

Expression of oestrus and timing of ovulation in pigs

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Oestrus is the period around ovulation in which sows show a standing response for boars, thus allowing the boars to mate with the sows. The duration of oestrus may vary between sows from 24 h up to 96 h, which is not related to systemic oestrogen concentrations. The moment of ovulation after onset of oestrus may vary from 10 h to 85 h. Consequently, onset of oestrus is not a good predictor for the time of ovulation. A reliable prediction of ovulation time would be worthwhile, since fertilization results are highly dependent on the moment of insemination relative to the moment of ovulation. However, at present, the duration of oestrus is the best 'predictor' of ovulation time and is independent of the duration of oestrus; ovulation takes place on average 70% of the way through oestrus. The following factors have been found to influence the duration of oestrus (and consequently the optimal time for insemination): boar-stimuli, stress, interval from weaning to oestrus, season and parity. Further study is needed to determine the causes of the variability in oestrus expression between sows, including the regulation of oestrus behaviour at the level of the brain.

Introduction

The period around and during oestrus is characterized by a combination of externally assessable changes of the vulva and behavioural changes, both of which show considerable variation between sows in intensity as well as in duration. Although in pigs little is known about the regulation of oestrous behaviour at the brain, many factors have been found that influence the duration of oestrus and these will be summarized.

The timing of insemination or mating in pig husbandry is normally based on the onset of (standing) oestrus. Since fertilization results are highly dependent on the time of insemination relative to ovulation (see Kemp and Soede, 1997), an important question is whether or not certain oestrous characteristics can 'predict' the time of ovulation. In this review, available data on the characteristics of oestrus in relation to ovulation time will be summarized.

In spontaneously ovulating sows, the duration of ovulation is only 1–3 h (Soede *et al.*, 1992) or at most 5 h under extreme chronic stress conditions (Soede *et al.*, 1997a) and studies relating oestrous characteristics to ovulation time only assess ovulation time with an accuracy of 4 h or more; in this review ovulation is regarded as taking place at one moment rather than during a period.

This review will not deal with factors affecting or regulating attainment of puberty in gilts or the intervals from weaning to oestrus in sows, which have been reviewed by Hughes *et al.* (1990) and Hemsworth and Barnett (1990) and Prunier *et al.* (1996) and Vesseur (1997), respectively.

Unless specified otherwise, in this review the expression 'oestrus' and 'duration of oestrus' is used for sows that show a standing response in the presence of a boar.

Externally Assessable Characteristics of (approaching) Oestrus

Vulva

The period of increasing follicular development and oestrogen production by the ovaries, during which symptoms of approaching oestrus can be observed, is called pro-oestrus (Willemse and Boender, 1966). During pro-oestrus, the vulva swells and becomes red(dish) under the influence of the higher oestrogen concentrations. Furthermore, the amount of vaginal mucus increases and also changes in fluidity, colour, conductivity, pH and crystallization pattern. During pro-oestrus, the swelling and redness of the vulva differ between animals, not only in intensity but also in duration. In primiparous sows, Sterning *et al.* (1994) showed that the reddening and swelling during pro-oestrus lasted 2.0 ± 1.5 days, with a range of 0 to 8 days in 158 sows during the first oestrus after weaning. The maximum intensity of the reddening and swelling (scored as 0, 1, 2 and 3) was 2.6 ± 0.6 and varied from 0 to 3. Not much is known about factors that influence the duration of pro-oestrus. Sterning *et al.* (1994) found indications of a seasonal influence; pro-oestrus was shorter in spring and summer (March–September; 1.5 days) than in winter (January–March; 2.3 days). In primiparous sows, the duration of pro-oestrus is not related to the duration of standing oestrus (Sterning *et al.*, 1994). It is unclear whether differences in vulval swelling and reddening between sows are related to differences in systemic oestrogen concentrations.

Behaviour

The differentiation of sexual behaviour, resulting in typical female and male sexual behaviour in pigs takes place after birth, as has been reviewed by Ford (1990). However, a very small part of the differentiation seems to take place during pregnancy, as is suggested by the fact that gilts that have been exposed to testosterone *in utero* show a decrease in oestrus expression (testosterone-treated: Ford and Christenson, 1987; gilts between two males *in utero*: Rohde-Parfet *et al.*, 1988).

In female mammals, the behaviour leading to mating is divided in proceptive and receptive behaviour. Proceptive behaviour has been defined as 'various reactions by the female towards the male which constitute her assumption of initiative in establishing or maintaining sexual interaction' and receptive behaviour is defined in terms of 'female responses necessary and sufficient for the male's success in achieving intra-vaginal (or intra-cervical) ejaculation' (Beach, 1976). Oestrus is defined as the period in which the sow shows receptive behaviour or, as defined by Willemse and Boender (1966), the only period in which the female animal permits mating.

Approaching and during oestrus, sows often show a reduced appetite, in general they have a higher level of activity and may show mounting behaviour. Proceptive behaviour in female pigs consists of boar-directed behaviour; given the opportunity, the sow will go to the boar and will stay close to the boar for longer periods of time approaching oestrus and during oestrus (Signoret, 1970; Bressers *et al.*, 1991; de Jonge *et al.*, 1994). Although receptive behaviour is normally the basis for oestrus detection, in group-housing systems, this (proceptive) boar-directed behaviour has been the basis for a system of automated oestrus-detection (Bressers *et al.*, 1991).

Sows show receptive behaviour by the so-called 'standing response'; the sow stands immobile, arches her back and cocks the ears (Signoret, 1970). Olfactory and tactile stimuli of the boar are particularly involved in evoking the standing response (Signoret, 1970). During oestrus, the standing response is not an all or none phenomenon; at the onset of oestrus, many (boar) stimuli may be needed to evoke the standing response, but later in oestrus, fewer stimuli are needed. Willemse and Boender (1966), therefore, divided oestrus into a first boar-period (standing response can be evoked by the boar, but not by the inseminator), an inseminator-period (standing response can also be evoked by the inseminator who performs the Back-Pressure-Test (BPT)), and a second boar-period. During the receptive period, not only receptivity but also proceptivity increases reaches a maximum and then decreases again (de Jonge *et al.*, 1994).

The duration of oestrus may vary considerably, both within and between experiments or farms; for example, Weitze *et al.* (1994) found that the duration of oestrus varied between 35 h and 96 h (on average 60 ± 15 h) in 483 sows and Soede *et al.* (1995a) found a variation of between 24 h and 88 h (on

average 50 ± 13 h) in 144 sows. Furthermore, when a similar strategy for detecting oestrus (twice daily with a boar) was used on 21 farms in The Netherlands, the average duration of oestrus varied between 38 h and 69 h (G. D. R. Groenland, unpublished).

The duration of the inseminator period (or standing oestrus in the absence of a boar) may also vary considerably; in gilts, Willemse and Boender (1966) found a variation in duration between less than 21 and more than 65 h (on average 43 ± 12 h; excluding the gilts that did not show oestrus in the absence of a boar) and in sows Soede *et al.* (1996) found a variation between 0 h and 64 h (on average 32 ± 14 h; including 8 of 144 sows that did not show oestrus in the absence of a boar). Not all gilts and sows that show a standing response for the boar also show a standing response for man. The proportion of oestrous gilts and sows that do not show oestrus in the absence of a boar was reported to be as high as 46% and 30% (gilts; Schenk, 1967 and Signoret, 1971, respectively) and 19% (sows; Schenk, 1967). However, in those studies, no account was made of the stage of oestrus of the animals. In studies in which oestrus detection was performed repeatedly at short intervals, the proportion of pigs at oestrus not showing oestrous behaviour in the absence of a boar was only 5% (gilts: Willemse and Boender, 1966; sows: Soede *et al.*, 1996).

From the few experimental data available, it seems that vulval and behavioural characteristics of oestrus are poorly related. For example, a significant difference in the duration of pro-oestrus (vulval swelling and redness) between the second and fourth oestrus of gilts was not accompanied by a change in the duration of standing oestrus (Andersson *et al.*, 1983). Furthermore, both gilts and sows may show vulval changes and ovulate, without showing a standing oestrus (see for example Ford and Christenson, 1987; Eliasson, 1991); not much is known about the cause of this 'silent' oestrus. However, it has been suggested that the occurrence of silent oestrus may be an indication that concentrations of oestrogen needed for initiation of the preovulatory LH peak are less than the concentration that is needed for initiation of oestrous behaviour (see for example Ford and Christenson, 1987).

Regulation of Oestrous Behaviour

Oestrous behaviour, like the preovulatory LH peak, is initiated by oestrogen produced by the growing follicles. From this it might be concluded that expression of oestrus is simply related to differences in systemic oestrogen profiles. In ovariectomized gilts, one injection with oestradiol benzoate can induce oestrous behaviour; higher doses of oestradiol benzoate result in a higher percentage of gilts that show oestrus and also increase the duration of oestrus in those gilts (for example Signoret, 1967; Esbenshade and Huff, 1989). Progesterone priming does not affect oestrous behaviour in pigs (Signoret, 1969) as it does for example in sheep. Furthermore, in pigs, GnRH and circulating LH and FSH do not seem to affect oestrus expression directly. This was shown by Esbenshade and Huff (1989) who eliminated these hormones by active immunization against GnRH and who, after subsequent ovariectomy, did not find any difference in expression of oestrus in these gilts compared with non-immunized ovariectomized gilts in several oestradiol benzoate treatments.

In intact animals, however, there does not appear to be a relationship between systemic oestrogen concentration and the duration of oestrus. Andersson *et al.* (1983) found higher oestrogen concentrations together with a shorter duration of pro-oestrus (but there was no relationship to the duration of oestrus) in gilts during their fourth compared with their second oestrus. In sows, no relationships were found between concentrations of oestrogen, LH or progesterone or their temporal relationships and the duration of oestrus (Soede *et al.*, 1994). Furthermore, in two groups of sows (tethered versus loose-housed) that differed in the duration of oestrus, no differences were found in profiles of oestrogen, LH or progesterone (Soede *et al.*, 1997a). In conclusion, even though oestrogen regulates oestrous behaviour, systemic concentrations of oestrogen do not seem to be related to differences in the duration of oestrus in pigs.

A considerable amount of literature, especially in rats, has shown that sexual behaviour in females is regulated for a major part by the ventromedial nucleus of the hypothalamus (VMH) and other areas of the brain that have a high density of oestrogen receptors (reviewed by

Pfaff *et al.*, 1994). Between and within these areas, there are complicated regulatory mechanisms that may affect oestrous expression depending on internal and external circumstances. In pigs, however, hardly any information is available on the regulation of expression of oestrus at the level of the brain.

Time of Ovulation in Relation to Characteristics of Oestrous Expression

Insemination more than 24 h before ovulation or insemination after ovulation result in a reduced fertilization rate and consequently a reduction in farrowing rate and litter size (reviewed by Kemp and Soede, 1997). Therefore, an important question for optimal detection of oestrus and management of insemination is: which characteristics of oestrus best predict the time of ovulation? In this section, current knowledge regarding this question is evaluated, taking into account both physical changes and behavioural parameters.

Vaginal mucus conductivity. During pro-oestrus and oestrus, the vaginal mucus changes in amount, consistency and conductivity. Several investigations have taken place in which changes in conductivity of the vaginal mucus have been used to determine the optimal time of insemination (e.g. Harbison *et al.*, 1987; Ko *et al.*, 1989). However, the reproductive success of sows inseminated based on vaginal mucus conductivity were at best similar to when inseminations were based on onset of oestrus. A study by Stokhof *et al.* (1996) has related vaginal conductivity to the timing of ovulation. They showed that, although vaginal conductivity increased slightly during oestrus, vaginal conductivity varied considerably between sows and there was no relationship between vaginal conductivity and ovulation time as determined by ultrasonography. In their study, even onset of oestrus was a better predictor for the moment of ovulation than was vaginal conductivity.

Body temperature. In contrast to cattle and humans, in pigs there appears to be no relationship between ovulation time and body temperature (Henne, 1991; Soede *et al.*, 1997b). In eight sows, continuous measurements of vaginal temperature did not show any consistent rises or falls between 4 days before ovulation and 2 days after ovulation (see Fig. 1).

Standing response for the boar. Until the early 1990s, sows were thought to ovulate at a relatively fixed time, at 38 to 40 h after the onset of oestrus. Studies in which ovulation was assessed by ultrasonography have shown that ovulation takes place at very variable moments after the onset of (spontaneous) oestrus in both German, Dutch, Danish and Swedish experiments (see Table 1). Although the average ovulation time is not very variable between the experiments (between 35 h and 48 h), the ovulation time of individual sows varies between 10 h and 85 h after the onset of oestrus. Therefore, although in practice onset of oestrus is the parameter used to assess insemination time, it is not a good predictor for the moment of ovulation.

Standing response for man (in absence of a boar). In 1966, Willemse and Boender found that gilts showed a positive standing response in the absence of a boar during the middle two-thirds of (boar) oestrus, the so-called inseminator period, irrespective of the duration of oestrus. However, in 1996, Soede *et al.* found that the duration of oestrus in the absence of a boar was only partly related to the duration of oestrus in the presence of a boar in 144 sows; time without boar (h) = $4.8 + 0.53 \times$ time with boar ($R^2 = 0.25$). In both experiments, oestrus was detected in the home-pen of the animals. In Soede *et al.* (1996), ovulation time (determined by ultrasonography) relative to the onset of oestrus as determined in the absence of a boar was found to be very variable, from -2 h to 50 h (on average 26 ± 9 h). Furthermore, eight sows did not show a standing response in the absence of a boar and 22 sows

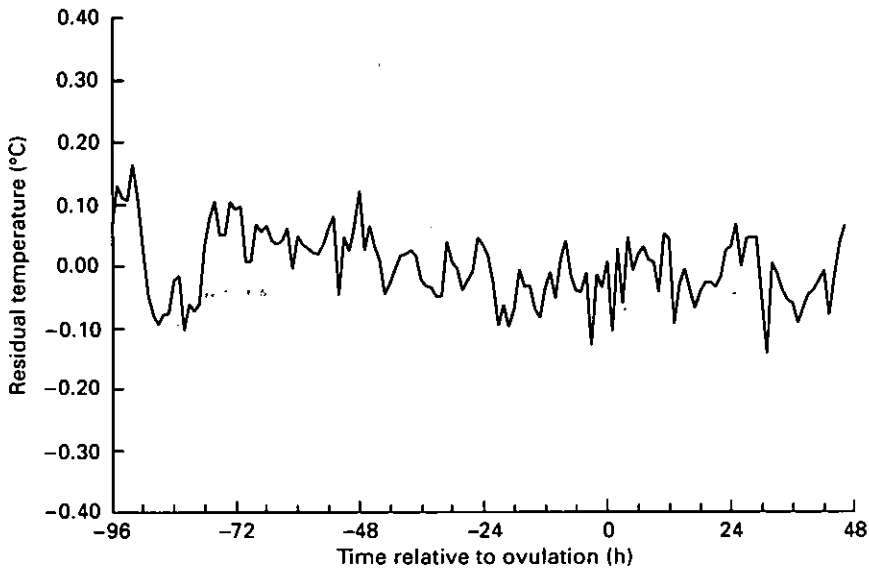


Fig. 1. Residual vaginal temperature (continuously recorded) of eight sows between 96 h before and 48 h after ovulation (checked every 2 h). Since the vaginal temperature is significantly affected by sow and time of day (h), the residual temperature (actual temperature minus estimated temperature) represents the deviation of the expected temperature for a specific sow and a specific time (h) of the day. (Reprinted from Soede *et al.*, 1997b with kind permission from Elsevier Science – NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.)

showed a standing response of only 8 or 16 h. Therefore, oestrus as determined in the absence of a boar cannot be used to predict ovulation time.

Duration of oestrus (standing response for the boar). In a number of recent German, Dutch, Swedish and Danish investigations using ultrasonography to assess ovulation in sows, the average timing of ovulation (percentage of oestrus) varies between only 64% and 72% (Table 2). In these experiments, the duration of oestrus explains as much as 50–60% of the variation in ovulation time in oestrus (see Table 2). The variation in ovulation time between individual sows still seems quite large (between 39% and 133%), but this is primarily caused by the sows with oestrus of a short duration (see also Fig. 2). Thus, the relative timing of ovulation during oestrus seems quite constant. Weitze *et al.* (1990a) showed that insemination with seminal plasma at the onset of oestrus may advance ovulation by up to 14 h. However, the effects on the relative timing of ovulation are limited (ovulation at 59% of oestrus), because the gilts concomitantly show a reduction in duration of oestrus of on average 8 h. Further studies have shown that the advancement of ovulation is caused by oestrogen and a peptide fraction in the seminal plasma that somehow result in a reduction in the interval from LH to ovulation (see review by Waberski, 1997).

From the above, it is clear that at the moment, the duration of oestrus as determined in the presence of a boar seems the best predictor for ovulation time during oestrus. Unfortunately, the duration of oestrus is highly variable and gives only a retrospective estimate of the time of ovulation. Therefore, research should be aimed at finding better prospective estimators for the timing of ovulation. The ultimate prediction would be to be able to monitor the rise in LH concentrations in a simple way, but for pigs this may still be impractical. Possibly, a combination of parameters (may be both physical and behavioural) can give a better estimate of ovulation time than only one parameter. However, at the moment, no such combination of parameters is known.

Table 1. Timing of ovulation (h after onset of oestrus) in sows and gilts, assessed by ultrasonography

Ovulation time		n	Treatment	Reference
Mean±SD	Range			
Gilts				
38±10	23–48	21	Saline-infusion	Weitze <i>et al.</i> , 1990b
45±5	39–48	21	None	Weitze <i>et al.</i> , 1990b
Sows				
39±12	20–64	15	None	Dalin <i>et al.</i> , 1995
ca 43	17–70	91	AI once	Nissen <i>et al.</i> , 1997
37±2	35–43	20	AI once	Mburu <i>et al.</i> , 1995
48±6	39–56	13	AI every day	Soede <i>et al.</i> , 1992
35±8	10–58	144	AI once	Soede <i>et al.</i> , 1995a
41±8	22–58	91	AI once or twice	Soede <i>et al.</i> , 1995b
45±13	15–85	427	AI	Weitze <i>et al.</i> , 1994

Factors Affecting the Duration of Oestrus

As already shown, a large variation is found in the duration of oestrus between sows and between experiments and farms. Sow factors and management factors that may influence the duration of oestrus are discussed below.

Consistency. The little information that is available shows that the consistency of oestrus duration is not high. In five gilts, the fourth oestrus differed from the second oestrus by –45 h, +3 h, +3 h, +9 h and +33 h (Andersson *et al.*, 1983). In 1996, Sterning found no correlation between the duration of oestrus at puberty and the duration of oestrus after weaning (both assessed twice a day) ($r = -0.03$, $n = 161$). Furthermore, in two consecutive parities, the percentage of sows with identical duration of oestrus (checked at 12 h intervals) was 29% (31 of 106 sows) and in 72% of the sows, the duration of oestrus did not differ by more than 12 h (either plus or minus) from the former parity (Weitze, 1996).

Genetic background. In practice, it is well known that differences occur in oestrous expression between the different breeds even though not much research has been done to substantiate this. Within breeds, Willemsse and Boender (1966) found that variation in the duration of oestrus within groups of sisters (gilts from 38 litters) was significantly smaller than the variation between groups of sisters, suggesting either a genetic or ontogenic influence on oestrous behaviour. In gilts selected for lean tissue growth rate, Rydhmer *et al.* (1994) found a genetic correlation of –0.49 between the duration of standing oestrus at puberty (1.8 ± 1.7 days) and growth rate to 90 kg (832 ± 97 g) in 600 gilts; the phenotypic correlation was not significant, nor were the genetic and phenotypic correlations with lean percentage. These data suggest that selection for production parameters may result in reduced oestrous expression. However, sows of sow lines (selected mainly for reproduction traits) and boar lines (selected mainly for production traits) were housed under identical conditions and were found to have a similar duration of oestrus (corrected for parity and interval from weaning to oestrus) of 56 h and 57 h, respectively (D. W. B. Steverink, unpublished). During the last 60 years, the performance of the sows (litter size) has changed markedly, while the duration of oestrus does not seem to have changed (in 1930, the duration of oestrus was reported to be on average 40–46 h (McKenzie and Miller (1930 in Gordon, 1997)); therefore, effects of selection for production on oestrous expression have been limited. Nevertheless, the results of Rydhmer *et al.* (1994) suggest that we may be approaching a limit.

Table 2. Timing of ovulation (% of oestrus) in sows, assessed by ultrasonography

Ovulation (% of oestrus)		n	Treatment	Reference
Mean \pm SD	Range			
71 \pm 14 ^a	ND	91	AI once	Nissen <i>et al.</i> , 1997
68 \pm 8	54–78	20	AI once	Mburu <i>et al.</i> , 1995
67 \pm 6	58–77	13	AI every day	Soede <i>et al.</i> , 1992
72 \pm 15 ^b	39–133	144	AI once	Soede <i>et al.</i> , 1995a
69 \pm 1 (\pm SEM)	ND	60	AI once	Soede <i>et al.</i> , 1995b
64 \pm 1 (\pm SEM)	ND	31	AI twice	Soede <i>et al.</i> , 1995b
68 \pm 10 ^c	ND	115	AI once	Steverink <i>et al.</i> , 1997
– ^d	ND	427	AI	Weitze <i>et al.</i> , 1994

^aTiming of ovulation (h after onset of oestrus) = 9.9 + 0.53 \times duration of oestrus (h) (R^2 = 0.49).

^bTiming of ovulation (h after onset of oestrus) = 11 + 0.48 \times duration of oestrus (h) (R^2 = 0.60).

^cTiming of ovulation (h after onset of oestrus) = 8.6 + 0.50 \times duration of oestrus (h) (R^2 = 0.59).

^dTiming of ovulation (h after onset of oestrus) = 1.79 + 0.7 \times duration of oestrus (h).

ND not determined.

Table 3. Sows classified according to interval from weaning to oestrus (classes of 24 h) and the interval from onset of oestrus to ovulation (classes of 8 h)

Onset of oestrus to ovulation (h)	Weaning to oestrus interval (days)				
	3	4	5	6	Mean
	n (%)	n (%)	n (%)	n (%)	n (%)
0–24	3 (8)	6 (5)	7 (16)	5 (45)	21 (10)
24–32	4 (13)	22 (19)	16 (36)	3 (27)	46 (22)
32–40	10 (27)	39 (34)	11 (25)	2 (18)	62 (31)
40–48	11 (30)	38 (33)	8 (18)	0 (0)	57 (27)
48–56	8 (22)	8 (7)	2 (5)	0 (0)	18 (9)
56–64	0 (0)	3 (2)	0 (0)	1 (9)	4 (2)
Total	36 (18)	116 (56)	44 (21)	11 (5)	208 (100)

From Kemp and Soede, 1996.

Gilts: cycle number. In six successive cycles in crossbred gilts, no influence of cycle number was found on the duration of standing oestrus, but the duration of pro-oestrus became significantly shorter in oestrus 3 to 6 in comparison with oestrus 1 and 2 (Andersson and Einarsson, 1980). Similarly, Andersson *et al.* (1983) studied second and fourth oestrus in crossbred gilts and did not find a difference in the duration of oestrus but did find a reduction in the duration of pro-oestrus; the authors suggested that the latter may have been caused by a change in sensitivity of vulval hormone receptors. In conclusion, in gilts, cycle number does not seem to influence the duration of oestrus.

Parity. The few data that are available are contradictory. Weitze *et al.* (1994) found that, only during summer time, sows of parity 2–4 had a significantly longer oestrus than sows of a higher parity (64 versus 60 h). In contrast, Steverink *et al.* (1997) found that the duration of oestrus (corrected for interval from weaning to oestrus) for sows of parity 1–2 was shorter than that for sows of higher parity (55 \pm 11 versus 62 \pm 12 h, P < 0.01).

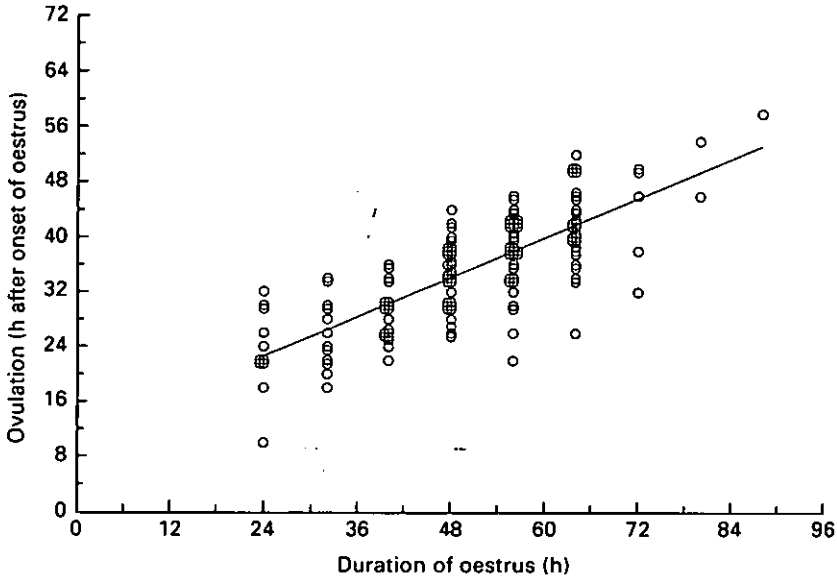


Fig. 2. Time of ovulation (OV) during oestrus in multiparous sows; $OV = 11 + 0.48 \times \text{Oestrus}$ ($R^2 = 0.60$, $P < 0.001$, $n = 144$) (Soede *et al.*, 1995b).

Season. There are very few experimental data on the effects of season on oestrus expression in sows. In the Netherlands, the combined data from several farms indicate that the duration of oestrus is on average longer in the summer months July, August and September (on average 53, 57 and 60 h) compared with the other months of the year (on average 46–50 h) (G. J. R. Groenland, unpublished). In Germany, Weitze *et al.* (1994) found a small increase in the duration of oestrus in summer compared with spring, whereas in Sweden, in primiparous sows, oestrus was of similar duration in the four seasons (Sterning, 1995). In ovariectomized sows, Cox *et al.* (1987) found that LH concentrations after an injection of oestradiol benzoate remained suppressed for longer in autumn and recovered more slowly (suggesting an increased sensitivity to oestrogen negative feedback). However, in autumn a reduction in oestrus expression was seen which was not related to post-injection concentrations of oestradiol (suggesting a decreased sensitivity to the oestrogen positive feedback). The authors suggested that environmental factors associated with season may alter responsiveness of the brain to oestradiol, consequently affecting sexual behaviour.

Weaning to oestrus interval. An increase in the weaning to oestrus interval (between approximately 3 and 6 days) is related to a decrease in the duration of oestrus (Rojkittikhun *et al.*, 1992; Weitze *et al.*, 1994; Kemp and Soede, 1996). This influence is quite large; an increase in weaning to oestrus interval of 3 days resulted in an average decrease in duration of oestrus of 24 h (Kemp and Soede, 1996). The decrease in duration of oestrus also resulted in a decrease in the interval from onset of oestrus to ovulation (Weitze *et al.*, 1994; Kemp and Soede, 1996). The percentage of sows that ovulate within 32 h from onset of oestrus increases from day 3 to day 6 after weaning from 21%, 24%, 50% to 72% (see Table 3). Rojkittikhun *et al.* (1992) found that the interval from the increase in oestradiol and the onset of oestrus was longer in sows with a prolonged weaning to oestrus interval, suggesting that these sows were less sensitive to oestrogen as a trigger for oestrous behaviour.

Chronic stress. It is generally known that stress conditions may affect several reproductive processes (reviewed by Varley and Stedman, 1994). For example, it is well established that rearing

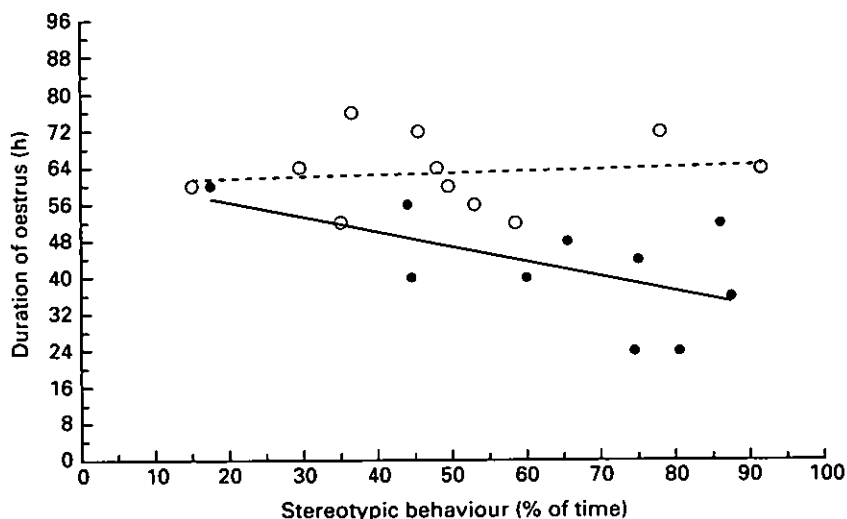


Fig. 3. Level of stereotypic behaviour during 1 h after afternoon feeding in sows between days 12 and 17 before oestrus (% of time) in relation to the duration of oestrus (h) in sows that had been tethered (●) or were housed loose (○) for 2 months after weaning. (Based on data from Soede *et al.*, 1997a.)

conditions (space allowance, group size, boar contact) influence the age of puberty in gilts (Hemsworth and Barnett, 1990). Rearing conditions may also influence oestrous expression; a reduction in space allowance (Hemsworth *et al.*, 1986) resulted in a reduction of the number of oestrous gilts that showed oestrus without the presence of a boar. Apparently, gilts under chronic stress conditions need more stimulation to express oestrus.

In addition, in sows, stressful conditions may influence oestrous expression. Pedersen *et al.* (1993) found that, in sows that were group-housed after weaning, the sows that were lowest in rank had the shortest duration of oestrus. However, no relation with concentrations of cortisol or oestrogen were found. In another study, in which sows were tethered by neck chains for 2 months after weaning, the duration of oestrus was significantly shorter than in sows that were individually housed in a pen of 6 m² during the same two months (42 ± 12 versus 63 ± 8 h; $P < 0.001$). In addition, in the tethered sows, the interval from onset of oestrus to ovulation, as detected by ultrasonography, was reduced (28 ± 6 versus 41 ± 6 h; $P < 0.001$). The changes in the duration of oestrus were not related to changes in oestradiol, LH or progesterone profiles of the sows, nor to cortisol concentrations (Soede *et al.*, 1997a). However, in the tethered sows, the duration of oestrus was negatively related to the level of stereotypic behaviour (an indication of chronic stress conditions) of these sows (see Fig. 3).

In general, oestrous behaviour seems to be sensitive to stressful conditions. The involvement of hormones of the hypothalamus–pituitary–adrenal (HPA) axis and endogenous opioid peptides (EOP) in oestrous behaviour have been shown in several experiments. Systemic injections with ACTH, cortisol and morphine (an EOP-agonist) reduced the duration of oestrus in pigs (Liptrap, 1970; Esbenschade *et al.*, 1983; Esbenschade and Huff, 1989). Esbenschade *et al.* (1983) concluded that '...it was not clear whether the competitive effects of cortisol and oestradiol on the expression of oestrus occurs at the level of the systemic circulation, at hypothalamic receptors or at higher brain centres'. This is still unclear. However, hormones of the HPA-axis have been found to affect LH release on all three concentrations. Therefore, oestrus expression may also be a resultant of interactions with hormones of the HPA-axis at the systemic, hypothalamic and higher brain level.

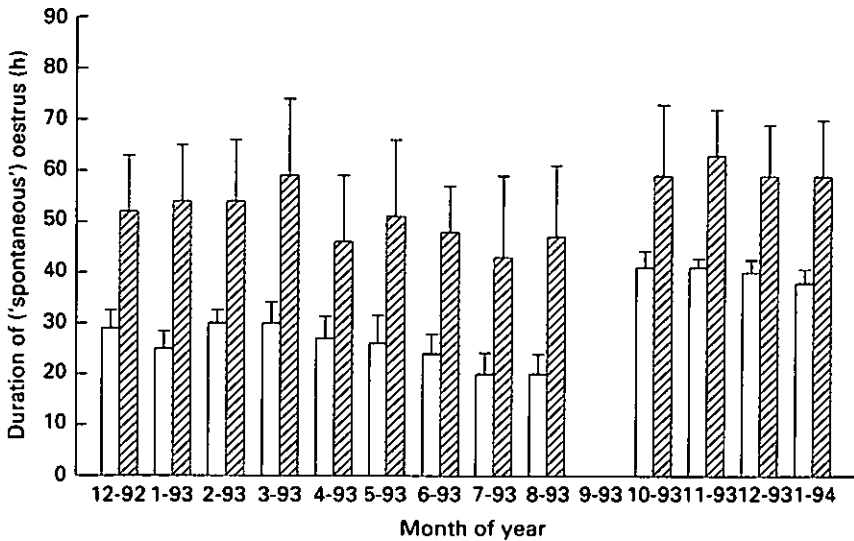


Fig. 4. The average duration of oestrus (□) and of the spontaneous standing response (▨; standing response in presence of the boar but before application of the back pressure test) per month in multiparous sows between 3 and 6 days after weaning in two experiments (Expt 1: December 1992 to August 1993, Expt 2: October 1993 to January 1994) that differed only in the boar that was used for detection of oestrus.

Boar stimulation. Many studies have been performed regarding effects of specific stimuli of the boar (visual, olfactory, auditory and tactile) on the attainment of puberty (reviewed by Hughes *et al.*, 1990), but only a few studies have incorporated the duration of oestrus.

An increase in the amount of boar stimulation during oestrus detection increases the expression of oestrus of sows. Jongman *et al.* (1996) even showed that stimulation by more than one boar (oestrus detection in a detection-mating-area where the sows are surrounded by several boars) increased the duration of oestrus by half a day. Between boars, variability in stimulation value (for a major part related to the olfactory stimuli), affect both proceptive and receptive behaviour (Hughes *et al.*, 1985) and, under multi-sire conditions, there was a certain partner preference (Tanida *et al.*, 1991). Boar variation was also found on our experimental farm, where we performed two 'identical' experiments with a different boar. The boar influence was quite large (Fig. 4). It is obvious that these experiments were not designed to study the influence of the boar and that other factors, such as season, may play a role here, but the results substantiate the importance of boar stimuli in oestrus expression of sows. However, it must be kept in mind that too long and too close contact with the boar has adverse effects on oestrus expression if gilts habituate to the boar stimuli (Hemsworth *et al.*, 1988). This has also been found in sows after weaning (Dyck, 1988).

Part of the influence of boar stimulation on the duration of oestrus may be explained by an involvement of prolactin, since Prunier *et al.* (1987) found that every introduction of a boar during oestrus causes a release of prolactin, and Van de Wiel *et al.* (1981) found that the duration of oestrus was positively associated with concentrations of prolactin.

Consequences of Variation In Expression of Oestrus for Insemination Strategy

As is clear from the outline above, many factors may be responsible for differences in expression of oestrus between farms and within farms, the most important factors (that have been identified as such): interval from weaning to oestrus, chronic stress and boar stimuli. Factors such as stress conditions and boar stimulation will be mostly responsible for differences in duration of oestrus

between farms. However, the interval from weaning to oestrus influences the variability in duration of oestrus within farms. Consequently, an optimal insemination strategy on farms (which implies a high farrowing rate and litter size with few inseminations or matings) varies between farms, but should also vary between sows on a farm depending on the interval from weaning to oestrus.

In several studies, an increase in the interval from weaning to oestrus has been found to cause a reduction in subsequent litter size and farrowing rate (see Vesseur, 1997). It has therefore been suggested that sows with a longer interval from weaning to oestrus are less fertile. However, in a study of Kemp and Soede (1996), fertilization results were high for sows that were inseminated between 0 h and 24 h before ovulation irrespective of the weaning to oestrus interval. This finding suggests that adverse effects of a longer weaning to oestrus interval might be a result of a suboptimal timing of insemination and not of poor fertility in these sows.

Concluding Remarks

Ovulation takes place at on average 70% of the way through oestrus in all experiments that have measured this parameter. At the moment, only one factor, insemination with seminal plasma at the onset of oestrus, is known to advance the relative timing of ovulation (to approximately 59%). Since the duration of oestrus is influenced by many factors, the duration of oestrus (and consequently the optimal time for insemination) is very variable within and between farms. However, the influence of some factors is quite fixed, resulting in, for example, a rather stable average duration of oestrus on a specific farm and a rather stable effect of the interval from weaning to oestrus on the duration of oestrus. Consequently, assessment of the average duration of oestrus of sows on a farm, taking into account the interval from weaning to oestrus, can be used for evaluation of the insemination strategy. For most factors that are known to influence the duration of oestrus, the mechanism behind the change in oestrus expression is unclear. Therefore, future studies are needed to determine causes of variability in oestrus expression between sows, including studies concerning the regulation of oestrous behaviour.

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