

Seasonal effects on fertility in gilts and sows

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The ancestral wild pig is a short day length seasonal breeder. The domestic pig appears to have retained some of this seasonality as evidenced by a reduction in fertility during the summer–autumn period. The most important aspect of this seasonality is a reduction in the number of mated sows that farrow. Many of these sows conceive and embryos develop normally for 20–25 days before pregnancy is terminated and the sow returns to oestrus (25–35 days after mating). In other species, transduction of photoperiodic information is achieved by release of melatonin during the dark period. In the pig, the pattern of melatonin secretion and the subsequent hypothalamo–pituitary–gonadal responses appear to be more complex. A relatively high light intensity is required for pigs to generate a distinct diurnal melatonin rhythm and they appear unable to respond appropriately to abrupt changes in photoperiod. Pigs on restricted feeding and maintained under long photoperiods (but not under short photoperiods) have higher concentrations of melatonin than do similarly maintained pigs fed *ad libitum*. Continuous release melatonin implants have a deleterious effect on farrowing rate, suggesting that the abnormally high melatonin concentrations observed in sows in summer–autumn play a role in the pathogenesis of seasonal infertility. *Ad libitum* feeding of sows during the first few weeks of pregnancy may prevent the increase in melatonin concentrations and so remove the seasonal influence on fertility. The pituitary response to different photoperiods is also somewhat confusing. Although there is some evidence of increased sensitivity to the negative feedback of ovarian steroids in the prepubertal gilts and weaned sows during summer–autumn, LH concentrations are increased in early pregnant sows. It is proposed that the failure of sows to maintain pregnancy in summer–autumn results from disruption of maternal recognition of pregnancy causing regression of the corpora lutea, loss of pregnancy and return of the sow to oestrus.

Introduction

The adverse seasonal effects on reproductive efficiency are of considerable economic significance to the pig industry worldwide. Efficient production requires a constant flow through the facility of growing pigs, and seasonal infertility in the summer–autumn period can dramatically disrupt this flow. A 10% reduction in the number of sows farrowing over 4 months is estimated to reduce profitability by \$Aus30 per sow per year (Cutler and Gardner, 1988). Decreases in productivity of this order or greater are not uncommon in Australia during the summer–autumn period.

It is now generally considered that photoperiod is the primary environmental cue to this seasonality and that the pig is essentially a short-day breeder. A considerable amount of research is being done to determine how pigs recognize and respond to changes in daylength. Current understanding of seasonal breeding stems largely from work in sheep, pronounced short-day breeders. The decreasing daylengths of late summer–autumn alter the diurnal profile of melatonin secretion and the duration of the period of

high concentrations of melatonin associated with darkness. This changed profile reduces the negative feedback of oestradiol on the GnRH pulse generator allowing the development of an LH surge and ovulation. Use of the sheep as a model for pigs has revealed some similarities and many differences in the way pigs interpret and respond to changes in daylength and these will be discussed in this review.

Seasonal Breeding in European Wild Boars

In attempting to understand the seasonal reduction in reproductive efficiency, it is useful to refer to the studies of the clearly seasonal European wild boar, from which the domestic pig is largely derived.

European wild boars are distinctly seasonal breeders, usually producing only one litter per year farrowed in the spring such that conditions in subsequent months are most conducive to the survival of both the sow and her progeny (Mauget, 1982). The rut or breeding season producing this litter occurs in late autumn–early winter; the timing of commencement of the rut is very much influenced by food availability. A plentiful supply of mast (nuts from forest trees such as the beech and oak) is associated with early breeding activity. Farrowing is followed by a long lactation of about 3 months during which the sow remains in anoestrus. Weaning is a gradual process and lactation normally ceases in mid- to late summer and the anoestrous state continues after weaning until the next rut. Wild sows can produce two litters per year if lactation is terminated by removal or death of the litters before midsummer. However, sows weaning a litter after the summer solstice are unlikely to come into oestrus and will remain in anoestrus until late autumn (Mauget, 1982). An interesting aspect of reproduction in wild boars is the synchrony of oestrous activity that occurs within any group of sows at the start of the breeding season. This occurs in the absence of the boar, indicating that there are significant interactions within the sow group (probably pheromonal) that affect reproductive activity (Delcroix *et al.*, 1990). The association of boars with a sow group is distinctly different from domestic arrangements. The boars are essentially solitary animals and only loosely and temporarily associated with a group of four or five sows at any time of the year (Signoret, 1980).

Domestic pigs are generally considered to be genetically remote from their wild ancestors. It certainly is in those characters which have a high heritability and have been strongly selected for in domestication (for example growth rate and carcass characteristics). However, there has been little deliberate selection pressure to negate the seasonal breeding pattern, because it has not been necessary. It is possible to take the wild pig producing one litter a year and convert her to a sow producing more than two litters per year simply by management practices normally used with domestic pigs. The most important practices are: (1) abrupt early weaning: as described above, the wild sow can produce two litters per year, even in the wild, if the litter is removed early in the lactation period; (2) the enforced presence of the boar and his influence on gilts approaching puberty and on sows at weaning: elimination of the boar influence by rearing gilts in the absence of boars to what is normally postpubertal age (Paterson *et al.*, 1991) or by ablation of the olfactory bulbs of sows (Booth and Baldwin, 1983) renders these animals much more responsive to seasonal influences; (3) provision of high levels of nutrition throughout the year: the commencement of the breeding season in late autumn is very much influenced by feed availability; when feed is plentiful, breeding commences some months earlier (Mauget, 1982).

Seasonal Infertility in Domestic Pigs

It is not surprising to see evidence of the propensity towards seasonal breeding in domestic pigs manifest as a moderate decrease in fertility during the period of the year when pigs under natural conditions would not be breeding at all. This seasonal infertility is reported to have a variety of manifestations: delayed puberty in gilts, prolonged interval from weaning to oestrus in sows, failure of mated sows to farrow and reduction in number of piglets born per litter.

Delayed puberty in gilts

There is some confusion in the literature about the effect of season on puberty. However, most reports indicate that puberty is delayed during the summer period (reviewed by Hughes 1982). The effect

on puberty is much more evident in the absence of boars. The intimate and continuous association of the boar, as occurs with domestic gilts, masks the innate seasonal breeding activity (Paterson *et al.*, 1991). In the many studies on the boar effect on puberty, the effect of season has been largely ignored but application of practices developed from these studies dramatically reduces the adverse effects of season on attainment of puberty.

Prolonged weaning to oestrus intervals

The literature on increased weaning to oestrus intervals during summer and autumn has been reviewed by Claus and Weiler (1985). During summer and autumn, most sows have a normal weaning to oestrus interval. A minority of sows (most evident in the parity one group) have a considerably prolonged weaning to oestrus interval (> 30 days) and this increases the mean figure (Hurtgen *et al.*, 1980; Mattioli *et al.*, 1987). The minority group of sows essentially behaves like its wild counterpart, in which weaning during the summer and autumn is followed by a prolonged period of anoestrus (Mauget, 1982). In Australia, this is a relatively minor component of the seasonal infertility complex. The importance of this manifestation of seasonal infertility has declined as weaning age has been reduced (3–4 week weaning), boar influence on the weaned sow has been optimized and feeding levels of sows during lactation and in the weaning to oestrus period have increased. The condition of the sow at weaning, reflecting the level of feeding during the previous pregnancy and lactation, influences the interval from weaning to oestrus (reviewed by Aherne and Kirkwood, 1985) at any time of the year, but it becomes critical during the summer–autumn period.

Reduced farrowing rate

The reduction in the proportion of mated sows that farrow is currently by far the most important aspect of the seasonal infertility. The annual farrowing rate pattern in a 3000 sow intensive piggery (Fig. 1) shows that farrowing rate is reduced for 16 weeks after the summer solstice. The most common evidence of this problem is delayed (> 24 days) return to oestrus (usually 25 to 35 days after mating) as illustrated in Fig. 2 (Love, 1981; Reilly and Roberts, 1992). Sows at this time may show normal oestrous behaviour or may have an undetected oestrus and go through further oestrous cycles of normal duration (21 days) before being remated (Stork 1979; Love, 1981; Mattioli *et al.*, 1987; Reilly and Roberts, 1992). Pregnancy losses also occur at later stages of pregnancy leading to the term 'autumn abortions' (Stork, 1979; Almond *et al.*, 1985). There is evidence that some sows do not develop corpora lutea after mating, and remain in anoestrus (Williamson *et al.*, 1980).

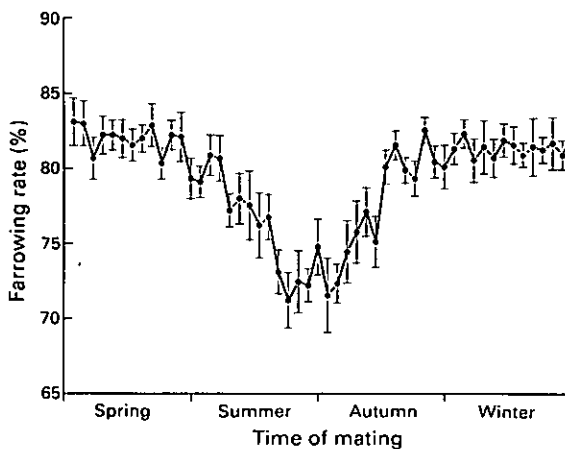


Fig. 1. Mean \pm SEM weekly farrowing rates for the period 1983–1991 for a 3000 sow intensive piggery. The sows are group housed from mating to farrowing.

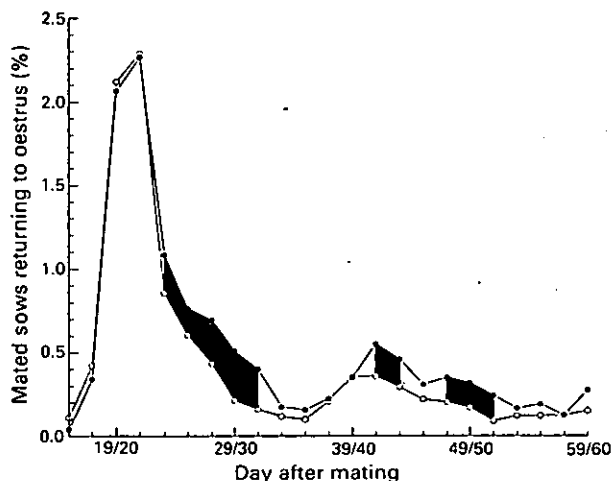


Fig. 2. Times of return to oestrus after mating for sows mated during (●) the period of seasonal infertility (weeks 1–15) or (○) during the remainder of the year (weeks 16–52). The number of sows returning for each two day interval was expressed as a percentage of the total sows mated in each period. The shaded area indicates where the two groups are significantly different ($P < 0.05$). Information was from a 3000 sow intensive piggyery for the years 1987–1991.

It would seem that in a large proportion of sows showing delayed return to oestrus, fertilization occurs normally and viable embryos, as indicated by high concentrations of oestrone sulfate, are present 22–25 days after mating (Y. S. Pan, personal communication; Mattioli *et al.*, 1987). The stage of pregnancy when sows are found not to be pregnant depends on the efficiency of oestrus detection and timing and accuracy of pregnancy testing. When a doppler type ultrasound pregnancy detector (which detects the increased blood flow in the uterine arteries associated with pregnancy) was used carefully during the fifth week after mating during a severe seasonal infertility problem, all sows diagnosed as pregnant at that time, farrowed (Love, 1981). Use of A-mode ultrasound instruments (which detect fluid accumulation in the uterus) during the fifth week after mating can lead to a considerable overestimate of the pregnancy rate and erroneous conclusions about the time of pregnancy loss.

Decreased litter size

Reports on the effect on litter size resulting from matings during the summer and autumn vary from no effect (Love, 1978; Paterson *et al.*, 1978; Mattioli *et al.*, 1987) to significant reductions in litter size (reviewed by Claus and Weiler, 1985). The effect of season on litter size can be confounded by the increased number of return matings which result in larger litters (Love, 1978), as well as increased numbers of gilt matings producing smaller litters. Less stringent culling of older sows aimed at offsetting the reduction in fertility by increasing the numbers of matings may also affect average litter size.

Photoperiod as the Environmental Cue to Seasonal Breeding

There is only limited direct evidence connecting photoperiod with seasonal breeding activity in pigs. Claus and Weiler (1985) provided convincing evidence of the effect of photoperiod on boars in which changes in semen and plasma testosterone can be readily quantitated. Evidence for photoperiodic influence on females is less substantial. These authors used a decreasing day length programme in an 80

sow piggery to simulate the natural decrease in autumn day length during summer. They demonstrated a reduction in interval from weaning to oestrus compared with the previous year in the same piggery.

Paterson and Pearce (1990), using controlled environment rooms, exposed prepubertal gilts from the vernal and autumnal equinox to photoperiods simulating the changes of summer and winter. In the absence of boar influence, puberty was inhibited in gilts exposed to the summer lighting regimen (only 3% reaching puberty by 225 days of age compared with 54%). The presence of a boar overrode this photoperiodic effect. This work provides convincing evidence of the importance of photoperiod on this aspect of seasonal infertility.

Transduction of Photoperiodic Information into Chemical Messenger

In all species studied, photoperiodic information is transduced into an endocrine response by release of melatonin from the pineal gland which then influences the hypothalamic–pituitary–gonadal axis and hence reproductive activity. In species other than the pig, this signal is relatively simple: melatonin synthesis and secretion are increased during the scotophase (darkness) and decreased during the photophase (light) and the change in secretion is recognized by the hypothalamus (reviewed by Lincoln, 1992). However, there has been considerable confusion about the presence or absence of such a diurnal pattern of melatonin secretion in domestic pigs. Many researchers have been unable to demonstrate a nocturnal rise in melatonin (Brandt *et al.*, 1986; Minton *et al.*, 1989; Diekman *et al.*, 1992); others have demonstrated such a rise only under equinoctial (12 h light:12 h dark) photoperiods and only in about half of the pigs studied (McConnell and Ellendorff, 1987; Minton *et al.*, 1989). However, Paterson *et al.* (1992a) demonstrated consistent nocturnal rises in melatonin concentrations under short, equatorial and long photoperiods in prepubertal gilts. To add to the confusion, De Boer and Hacker (1986) found distinct and consistent increases in melatonin during daylight hours.

A number of factors have now been recognized that help to explain these variable results.

Light intensity

In humans there is an inverse linear relationship between light intensity and melatonin plasma concentrations during the photophase. The greater the suppression of melatonin in the light phase the higher the concentrations of melatonin during the dark phase (Lewy *et al.*, 1980). Adequate light intensity is therefore critical to the generation of a distinct circadian rhythm of melatonin.

Griffith and Minton (1992) showed that a light intensity of 113 lux is insufficient to induce a circadian rhythm in melatonin in pigs. However, intense illumination (1783 lux) induced a clear rise in the scotophase melatonin concentrations indicating that light intensity is critical to entrainment of circadian rhythms. The critical light intensity has not been determined but reliable induction of a nocturnal melatonin rise would appear to require a light intensity of 200–300 lux. Paterson *et al.* (1992a), using 270 lux 400 mm above the floor, reliably induced nocturnal rises, whereas Minton and Cash (1990) using 202 lux 650 mm above floor level induced rises in only half of the pigs. Many of the lighting regimens used when investigating melatonin concentrations in pigs have involved intensities of less than 200 lux.

Duration of photophase

Pigs housed in continuous light (202 lux) or dark have a melatonin rhythm with a periodicity close to 24 h (Griffith and Minton, 1991). The pigs on continuous light have significantly higher concentrations of melatonin with much greater variability than those maintained in darkness.

Some studies have found equinoctial photoperiod regimens (12 h light:12 h dark) to be effective inducers of nocturnal increases in melatonin concentrations (McConnell and Ellendorff, 1987; Minton and Cash, 1990), whereas short (8 h light:16 h dark) and long (16 h light:8 h dark) photophases were ineffective (McConnell and Ellendorff, 1987). However, Paterson *et al.* (1992a) were able to demonstrate nocturnal rises in melatonin in short, equinoctial and long photophases.

Rate of change in photophase

Most studies involving artificial lighting have used abrupt and extreme changes in photoperiod (from 8 to 16 h of light in one change). Paterson *et al.* (1992a) increased or decreased the photoperiod incrementally from 12 h light:12 h dark mimicking the natural rate of change in daylength and introduced the pigs into the controlled lighting conditions at the spring equinox. It is under these conditions that nocturnal increases in melatonin have been observed most consistently. As suggested by these authors, pigs may be unable to respond appropriately to sudden changes in photoperiod. In contrast, sheep show immediate and appropriate changes in melatonin when exposed to an abrupt change in photoperiod (Cutler, 1988).

Season

Exposure to natural light with the gradual decrease and increase in intensity at dusk and at dawn could provide quite a different stimulus to the on-off lighting situation that occurs in controlled environments used in many experiments. When early pregnant sows were exposed to natural light in an open-sided building, demonstrable nocturnal rises in melatonin during the night were seen only in spring and summer (Fig. 3). In this experiment the spring and autumn light periods would approximate 12 h light:12 h dark, the summer 15 h light:9 h dark and winter 9 h light:15 h dark at this latitude. The other aspect of the melatonin profiles in this experiment was that overall concentrations in plasma were lowest in winter and highest in summer and autumn. Similar seasonal differences in melatonin concentrations were found by Peacock *et al.* (1991). The low winter concentrations of melatonin found were similar to those produced by pigs in continuous darkness (Griffith and Minton, 1991), and may reflect the lower light intensity during winter. However, the midday light intensity to which these sows were exposed was greater than 300 lux in mid-winter and was as high as could be achieved in housed pigs without exposure to direct sunlight. The high concentrations of melatonin in plasma in summer-autumn may also be similar to the higher concentrations observed under continuous illumination (Griffith and Minton, 1991).

Physiological state

Most studies investigating changes in melatonin concentrations have used young boars (Minton and Cash, 1990), castrates (Griffith and Minton, 1992) or gilts (Diekman *et al.*, 1992; Paterson *et al.*, 1992a). Others have used lactating sows (De Boer and Hacker, 1986), cyclic sows (McConnell and Ellendorff, 1987) or pregnant sows (Peacock *et al.* 1991). Nocturnal increases in melatonin have been demonstrated in at least one study in all these classes of pig except for the lactating sow. The lactating sow is remarkable in that daytime increases in melatonin were observed in sows and these were related to feeding (De Boer and Hacker, 1986).

Age

The amplitude of the nocturnal melatonin rise declines with age in rats (Pang *et al.*, 1984) and humans (Waldhauser *et al.*, 1988). Recent work in our laboratory has shown that distinct nocturnal increases in melatonin were more obvious in young pigs (7 weeks of age) than in prepubertal gilts or multiparous sows (C. Klupiec, R. Love and G. Evans, unpublished).

Level of feeding

The level of feeding affects melatonin secretion in species other than pigs. Three weeks of 50% feed restriction in rats caused increased scotophase melatonin concentrations (Chik *et al.*, 1987) and complete deprivation in post-menopausal women caused a dramatic and immediate increase in daytime melatonin (Beitins *et al.*, 1985). Diurnal profiles were not determined in the latter experiment. Melatonin concentrations are also known to be considerably increased in anorexia nervosa and abnormal in other eating disorders in humans (Ferrari *et al.*, 1989). Most of the experiments studying the melatonin concentrations in pigs have used various degrees of feed restriction (estimated as 60–80% of *ad libitum* intake). We

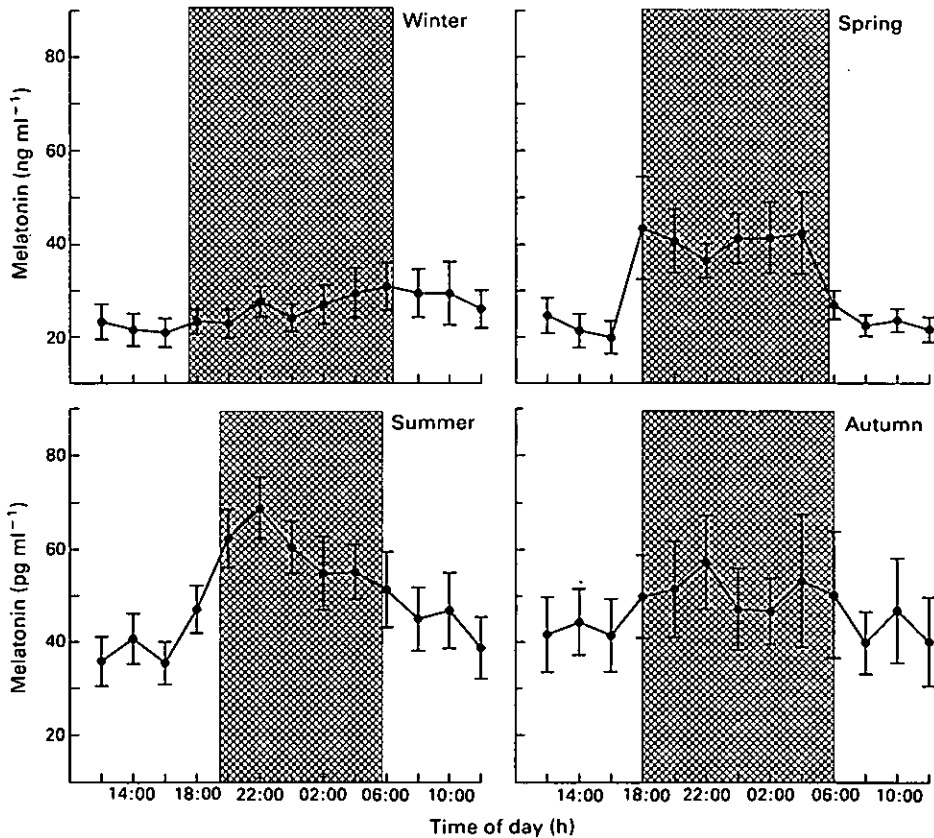


Fig. 3. Mean plasma melatonin concentrations for 4-week pregnant sows in the four seasons. Groups of eight sows exposed to natural lighting conditions were sampled at intervals of 2 h for 26 h. The shaded areas represent the period from sunset to sunrise for each season.

examined the effect of a three week period of food restriction to 60% of *ad libitum* intake on 24 h melatonin profiles of prepubertal gilts on short (9.5 h) or long (14.5 h) photophases. Feed restriction caused a dramatic rise in melatonin concentration in pigs maintained under long photophase, but had no effect on pigs maintained under short photophase (Fig. 4). This finding could explain the higher melatonin concentrations in sows in summer–autumn, as pregnant sows have a restricted feed intake (usually about 60% of *ad libitum* intake). In commercial piggeries the amount of feed restriction is usually greatest for the first few weeks of gestation to minimize the adverse effects of ‘overfeeding’ on embryonic mortality and hence litter size.

In summary, it would appear that nocturnal increases in melatonin are most likely to occur in pigs maintained under high light intensities and fed *ad libitum*. Changes in the duration of the photophase should be incremental rather than abrupt to allow pigs to gradually alter their melatonin response.

Seasonal Effects on the Hypothalamic–Pituitary–Ovarian Axis

In sheep, distinctly short day breeding animals, changes in day length alter the activity of the GnRH pulse generator in the hypothalamus increasing or decreasing release of LH from the pituitary. Changes in photoperiod have both steroid-dependent and steroid-independent effects on GnRH release. Long photoperiods increase the sensitivity of the GnRH pulse generator to the negative feedback effects of oestrogens, markedly decreasing LH pulsatility. In the absence of ovarian steroids, long photoperiods have considerably less influence on LH pulsatility.

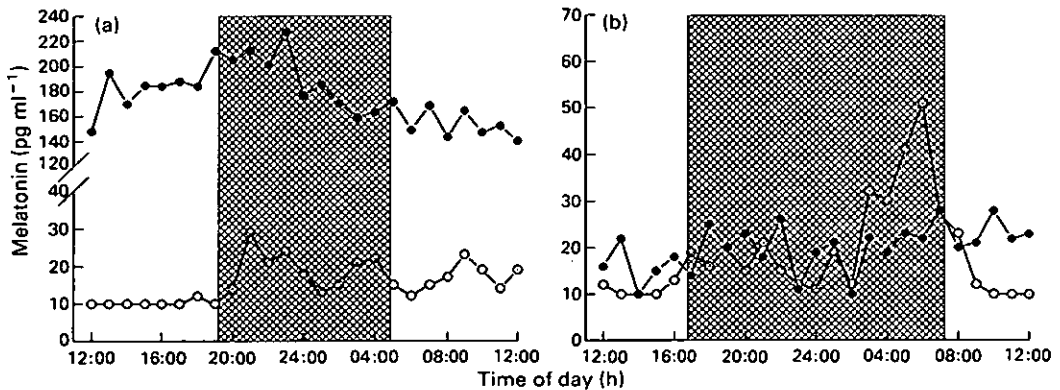


Fig. 4. Twenty-four hour profiles of concentration of melatonin in plasma in pairs of pigs of the (a) long photoperiod (14.5 h light:9.5 h dark) and (b) short (9.5 h dark:14.5 h light) photoperiod. Melatonin concentrations were determined while pigs were (o) *ad libitum* fed and (●) after 3 weeks of feed restriction to 60% *ad libitum* intake. The shaded areas indicate the periods of darkness.

There is evidence from pharmacological studies that both the catecholamine (Meyer and Goodman, 1985) and the endogenous opioid neurotransmitter systems (Ebling and Lincoln, 1985) are involved in the inhibition of GnRH secretion in sheep. Catecholamine inhibition is stronger during the non-breeding season, whereas the effect of endogenous opioids is greatest during the breeding season (Ebling and Hastings, 1992). The endogenous opioids function as part of the steroid feedback system; increasing endogenous opioid tone increases sensitivity to the negative feedback effect of the steroid suppression of GnRH secretion.

The precise mechanism by which the pattern of melatonin secretion, reflecting the changing photoperiod, influences GnRH release is not known (reviewed by Lincoln, 1992). In humans, acute melatonin treatment has been shown to block the LH rise induced by the endogenous opioid antagonist, naloxone (Esposti *et al.*, 1988). However, the dosage of melatonin used may have produced pharmacological rather than physiological responses. Nevertheless, these results suggest that the endogenous opioid system plays a role in mediating the effects of melatonin. Whatever the mechanism, a period of 6–7 weeks exposure to a different photoperiod or melatonin supplementation is required for effects on reproductive activity to become evident (Karsch *et al.*, 1984).

The experimental model that has been used extensively to study the seasonality of sheep is the ovariectomized ewe with or without oestradiol implants. In long-term ovariectomized ewes, LH pulses are relatively infrequent and of large amplitude during the long days of summer and become more frequent and of lower amplitude in winter. Oestradiol implants in ovariectomized ewes cause virtually complete suppression of LH pulsatility under long photoperiods but have little effect under conditions of short days (reviewed by Karsch *et al.*, 1984). In ovariectomized pigs, Cox *et al.* (1987) found an increase in LH pulse amplitude and in baseline concentrations but no change in pulse frequency during summer compared with other seasons. However, Smith *et al.* (1991) could not demonstrate any such change with season.

Ovariectomized pigs maintained in controlled temperature environments and exposed to long photoperiods (16 h light:8 h dark), had higher basal concentrations of LH but similar pulse frequency and amplitude to animals maintained on short photoperiods (8 h light:16 h dark) (Peacock, 1991). Chronic oestradiol implantation of ovariectomized pigs under these conditions reduced pulse frequency, amplitude and basal LH compared with non-implanted animals. The reduction in basal LH and pulse amplitude was significantly greater under short photoperiods (8 h light:16 h dark), but pulse frequency was not significantly different (Peacock, 1991). It would appear that there are both steroid-independent and steroid-dependent effects of photoperiod on LH in ovariectomized sows as in ewes, but the effects are quite different. Rather than LH being reduced during the non-breeding season, it is actually increased without a change in pulse frequency.

Intact, anoestrous, recently weaned sows have been shown to have lower hypothalamic GnRH content and lower concentrations of LH in the anterior pituitary in summer compared with sows weaned in winter. Serum LH concentrations were marginally lower at the time of weaning and 24 h later but were similar 48 and 72 h after weaning for the two groups of sows (Armstrong *et al.*, 1986). These authors suggested that inadequate production of GnRH in summer led to postweaning anoestrus. An alternative interpretation of low hypothalamic GnRH and low pituitary LH could be that increased secretory activity depletes stores of these hormones.

Other studies have looked for differences between sows that have a normal post-weaning oestrus (less than 7 days after weaning) and sows that have a prolonged postweaning anoestrus. These seasonally anoestrous sows respond normally to pulsatile administration of GnRH (Armstrong and Britt, 1985), exogenous gonadotrophins (Dial *et al.*, 1984; Britt *et al.*, 1986) and exogenous oestrogen (Cox *et al.*, 1983; Dial *et al.*, 1984; Almond and Dial, 1990). Apparently the hypothalamic-pituitary-ovarian axis is fully functional, suggesting that alterations in the GnRH pulse generator are responsible for this seasonal anoestrus.

In early pregnant sows, mean plasma LH concentrations are higher in summer than in winter (Peacock, 1991; Smith and Almond, 1991). The LH profiles of sows in summer are very irregular compared with those in winter (Peacock, 1991) making estimates of pulse frequency difficult (Fig. 5). This pattern of LH secretion suggests a decreased response to the negative feedback effect of steroids. Concentrations of progesterone in plasma are marginally lower in the summer and autumn (Wrathall *et al.*, 1986; Peacock, 1991), whereas concentrations of oestradiol in early pregnancy are apparently unaffected by season (Smith and Almond, 1991) and oestradiol is considered to be the more potent suppressor of LH secretion. It therefore seems unlikely that reduced steroid concentrations are responsible for this increase in LH. Smith and Almond (1991) also showed that in early pregnant sows, release of LH in response to exogenous GnRH was not affected by season. Later in pregnancy, gilts had lower mean and baseline LH concentrations in summer than in winter and this was suggested as the cause of the 'autumn abortion syndrome'.

Despite the higher concentrations of LH in early pregnant sows during summer, plasma progesterone concentrations are lower at this time of the year (Wrathall *et al.*, 1986; Peacock, 1991). These lower concentrations during summer may result from an increased rate of clearance of progesterone rather than from reduced secretion. Weaned sows cleared an intravenous bolus of progesterone more quickly in summer than during winter (Peacock, 1991).

The higher concentrations of LH in sows in early pregnancy during the summer period is difficult to reconcile with information from other seasonal breeders in which LH concentrations are decreased in the non-breeding season. It is conceivable that these high plasma concentrations of LH in sows during early pregnancy provide an inappropriate stimulus to ovarian receptors (causing downregulation), resulting in lower progesterone production and, in some sows, failure to maintain the corpora lutea.

The endogenous opioid system has been shown to be important in regulating hormones secreted by the adenohypophysis in many species. It appears that the endogenous opioids influence, or are an integral part of, the steroid-dependent feedback regulation of LH secretion (reviewed by Barb *et al.*, 1991). β -Endorphin (Parvizi and Ellendorff, 1980) decreases LH secretion in pigs and naloxone, an opioid antagonist, in the presence of progesterone, causes a dramatic increase in both LH and prolactin (Barb *et al.*, 1986). The increase in LH in early pregnant sows in summer could reflect a decrease in endogenous opioid tone, reducing the negative steroid-dependent feedback.

It may be that the unusually high concentrations of melatonin in plasma seen in sows during summer influence endogenous opioid tone and thus increase release of LH. In humans, melatonin supplementation has been shown to reduce LH (Voordouw *et al.*, 1992) and the LH increase following naloxone infusion (Esposti *et al.*, 1988). Although not consistent with the high melatonin-high LH findings in sows, this result does indicate that melatonin can influence the endogenous opioid system and LH secretion.

Manipulation of Photoperiodic Response by Melatonin Supplementation

The seasonal pattern of fertility in sows indicates that pigs, like sheep, are short day breeders. Administration of melatonin in the afternoon, prolonging the nocturnal rise in melatonin, or continuous release implants during summer, advances the onset of the breeding season in sheep (English *et al.*, 1986).

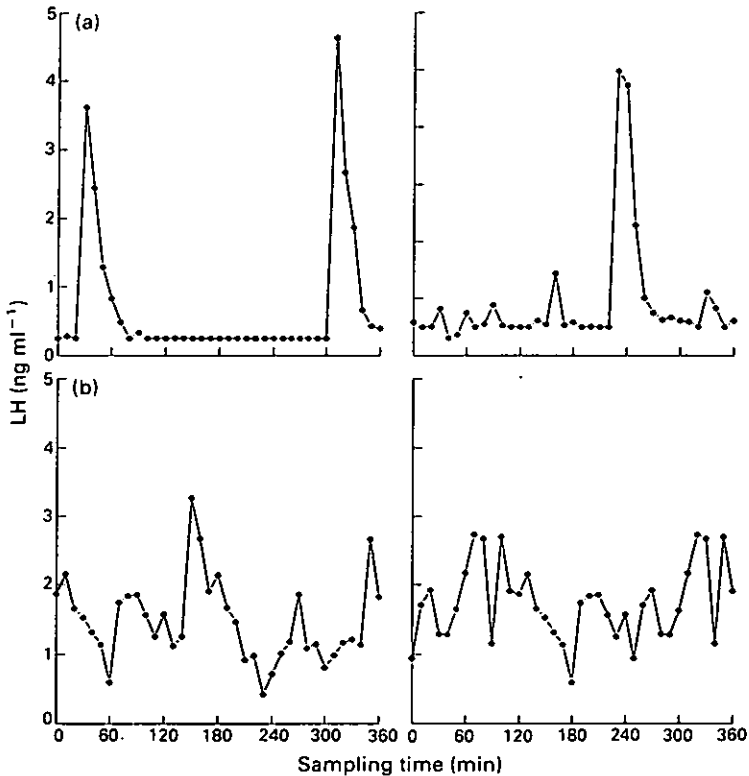


Fig. 5. Six hour profiles of plasma LH concentrations in two 4-week pregnant sows representative of (a) the winter period and (b) the summer period. Redrawn from Peacock (1991).

Afternoon in-feed administration of melatonin to prepubertal gilts from midsummer increased the proportion of gilts reaching puberty by 221 days of age (56% versus 24%, Paterson *et al.*, 1992b). Diekman *et al.* (1991) found that daily melatonin supplementation increased the number of gilts reaching puberty in both autumn and spring. Inducing a marked nocturnal rise in concentration of melatonin in plasma appears to advance puberty in any season. The sustained increased concentration of melatonin following oral administration (> 8 h) was similar to that reported for sheep and goats but was in contrast to work in humans in which only a transitory rise in melatonin plasma concentrations occurred (Wetterberg *et al.*, 1977). The difference between the ruminants and humans was explained previously on the basis of retention of the oral dose in the rumen and gradual release to the lower intestinal tract for absorption (Kennaway and Seamark, 1980). Evidently the absorption of melatonin is different in the two aforementioned monogastrics.

Continuous release melatonin implants have no effect on the age at which gilts reach puberty during the summer–autumn period (Peacock *et al.*, 1991; Paterson *et al.*, 1992b). These implants have also been used in sows in an attempt to improve farrowing rate during the summer–autumn period. In this trial, half of the gilts were implanted 6 weeks before entry into the boar shed for mating; half the parity 1 sows were implanted at weaning approximately 4 weeks before mating (this parity group was mated at the second post-weaning oestrus); and half the older sows were implanted during the second week of lactation (approximately 3 weeks before the next mating). This implant regimen had no effect on the interval from weaning to oestrus or litter size but did have a significant deleterious effect on the farrowing rate in the more numerous older sow group (Table 1).

Sows during the summer–autumn period have been shown to have unusually high plasma melatonin throughout the 24 h period. These high concentrations may be involved in the pathogenesis of seasonal

Table 1. The effect of continuous-release melatonin implants on fertility of gilts and sows during the summer–autumn period

Parameter	Parity 1		Parity 2*		Parity > 2	
	Implant	Control	Implant	Control	Implant	Control
Number of animals	41	94	77	93	122	152
Weaning to mating interval (days)	—	—	26.6 ± 5.8	26.8 ± 6.5	5.6 ± 1.4	5.3 ± 1.3
Farrowing rate %	70.7%	83.0%	74.7%	82.8%	73.7%	86.2%
	P = 0.1065		P = 0.1972		P = 0.0097	
Litter size	10.0 ± 2.1	9.6 ± 2.8	12.3 ± 2.4	11.6 ± 3.1	11.2 ± 3.0	11.5 ± 3.1

Implants were placed six (parity 1), approximately 4 (parity 2) and approximately three (parity > 2) weeks before mating. *This parity group was mated at the second oestrus after weaning.

infertility and hence in the adverse effect of the constant high concentration of melatonin produced by the implants. The failure of implants to adversely affect attainment of puberty in gilts or intervals from weaning to oestrus in sows suggests that pregnancy failure associated with seasonal infertility may have a different pathogenesis.

Other Factors Interacting with Photoperiod

If change in daylength *per se* was the cause of seasonal infertility, then the problem would be much more predictable throughout the summer–autumn period. A feature of seasonal infertility is the extreme variability from piggery to piggery, from week to week within the same piggery (Love, 1981) and even from pen to pen of sows mated in the same week. It would appear that long daylengths are fundamental to inducing seasonal infertility and increase the sensitivity of the sow to other aspects of her environment. A number of factors may be responsible for this variability.

Nutrition

In wild boars, it appears that cessation of breeding activity is independent of the plane of nutrition but commencement of the breeding season is very dependent of food availability (Mauget, 1982, 1987). In domestic gilts many trials have been carried out to investigate the effect of various degrees of feed restriction on puberty (reviewed by Aherne and Kirkwood, 1985). The effect of season in which these trials have been conducted has largely been ignored and may explain the variable effect of feed restriction from delaying puberty to enhancing puberty. It may be that, like boar influence, *ad libitum* feeding may tend to negate the photoperiodic effect on puberty. The rat, a species considered unresponsive to photoperiod, is rendered responsive to photoperiod by feed restriction (Sorrentino *et al.*, 1971).

It is well established that feeding level during lactation, or more precisely, excessive loss of body condition, extends the interval from weaning to oestrus (reviewed by Aherne and Kirkwood, 1985). Appetite is adversely affected by high temperatures and possibly also by season independent of temperature (Mauget, 1987), resulting in greater loss of body condition and extending the interval from weaning to oestrus.

Autumn abortions have been shown to be prevented by either increasing the temperature in the sow house or increasing feeding levels during autumn. The occurrence of abortions appeared to be unrelated to body condition and was considered to be associated with the increased energy demands of the cooler autumn months (Almond *et al.*, 1985).

Social interactions

The pig has an extremely well developed olfactory and vomeronasal system that can detect signalling and priming pheromones. It seems likely that there is a spectrum of pheromonal communication in pigs similar to that described in rodent species. In rodents there are both male–female and female–female pheromonal interactions (reviewed by Vandenberg, 1983). The positive effect of boar pheromones on puberty in gilts and intervals from weaning to oestrus in sows is well known. More recently it has been shown that sows at oestrus have a stimulatory effect on weaned sows, inducing oestrus (Pearce and Pearce, 1992). The synchronous oestrous activity in European wild boars, in the absence of male influence, has been attributed to sow–sow interactions (Delcroix *et al.*, 1990).

However, in addition to positive priming pheromones, a number of inhibitory pheromonal influences have been described in rodents. The most notable of these pertinent to domestic pigs are the effect of group size and crowding on attainment of puberty in young females and oestrous expression in mature females. These effects are most evident in the absence of males but are still expressed if the ratio of females to males is sufficiently high. The end result is determined by the balance between the stimulating effect of the males and the inhibitory influences of other females. This, together with other inhibitory pheromonal influences (e.g. dominant female on subordinate females), may act within the artificial population structure imposed on domestic pigs to affect reproductive success. For most of the year, the positive effects probably outweigh the negative influences except when reproductive impetus is at its lowest during the summer–autumn period.

Demonstration of such inhibitory social influences is logistically difficult in pigs. However, gilts exposed to urine collected from crowded gilts inhibited puberty in non-crowded gilts (Clark *et al.*, 1985), suggesting that population density in pigs had similar effects to those demonstrated in rodents. Mixing of older pregnant sows with young newly mated sows under normal crowded conditions of domestication had an adverse effect on pregnancy rate in the younger sows, suggesting an effect of dominance on reproductive success (Wilson and Love, 1990).

Such apparently nebulous influences may explain the dramatic variation in the adverse effects of seasonal infertility on groups of sows. It is not unusual for a pen of 20 sows to achieve a farrowing rate of less than 50%, while a second pen of sows mated in the same week and maintained in the same building have a normal farrowing rate. It appears that there are some group associated influences that determine reproductive success.

Temperature

Heat stress has been proposed by many as the cause of seasonal infertility (reviewed by Wettemann and Bazer, 1985). The strongest argument against heat stress playing a direct role in the pathogenesis of seasonal infertility is the timing of this problem. The period when seasonal infertility operates commences in midsummer and extends well into the autumn period when temperatures are very mild and certainly less severe than in the early summer period (Fig. 1). Provision of cooling in commercial piggeries has also failed to reduce the severity of seasonal infertility (Hurtgen and Leman, 1980). Rather than high environmental temperatures being involved, there is evidence that low temperatures or cold stress without an adequate compensatory increase in feeding level is responsible for the 'autumn abortion syndrome' (Almond *et al.*, 1985). Sows can maintain pregnancy in midwinter on these relatively low feeding levels. It therefore appears that sows in this period are more sensitive to energy requirements than at other times.

Housing

Provision of individual stalls for mated sows significantly improves the farrowing rate during the summer–autumn period (Hurtgen and Leman, 1980). One large piggery in Australia has half its sows in stalls for the first few weeks of pregnancy and the other sows are maintained in groups of about 20; only the grouped sows show any evidence of seasonal infertility. There is also some evidence that group size is important, groups of five or six sows appear to be less affected by seasonal infertility than do large groups. It is not known how use of individual stalls reduces seasonal infertility: it may be a reduction in

stress; it may ensure each sow receives an adequate level of nutrition; or it may be that use of individual stalls disrupts the group social interactions that have negative effects on fertility.

The Effector Mechanism Disrupting Pregnancy

Delayed puberty in gilts and anoestrus in sows have counterparts in other seasonal breeding species. However, the failure of sows to farrow that apparently ovulate normally and develop normal embryos into the fourth week of gestation is not a common reproductive strategy and appears to be a metabolically wasteful process. A similar phenomenon has been described in a tropical rodent (cloud forest mice) in coping with precarious food and water supplies. Mild restriction of either commodity in this species causes pregnancy failure and return to oestrus (Heideman and Bronson, 1992).

It has been suggested that pregnancy failure in sows is the result of inadequate pituitary support (Wrathall *et al.*, 1986). Once ovulation has occurred in pigs, the corpora lutea function autonomously for the first 14 days and it is only after this time that pituitary support, in the form of LH, is required (reviewed by Flint *et al.*, 1982). Failure of adequate pituitary support at the time of transition of the corpora lutea to pituitary dependence fits well with the increased returns to oestrus 25–35 days after mating. In pregnant pigs with sectioned hypophyseal stalk, there was a gradual decline in corpus luteum function and death of embryos between 16 and 20 days after mating (Anderson *et al.*, 1967).

Flushing embryos from the uterus 13 days after mating results in sows returning to oestrus 25–30 days after mating (van der Meulen *et al.*, 1988). Persistence of the corpora lutea, necessary for the continuation of pregnancy, requires a second signal from the embryo in the period 15–30 days after mating. Killing the embryos at 22 days results in half the sows returning to oestrus and half remaining pseudopregnant (Love, unpublished observations), whereas death of the embryos at day 30 results consistently in pseudopregnancy (Webel *et al.*, 1975). This second signal can be mimicked in nonpregnant sows by injection of oestradiol 15–20 days after oestrus (Geisert *et al.*, 1987). Together with the evidence for biphasic production of oestrogens by embryonic tissues (Geisert *et al.*, 1990), this finding indicates that the second signal is provided by oestrogens, but its mode of action has yet to be determined.

It seems more than coincidence that disruption of the second phase of the embryonic signal (required for the pregnant state to be maintained) results in return to oestrus at the same time as frequently occurs in seasonal infertility. Failure of the second embryonic signal could provide the basis for pregnancy failure in seasonal infertility. However, the presence of the viable embryos producing apparently normal concentrations of oestrone sulfate (Y. S. Pan, personal communication; Mattioli *et al.*, 1987) suggests that, rather than a failure of production of this signal, there is a failure to respond to it. Such a hypothesis suggests that the function of the second signal is different from the first and may be, as suggested by Garverick *et al.* (1982), to increase LH receptors in the corpora lutea. Failure of maintenance of the corpora lutea could then result from inadequacy of the signal (removal of the embryos) or failure of effective occupancy of receptors (seasonal infertility), both situations resulting in delayed return to oestrus.

The unusually high concentrations of melatonin in plasma observed in early pregnant sows in summer–autumn during the period of seasonal infertility and the adverse effect of melatonin implants on farrowing rate suggest that these high concentrations are the cause of the pregnancy failures. High melatonin may exert its effect on LH secretion or, alternatively, by direct effects on the ovary. High concentrations of melatonin occur only in pigs under long photoperiods when feed supply is restricted, if sows are therefore fed *ad libitum* during the summer–autumn period, melatonin concentrations will remain low and seasonal infertility not occur. Trials are being conducted to test this hypothesis by feeding sows liberally during the first four weeks of gestation.

Similar interactions between photoperiod and level of feeding have been described in male deer mice. These animals exhibit greater testicular regression in response to food restriction when maintained on short photoperiods than on long photoperiods (Nelson *et al.*, 1992).

Sow diets are formulated to satisfy the nutrient requirements of the animal rather than appetite. Thus it has been suggested that sows spend much of each day hungry (Hutson, 1989) because they perceive that their food supply is inadequate. If the appetite of the sow is satisfied by feeding the same nutrients in a bulkier diet, there may be benefits to both sow welfare and productivity (Brouns and Edwards, 1992).

Conclusion

It is clear that domestic pigs are seasonal breeders regulated primarily by photoperiod and seasonality is often manifest by a reduction in fertility in the summer–autumn period. Other environmental factors interact with photoperiod to potentiate or exacerbate the problem of summer–autumn infertility and, in early pregnant sows at least, nutrition may be the most potent of these factors. Although pigs behave as short-day breeders, transcription of environmental stimuli is not typical of a classic short-day breeder such as sheep. Melatonin concentrations are often highest during the infertile period and these are associated with, but not yet directly related to, higher mean LH concentrations. The mechanisms by which melatonin acts as a photoperiodic transducer, if indeed it does so in pigs, remain poorly understood.

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