

Influence of light and photoperiodicity on pig prolificacy

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Summary. In the wild pig mating activity is seasonal. The main breeding period is in late autumn but a second period may occur around April. It is known from other species that seasonal variations in breeding activity are mainly regulated by photoperiod.

In the domestic pig seasonal influences on prolificacy still exist: for example, AI boars not only show decreased steroid synthesis, sperm counts and libido in summer compared with the optima which occur in winter but also a biphasic pattern with a transient increase in spring. In cyclic sows ovarian function may be affected with anoestrus mainly in summer and occasionally in February/March. Additionally ovulation rate may be lower in summer and the duration of oestrus prolonged compared with that in late autumn and winter. In consequence the interval from weaning to oestrus is prolonged in summer and mating during this season leads to lower conception rates and slightly smaller litters. Light programmes which extend the daily light period to a constant 15–16 h seem to be ineffective in improving reproductive characteristics of the sow but stimulate the sucking frequency of piglets and increase survival of piglets with a low birthweight. Simulation, in summer, of the decreasing photoperiod (naturally occurring in autumn) stimulates the reproductive characteristics of AI boars, optimizing testicular steroid production, libido and semen composition. Similarly, a programme of decreasing light (20 min decrease/week) from May to August removed the seasonal increase (June–August) of the weaning-to-oestrus interval which was 5–7 days (compared with 23–6 days for the controls).

An interaction between photoperiod and puberty attainment seems to exist for male and female pigs. Further experiments with appropriate light programmes, however, are necessary to clarify this interaction.

Photoperiod as an environmental factor controlling seasonal reproduction in mammals

Seasonal reproduction is a well known phenomenon in animals living in the wild and is still obvious in some domesticated animals. It ensures that the offspring are born when chances of survival are at their optimum. The anticipated time of conception is controlled by the variation in the duration of daylength, as this is the only highly repeatable environmental factor available (Ortavant, Mauleon & Thibault, 1964; Turek & Campbell, 1979; Lincoln & Short, 1980). Consequently, light programmes may be used to influence reproduction. Neither the light intensity nor the wavelength seem to be the crucial features for a light programme in mammals (Lincoln & Short, 1980). In the sheep it has been shown that it is the change from long daily light periods to short periods which is the effective stimulus (Ducker, Thwaites & Bowman, 1970a, b).

In the wild pig reproduction is clearly seasonal with a biphasic pattern. While the main breeding season is in late autumn, second one may occur around April so that the farrowing percentage of sows is highest in April with another increase around August. From July to September all the sows in the population are anoestrous (Mauget, 1982). Measurements of testicular steroids in seminal

plasma of a wild boar routinely used for semen collection have revealed the highest concentrations in late autumn. In summer libido decreased, so that in August and September the boar has been shown to refuse to mount the dummy (Schopper, Gaus, Claus & Bader, 1984).

In the domestic pig, sensitivity to photoperiodic stimuli does not seem to have disappeared and this paper considers the influence of photoperiod on various reproductive characteristics. In addition, the still limited attempts to improve prolificacy with light programmes are discussed.

Light and reproduction of male pigs

Seasonal variations in reproductive characteristics of the mature boar

A pronounced seasonal pattern of testicular steroid production has been shown by measuring 5 α -androst-16-en-3-one (5 α -androstene; boar taint steroid) in adipose tissue of boars at weekly intervals. Maximum concentrations were found around November and were about 5-fold higher than at other periods of the year (Claus, 1979). Such measurements are useful to determine the endocrine status of the testes (Claus & Alsing, 1976).

Seasonal differences in the total number of spermatozoa have been well established. A significant difference ($P < 0.001$) was found between ejaculates from September until February (72×10^9) and from March until August (56×10^9) (Peter, Frank, Mudra & Ueckert, 1981). Higher numbers of spermatozoa per ejaculate in winter may be achieved by increased volumes (Podzo & Varadin, 1983) or by higher sperm concentrations (Peter *et al.*, 1981). Additionally, in summer an increase in the number of morphologically abnormal spermatozoa and spermatozoa with cytoplasmic droplets may occur (Cеровsky, 1978; Kopriva & Pikhard, 1981; Louda, Smerha & Bachtik, 1983). The viability of spermatozoa 24 or 48 h after extending the semen is higher in ejaculates obtained in winter (70% and 55% respectively) than in summer (65% and 44% respectively) (Antonyuk, Il'inskaya & Bezlyundikov, 1982).

Andrological characteristics of the domestic boar may vary throughout the year in a biphasic manner as they do in wild boar. Jaussiaux (1964) has described changes in the number of spermatozoa per ejaculate with a maximum in November, a decrease in February followed by a moderate increase in April/May and a nadir in June. A biphasic pattern has also been found for the ejaculate volumes of boars used for AI (Schindler, 1980) and has been reported for the number of motile spermatozoa per ejaculate (Louda *et al.*, 1983).

Influence of light programmes on reproductive characteristics of the mature boar

Only a few studies of light programmes with mature boars have been reported. Mazzari, du Mesnil du Buisson & Ortavant (1968) changed the light conditions of boars from the natural photoperiod (duration was not given) to 10 h or 16 h light per day. Environmental temperature was kept constant at 15 or 35°C. Boars subjected to short daylength had an increased total number of spermatozoa ($\times 10^9$) compared with those exposed to long daylengths in both temperature groups (15°C: 67.7 ± 2.8 (s.d.) vs 47.8 ± 2.6 ; 35°C: 59.9 ± 2.5 vs 46.9 ± 2.9). It was concluded that photoperiod changes sperm production by influencing the hypothalamo-pituitary status, whereas high temperature has a direct destructive effect on the germ cells (Mazzari *et al.*, 1968).

In experiments with 8 boars which were routinely used for AI, 4 (daylight boars) were subjected to continuous changes of the natural photoperiod (longest day, 17 h light per day, in June; shortest day, 8 h light per day, in December). The other 4 (light programme) boars were kept in a dark building with a light programme which simulated the changes of the natural photoperiod with a delay of half a year (longest day, 17 h light, in December; shortest day, 8 h light, in June). One of the two ejaculates collected weekly was evaluated. Before ejaculation the reaction time was measured as a criterion of libido and blood samples were taken weekly from the ear vein during mounting of

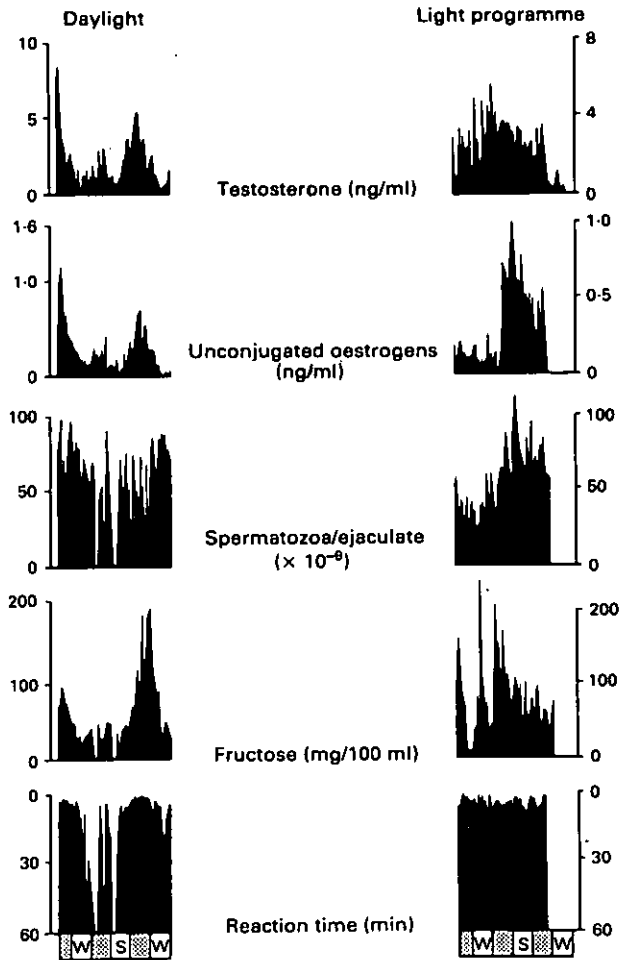


Fig. 1. Seasonal variations of steroid concentrations in blood plasma and several andrological characteristics of individual boars as influenced by the natural photoperiod (daylight) or a light-reversal programme (light programme). (After Claus *et al.*, 1985a, b.)

the dummy. Annual profiles of andrological characteristics (Claus, Schopper & Wagner, 1983; Claus, Schopper, Wagner & Weiler, 1985a; Claus, Weiler & Wagner, 1985b) of individual boars from both light regimens are shown in Fig. 1. In the daylight boars, the optima occurred in autumn and winter and an additional slight improvement was noted in spring. Thus in these boars the characteristics studied followed the usual biphasic pattern.

In the light-programme boars (Fig. 1) all characteristics were optimal in summer. Unconjugated oestrogens and spermatozoa/ejaculate apparently reacted with some delay and optimal values were found during July–September. An improvement in summer was also obvious when the mean values of several characteristics were compared for the 4 boars from both groups in July–September (Table 1).

Sperm production was expressed as 'spermatozoa/mounting attempt' to correct for elevated sperm counts in the ejaculates after refusals to mount. Additionally, to correct for differences in the overall level of spermatogenesis the figures are given as percentage of the initial period. This criterion is shown for the daylight boars and the light-programme boars according to the meteorological seasons in Fig. 2 and points to the stimulating effect of a decreasing natural or artificial photoperiod.

Table 1. Mean values of reproductive characteristics during the period from July to September for 'daylight boars' and 'light programme boars' (from Claus *et al.*, 1984, 1985a,b)

Measurement	Daylight boars	Light programme boars	Significances
Testosterone (ng/ml blood plasma)	1.92	2.82	$P < 0.001$
Unconjugated oestrogens (ng/ml blood plasma)	0.18	0.35	$P < 0.001$
Fructose (mg/100 ml seminal plasma)	44.9	86.2	$P < 0.001$
Reaction time (min)	11.8	5.1	$P < 0.01$

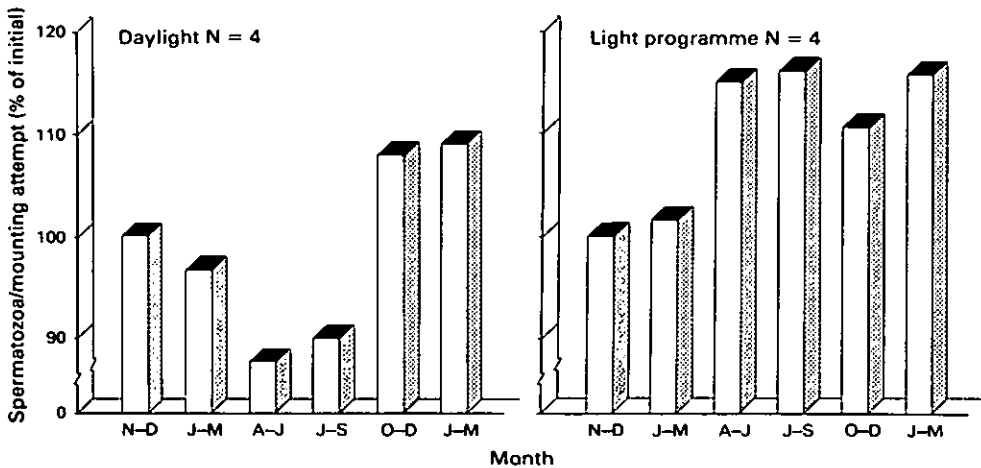


Fig. 2. Influence of the natural photoperiod (daylight) or a light-reversal programme (light programme) on spermatozoa/mounting attempt (see text) of AI boars. (After Claus *et al.*, 1985b.)

The same programme was meanwhile applied in a large German AI station to half the boars. So far (U. Weiler, unpublished observations) the results show that from October to December the daylight boars ($N = 54$) were significantly better than the light-programme boars, with respect to libido, ejaculate volume, spermatozoa per ejaculate and the number of doses obtained per ejaculate. Light-programme boars ($N = 59$), with a variable degree of significance for each month, had improved values for these characteristics from June to September, thus confirming the results of the pilot study.

Influence of light on pubertal development of male pigs

Puberty in the boar becomes obvious at about 3 months of age when Leydig cells differentiate (Colenbrander, Frankenhuis & Wensing, 1982) and testicular steroid synthesis starts to increase (Booth, 1975; Claus & Hoffmann, 1980; Allrich, Christensen, Ford & Zimmermann, 1982). Spermatogenesis, however, is not completed before an age of 4–5 months (Schilling, 1968).

According to the experiments on the influence of light on mature boars, it may be assumed that pubertal development is stimulated by decreasing (stimulating) photoperiod and is delayed by increasing photoperiod. Based on this hypothesis the development of puberty was evaluated by the determination of testicular steroids in two consecutive groups of growing boars (half-sibs) (R. Claus, unpublished observations). The first group (N = 20) was raised during the maximum increase of photoperiod starting at an age of 13 weeks on 10 March; the second group (N = 20) was raised during the maximum decrease of photoperiod (13 weeks; 1 September).

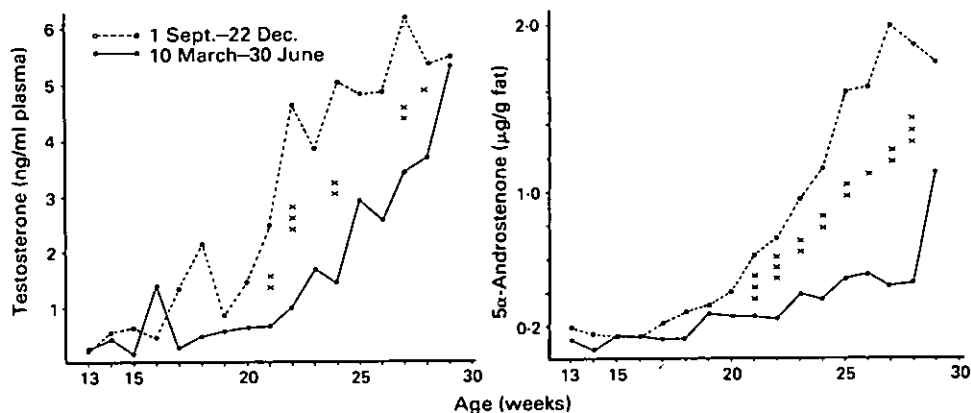


Fig. 3. Testicular steroids in male pigs raised during increasing (solid line, —) or decreasing (broken line, ---) photoperiod. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. (R. Claus, unpublished observations.)

Testosterone concentrations in blood plasma, taken at weekly intervals from the ear vein of 5 pigs from each group, increased more rapidly in the boars raised under decreasing daylength than in those raised in increasing daylength (Fig. 3). The differences were significant at 16, 21, 23, 24, 27 and 28 weeks of age. Similarly, the concentrations of 5 α -androstenone in adipose tissue were significantly higher throughout the period of 21–28 weeks of age for the boars raised under decreasing photoperiod. In addition blood and adipose tissue from the other 15 animals in each group were collected at a weight of 100 kg (about 24 weeks of age). Testosterone concentrations were more than 3-fold higher in the boars exposed to decreasing daylength ($P < 0.001$) and 5 α -androstenone concentrations in adipose tissue were also significantly ($P < 0.001$) higher for the same group.

The results with controlled light conditions do not provide a definite conclusion. Pubertal development of boars kept with constant light of 8 or 16 h per day showed no differences for testicular and epididymal weight, epididymal sperm numbers and serum LH concentrations. However, testicular sperm numbers and testosterone concentrations in blood plasma tended to be higher (not significantly) in the boars exposed to 16 h light (Minton, Fent & Wettemann, 1980). The effects of supplemental light (15 h light/day) have been compared to the natural photoperiod during various seasons of the year (Mahone, Berger, Clegg & Singleton, 1979; Berger, Mahone, Svoboda, Metz & Clegg, 1980; Greenberg & Mahone, 1981; Hoagland & Diekman, 1982). No definite influence on the onset of spermatogenesis (e.g. appearance of first spermatozoa in urine or preputial fluid) and later differences in semen composition were obvious. In some studies libido scores tended to be improved for the boars with supplemental light.

As a comparison of pubertal development under decreasing or increasing light programmes has not yet been undertaken, light–puberty interactions in the boar need further investigation.

Light and reproduction of the female pig

Annual differences of reproductive phenomena which contribute to prolificacy in the sow have attracted considerable interest. Results from many countries where various reproductive traits have been examined confirm the existence of a period of lowered fertility in summer (Fig. 4). Seasonal changes of traits influencing farrowing interval and litter size are considered further.

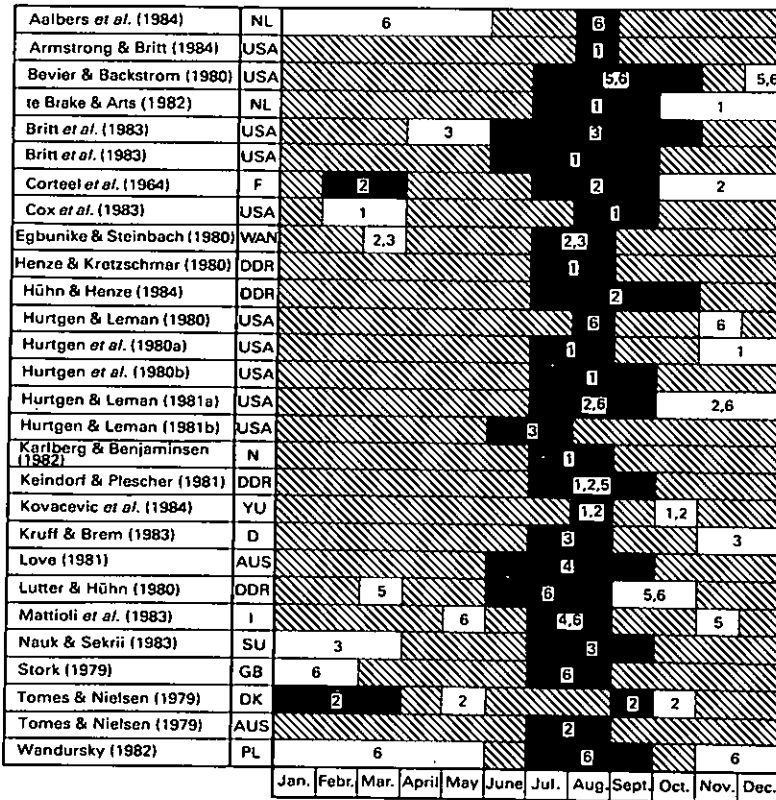


Fig. 4. Investigations on seasonal reproductive problems in the sow. Black bars indicate periods with lowered reproductive measures, white bars of improved measures compared with the rest of the year (southern hemisphere adapted to northern hemisphere). 1 = Weaning-to-oestrus interval; 2 = conception rate; 3 = weaning-to-conception interval; 4 = embryonic loss; 5 = litter size, depending on the month of conception; 6 = farrowing rate, depending on the month of conception.

Seasonal variations in reproductive characteristics of the sow

Weaning-to-oestrus interval. After weaning the piglets, a sow should return to oestrus within 7 days. This weaning-to-oestrus interval, however, is generally prolonged during summer and tends to be improved during October to January (Corteel, Signoret & du Mesnil du Buisson, 1964; Hurtgen & Leman, 1981a, b; Keindorf & Plescher, 1981; te Brake & Arts, 1982; Britt, Szarek & Levis, 1983; Noguera, Felgines & Legault, 1983). The use of cooling systems has not yet prevented the increased interval in summer (Hurtgen, Leman & Crabo, 1980b; Britt *et al.*, 1983; Cox, Britt, Armstrong & Alhusen, 1983).

The percentage of sows returning to oestrus within 7 days was only 68.6% during July to September, compared with 82.0% during the rest of the year (Hurtgen *et al.*, 1980a); a similar result (50.5 and 72%) has been reported by te Brake & Arts (1982). Average intervals of 23.6 days in summer and 10.8 days in autumn have been reported by Claus, Schelkle & Weiler (1984) and of 28 and 17 days by Aumaitre, Dagorn, Legault & le Denmat (1976). Additionally, the chance of an abnormally prolonged interval until first oestrus (more than 30 or even 45 days) is two-fold greater in summer than at other times of the year (Corteel *et al.*, 1964; Hurtgen *et al.*, 1980a) and may lead to replacement of multiparous sows by gilts. In primiparous sows, however, the interval is even more prolonged in summer (Hurtgen *et al.*, 1980a; Britt *et al.*, 1983).

Progesterone concentrations in the blood plasma are constantly low until the first observed oestrus (Armstrong & Britt, 1984; Claus *et al.*, 1984; Kovacevic *et al.*, 1984), and so silent oestrus seems to be the exception.

Increased intervals to oestrus seem to occur when weaning coincides with a period of lowered ovarian activity. In a slaughterhouse study Hurtgen & Leman (1978) found more than 40% of sows with inactive ovaries in August (Fig. 5). Ovarian inactivity is also obvious in a current study in which the annual progesterone profiles of cyclic sows are being obtained (R. Claus, unpublished observations). Figure 6 shows the pattern from one animal which spontaneously ceased cycling

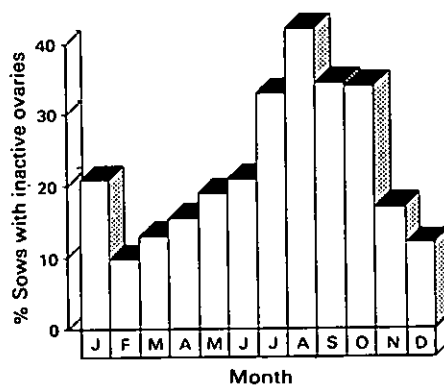


Fig. 5. Seasonal distribution of the percentage of sows with inactive ovaries as found in a slaughterhouse study. (After Hurtgen & Leman, 1978.)

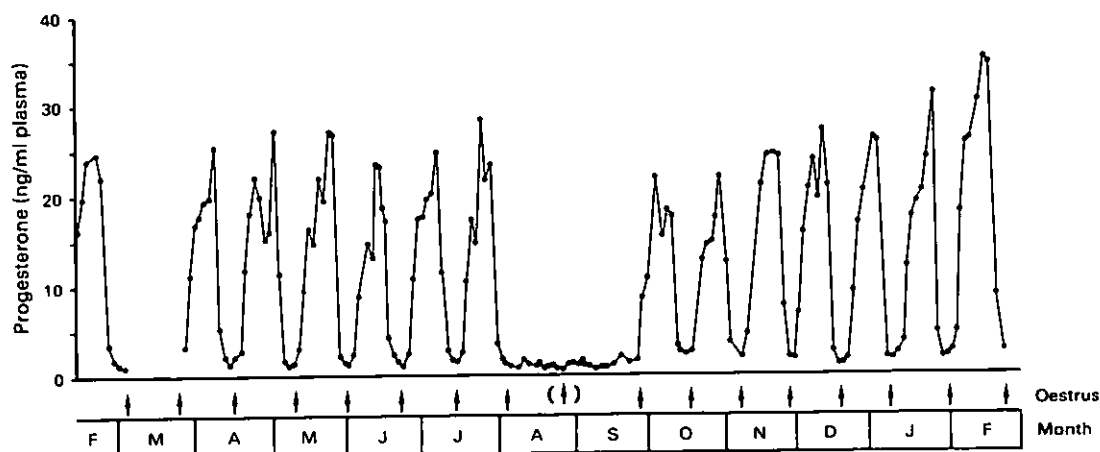


Fig. 6. Annual profile of progesterone concentrations in a cyclic sow. Catheter failure in March; weak symptoms of oestrus at the end of August during the acyclic period. (R. Claus, unpublished observations.)

from the beginning of August until the end of September and then resumed cyclic activity. Anoestrus was obvious in this study in the period of July to October in 6 out of 15 sows and in 3 sows also during February and March. Anoestrus did not occur in December to January and April to June.

Conception and farrowing rate. Farrowing rate is generally suboptimal when insemination or mating take place between July and September (Stork, 1979; Hurtgen & Leman, 1980; Wandursky, 1982; Aalbers, Johnson, Rademaker & Grooten, 1984). This annual decrease may arise as early as May or June (Lutter & Hühn, 1980; Bevier & Backstrom, 1980; Hurtgen & Leman, 1981b) and extend to September or October and is not prevented by cooling methods (Hurtgen & Leman, 1981a). Farrowing rates above the average were found when insemination took place between late autumn and early spring (Stork, 1979; Hurtgen *et al.*, 1980a; Hurtgen & Leman, 1981a; Wandursky, 1982; Aalbers *et al.*, 1984). The main explanation is that conception rate is decreased in summer and tends to be elevated in autumn and winter (Keindorf & Plescher, 1981; Britt *et al.*, 1983; Dobao, Rodriganez & Silio, 1983; Mattioli, Taschini, Galeati & Seren, 1983). The percentage of sows not conceiving in summer varies considerably and may be as high as 35.5% compared with 23.5% in winter (Dobao *et al.*, 1983) and 56% for gilts in summer (Kovacevic *et al.*, 1984). The biphasic pattern of conception rate reported by Corteel *et al.* (1964) is shown in Fig. 7.

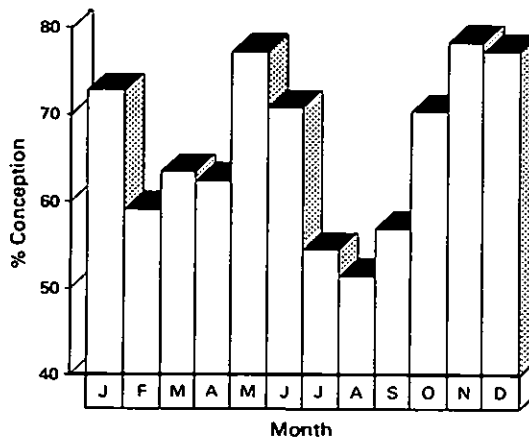


Fig. 7. Annual biphasic pattern of the conception rate. (After Corteel *et al.*, 1964.)

An explanation of the annual differences in conception rate may be the problem of timing of AI or mating during the oestrous period. The time of ovulation within the oestrous period varies considerably (Foxcroft & van de Wiel, 1982) and it is known that during summer the duration of oestrus is prolonged compared with autumn/winter (Signoret, 1967; Nauk & Sekrii, 1983).

In addition, embryonic loss may cause a reduced farrowing rate (Stork, 1979; Mattioli *et al.*, 1983): the highest incidence of abortions occurs in September/October mainly in sows mated between June and September. From all sows that were successfully inseminated during the period June to August (oestrone sulphate determination at Day 25), 25–30% did not farrow, compared with only 4 and 6% of sows successfully inseminated in May and November respectively (Mattioli *et al.*, 1983).

Litter size. Litter size is generally increased after mating in autumn and winter compared with summer (Tomes & Nielsen, 1979; Keindorf & Plescher, 1981; Bevier & Backstrom, 1981; Dobao *et al.*, 1983; Mattioli *et al.*, 1983; Noguera *et al.*, 1983; Aalbers *et al.*, 1984). Litter size from matings in summer is usually at least 1 piglet less than that from autumn and winter matings (Bevier & Backstrom, 1981; Mattioli *et al.*, 1983). Increased litter size may also result from mating in

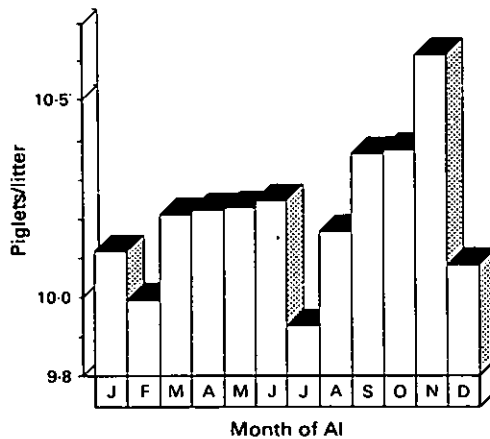


Fig. 8. Annual biphasic pattern of the litter size, depending on the month of AI. (After Mezger, 1984.)

April–May (Bevier & Backstrom, 1981) and this fits with the biphasic pattern obtained by analysis of 9000 litters as shown in Fig. 8 (Mezger, 1984).

In mature sows, litter size seems to be determined mainly by uterine capacity which limits the number of embryos (Dziuk, 1977). In summer, however, reduced ovulation rate may also limit the litter size. Counting the corpora lutea of sows slaughtered 30 days after mating has shown that the ovulation rate appears to be at a maximum in autumn ($N = 17$) and at a minimum ($N = 15$) from the end of winter to spring (Martinat-Botte, Dando, Gautier & Terqui, 1981); figures were not given for May–August because of the limited number of sows slaughtered. A tendency for increasing progesterone concentrations during consecutive luteal phases from summer to winter is obvious for the sow shown in Fig. 6. In the same study, statistical evaluation of 11 luteal phases for each month revealed that progesterone concentrations were significantly ($P < 0.001$) lower in August than in November, December and January (R. Claus, unpublished observations).

Progesterone concentrations in early pregnancy (Days 10–60 after AI) are significantly lower in August–September (21.5 ng progesterone/ml plasma) than in all other periods (32.4–40.3 ng/ml) (Bielanski & Kremer, 1983). No differences, however, were found in the maximum progesterone concentrations during the luteal phase of gilts investigated in June–September or February–March (Perotti, Enne, Meggiolaro & Delrio, 1979).

Influence of light patterns on reproductive characteristics of the sow

Constant photoperiod. Several experiments were designed to study the effects of supplemental light (daily light period artificially extended to 16 h) compared with the natural photoperiod or a constant 8-h light per day on reproductive characteristics of the sow. The light regimen was changed at the end of pregnancy and was kept constant thereafter. No effect was found for the weaning-to-oestrus interval, conception rate, farrowing rate, or litter size (Greenberg & Mahone, 1982; Mabry, Cunningham, Kraeling & Rampacek, 1982; Mabry, Coffey & Seerly, 1983). A late change from natural photoperiod (1 day after weaning) to 24 h dark or 24 h light or 12 h dark/12 h light per day did not influence these values (Perera, Hacker & King, 1980; Perera & Hacker, 1984). Long periods of light per day, however, prolonged manifestations of behavioural oestrus (Perera & Hacker, 1984) similar to the natural photoperiod in summer.

Extending the photoperiod (16 h vs 8 h) caused an increase of milk yield of nursing sows by 20–24% (Mabry *et al.*, 1982, 1983), so that the survival rate of the piglets born with low birth weights was improved (Mabry *et al.*, 1982, 1983; Stevenson, Pollman, Davis & Murphy, 1983). This

is explained by an increased suckling frequency of the piglets (Mabry *et al.*, 1983), which in turn both increased their nutrient supply and stimulated milk production.

Decreasing photoperiod. A decreasing light programme simulating the natural decrease of daylength in autumn was applied during summer in a piggery with 80 sows to improve the weaning-to-oestrus interval (Claus *et al.*, 1984). At this farm the interval had been recorded in the year preceding the use of this light regimen and was found to increase to an average of 31.6 days in August (Fig. 9a). The programme started in May (15 h 20 min light) about 1 month before the expected seasonal increase of the weaning-to-oestrus interval. The daily light period was weekly diminished by 20 min until the end of August. After this period the sows returned from 10 h artificial to 13.5 h natural light, followed by the seasonal decrease of natural daylength. As shown in Fig. 9(b) the light programme markedly decreased the interval to an average of 5.7 days in June–August (28 sows weaned), compared with 23.6 days in the same period of the preceding year.

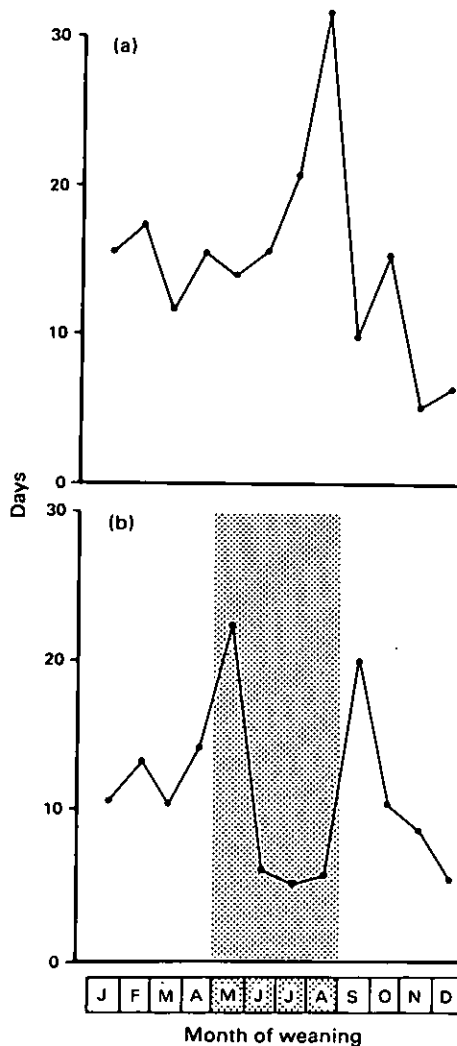


Fig. 9. Annual pattern of the weaning-to-oestrus interval as influenced by the natural photoperiod (a) or a decreasing-light programme (shaded area, b). (From Claus *et al.*, 1984.)

The return to the natural photoperiod at the end of August (sudden increase of photoperiod) resulted in a transient increase of the interval in September, which fell again as natural daylight decreased. The average monthly temperature in July and August was higher in the experimental year (20.1°C) than in the previous year (18.2°C).

Light and puberty in the gilt

Conflicting results have been obtained from studies on the effects of season on the attainment of puberty in the gilt (see review by Hughes, 1982). A delayed puberty in summer has been reported (Christenson, 1981), and a biphasic annual profile was obvious for the percentages of gilts showing first oestrus (Willecke, Metges & Oster, 1984) and reaching puberty by 8 months of age (Maksimovic, 1983).

The influence of light programmes (constant duration of light/day) has also been reviewed (Hughes, 1982) and the conflicting nature of the results shown. Recent experiments with comparable light regimens have contributed to the conflict by confirming the suggested positive effect of long days (Dickman & Hoagland, 1983) or finding a contradictory or no effect (Wise, Jones, Allrich & Zimmermann, 1980; Christenson, 1981). The only light-decreasing regimen (Wright, English & Robertson, 1984) was applied for 1 month only and did not allow conclusions to be drawn.

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