing rate is commonly seen later in autumn, when high ambient temperatures may no longer be a problem.

A number of studies have investigated the effectiveness of hormone treatments, such as gonadotrophin analogues, prostaglandins, melatonin and oxytocin to overcome problems with seasonality of reproduction in the pig and sheep (Safranski *et al.*, 1992; Pena *et al.*, 1997; Pena *et al.*, 2000; Pena *et al.*, 2001; Basset *et al.*, 2001). Seasonal anoestrus is considered to be similar to the prepubertal period with regard to the responsiveness of females to exogenous gonadotrophin analogues (Stevenson *et al.*, 1985; Safranski *et al.*, 1992). Therefore, it is not surprising that gonadotrophin analogues appear to be effective in induction of oestrus in seasonally anoestrous gilts and sows. However, although oestrus may have been induced, fertility

results were not promising (Pena *et al.*, 2001), and an additional caveat is that consumers demand that no hormonal treatments be used on a routine basis. Therefore, this approach is not a practical sustainable solution to avoiding seasonal effects on reproduction in the domestic pig.

Conclusion

While the pig has been domesticated indoors, genetically selected for better reproductive performance and provided with environment and feed which enable year around production of piglets, she has retained some of the original circannual rhythm in reproductive function. Farrowing rate, proportion of gilts in puberty at the expected time and proportion of sows in oestrus when expected are lower in late summer and autumn compared to other seasons of the year. Seasonal changes in environment are perceived through seasonal changes in photoperiod and this information is transferred through the SCN and the pineal gland to the GnRH pulse generator. Eventually, through involvement of the pituitary gonadal axis, seasonal changes in the progesterone environment in the gonadal circulation and within the uterus affect development of the embryos. Seasonal infertility can be avoided by adequate lighting programs involving alternation of short and long days, by providing female pigs with abundant feed, by using breed records for genetic selection and by using cooling systems where the upper thermal comfort zone is exceeded.

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