

Ovarian Activity and Oestrous Signs among Group-Housed, Lactating Sows: Influence of Behaviour, Environment and Production

F Hultén¹, A Wallenbeck² and L Rydhmer²

¹Department of Clinical Sciences, Division for Comparative Reproduction, Obstetrics and Udder Health; ²Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, Uppsala, Sweden

Contents

Animal welfare concerns require the development of housing systems that allow the animals to express their natural behaviour. One example of this is the group-housing system for lactating sows. The present study aimed at exploring ovarian activity in such a system. Thirty-eight sows farrowing individually outdoors during spring and summer, and indoors during autumn and winter, and group-housed in groups of four during weeks 3–7 of the lactation period, were monitored regarding reproductive functions, behaviour and production during their first to fourth lactation period. Average ovulation frequency during lactation was 47%. Only 50% of these ovulating cases were accompanied by a standing oestrus. Lactational ovulation frequency was higher in later parities ($p < 0.001$). Ovulation frequency was higher ($p < 0.05$) during winter (74%) and spring (69%), than during summer (10%) and autumn (23%). Occurrence of lactational ovulation was associated with some aspects of suckling behaviour and also with litter weight gain ($p < 0.05$). Forty-nine per cent of the lactational ovulations occurred during the seventh week of lactation. Timing of ovulation seemed positively ($p = 0.08$) associated with weight loss during lactation. Compared with the sows that were anoestrus during lactation, oestradiol-17 β values were higher ($p < 0.05$) only in the week before occurrence of lactational ovulation. Weaning-to-oestrous interval was prolonged ($p < 0.05$) among the sows that ovulated during lactation. The present study identifies several factors influencing ovarian activity among group-housed sows, thereby providing tools for the control of lactational ovulation in group-housing systems.

Introduction

Suckling stimulus has a strong inhibitory influence on ovarian activity and thus the ovaries are most often quiescent during the lactation period in individually housed sows (Baldwin and Stabenfeldt 1975; Kunavongkrit et al. 1982; Hultén et al. 1999). However, this inhibitory effect is constantly challenged by the stimulatory influence arising from, e.g. a generous feeding regime and thus a good body condition (Zak et al. 1997; Quesnel et al. 1998), seasonal shifts (Peltoniemi et al. 2000), boar contact (Mota et al. 2002) and factors that disturb the suckling process or the mother–infant relationship. The last-mentioned situation occurs if litter size is reduced or if suckling is interrupted (Newton et al. 1987a,b; Matte et al. 1992; Kuller et al. 2004). A similar stimulatory effect of group-housing on lactating sows is evident by the fact that signs of oestrus and ovulation occur in varying proportions of grouped sows (Petchey et al. 1978; Rowlinson and Bryant 1982; Hultén et al. 1995a). Some factors promoting lactational ovulation in group-housed sows have been revealed

(Rowlinson and Bryant 1982). However, the complex interaction between these factors, leading to the great variation in ovulation frequency seen between different groups of sows, has not yet been fully elucidated. Previous studies have either focused on oestrus signs or occurrence of ovulation, indicating that the relationship between ovarian activity, signs of oestrus and occurrence of ovulations is not known. A sow age-dependent reduction in mother–infant relationship has been suggested as cause for lactational ovulation in one type of group-housing system (Hultén et al. 1995a,b), but these indications need to be further tested in behavioural studies.

Welfare concerns promote the development of management systems better adapted to the natural behavioural repertoire of the animals. In this context, an extended lactation period is desired, but the effects on ovarian activity, productivity and post-weaning performance have not yet been explored in such a system. In Europe, group-housing of lactating sows is practised in commercial farms and most often involves a period of separation of the sow and the newborn litter, either indoors in individual pens (Hultén et al. 1995b), or by temporary thresholds in outdoor settings (Larsen and Jørgensen 2002).

The aim of this long-term study was to explore the influence of management, performance and behaviour on ovarian activity, occurrence of oestrous signs and ovulation during lactation, in a system where sows farrow individually and are kept in small groups from 2 weeks after farrowing, during a 7-week-long lactation period.

Material and Methods

Forty crossbred Swedish Yorkshire, Swedish Landrace gilts, divided into two equally large batches (1 and 2), were monitored during their first four parities. To keep the farrowing periods as short as possible within a batch, approximately five sows showing a delay in post-weaning oestrus were shifted between the two batches during the study period.

Housing and management

During each mating and gestation period, the sows were group-housed indoors on deep-litter straw bedding. Five days (5.2 ± 1.6 days) before the expected farrowing, they were moved to the farrowing unit. At the first and third parity (spring/summer period), the sows farrowed

Table 1. The farrowing period, the sow location during lactation and the lactational oestrus frequency within sow batch and parity

Parity	Batch					
	1			2		
	Period	Location	Oestrus	Period	Location	Oestrus
1	6 April to 18 May	Out	47% (19)	28 July to 17 September	Out	0% (18)
2	25 September to 1 November	In	21% (14)	17 January to 2 March	In	68% (19)
3	18 March to 10 April	Out	58% (12)	18 July to 18 August	Out	37% (16)
4	21 September to 25 October	In	67% (12)	5 January to 22 February	In	93% (14)

Out, outdoors; In, indoors.

Figures within parentheses denote the number of animals per group.

individually in a straw-provided hut (3.9 m², height 1 m, 'Salling hytten', Kjeldgårdsvej 18, Selde, Roslev) placed in an outdoor paddock. Two weeks after farrowing, they were moved to a 1.5-ha paddock shared by four sows, which was provided with one family hut (four walls) 13.0 m² and one rain-shed (roof) 11.0 m². At the second and fourth parity (autumn/winter period), the sows farrowed indoors in individual 7.6-m² large pens provided with straw bedding and rails along the walls. Two weeks after farrowing, they were moved to a ≥52-m² large pen shared by four sows, located in an uninsulated building with straw bedding. The average difference in the farrowing date within each group of four sows was 4.1 (± 3.2) days. The sows did not have contact with any boar during the lactation period. The housing conditions and farrowing period for each batch and parity are presented in Table 1.

After a 7-week-long lactation period, each group of four sows was moved to the breeding unit. They were checked for standing oestrus twice daily in front of a boar, inseminated twice with mixed semen and pregnancy check was performed 4 weeks later. At that time, each group of four sows was mixed with the other sows within the same batch. The same mating procedure was used for the gilts. Sow feed was made of oats (40%), wheat (16%), rapeseed cake (15%), wheat bran (10%), triticale (6.9%), peas (5.9%), potato protein (2.5%), vitamins and minerals.

During gestation, the sows were provided 2.5 kg of dry feed twice daily containing 12.2 MJ/kg and 12.26% digestible protein. After farrowing, the same feed was used and the ration was gradually increased to reach *ad libitum* levels at time of grouping. At weaning, the feed ration was decreased to 4 kg/day and after mating it was adjusted to gestation level. The piglets had access to sow feed from 2 weeks after farrowing and castration of male piglets was performed on day 4 after farrowing. Teeth were not cut or grinded and iron was only provided indoors. Water was provided *ad libitum* to the sows and piglets.

Detection of sow and piglet performance

Sow weight and backfat thickness were determined 5 days before the expected farrowing, 14 days after farrowing and on the day of weaning. Litter size and individual piglet weight were determined on days 4 and 14 of lactation and on the day of weaning. In addition, litter size and stillbirths were recorded at first time the sow was attended to after farrowing. Reasons for

slaughter were recorded for those sows removed from the study.

Oestrus detection

During the group-housing phase of the lactation period (weeks 3–7 of lactation), trained technicians performed oestrus detection once daily. Standing oestrus was determined by the back-pressure test and the degree of swelling and/or reddening of the vulva was recorded according to Eliasson (1989). After weaning, the same oestrous detection procedure was performed twice daily in front of a boar. A sow not showing signs of oestrus within 30 days after weaning was considered anoestrus.

Blood sampling and hormonal analyses

From day 21 after farrowing until the day of weaning, weekly blood samples were collected in heparinized tubes through jugular vein puncture for progesterone and oestradiol-17 β analysis. One final sample was collected for progesterone analysis 10 days after weaning if oestrus symptoms had not occurred at that time. The tubes were immediately centrifuged (1500 \times g, 10 min) and the plasma collected was frozen and stored at –20°C.

The progesterone concentration in blood plasma was determined using enzyme immunoassay (Amerlite; Kodak Clinical Diagnostics Ltd, Amersham, UK). The kit was used according to the manufacturer's instructions with certain modifications (Razdan et al. 2001) and validation for the pig species was previously performed (Razdan et al. 2001). The blood plasma levels of oestradiol-17 β were determined by radioimmunoassay (double antibody oestradiol, Diagnostic Products Corporation, Los Angeles, CA, USA) as previously described and validated for the pig species (Mwanza et al. 2000).

Behavioural observations

The fourth and the sixth week of the lactation period, the number of nursings, the time spent for each nursing occasion and the number of cross sucklers per nursing was recorded by direct observations of each sow, by the same person, during 6 h, between 9 AM and 3 PM. Nursing was considered to occur when more than 50% of the sows own piglets suckled the udder for more than 60 s.

Udder examination

At the day of weaning, the udder was examined regarding the distension of each udder part, indicating the degree of milk production (Hultén et al. 2003). A pre-weaning cease of milk production was recorded if all mammary glands showed a complete atrophy on the day of weaning.

Statistical analyses

To distinguish between follicular phase and luteal phase levels of plasma progesterone, a threshold level previously established, using the same assay system on sows showing normal oestrus cycles, was used (Hultén et al. 1995a,b). Thus, by use of this threshold (2.0 nmol/l), occurrence of ovulation could be determined.

All statistical analyses were performed using the Statistical Analysis System, version 9.1 (SAS Institute Inc., Cary, NC, USA). Repeated within-sow measurements were accounted for by including 'sow' as random term [the GLIMMIX procedure] or by using the repeated option (the MIXED procedure). To identify those factors influencing the occurrence of lactational ovulation (yes or no) the GLIMMIX procedure was used. Primary models were developed by separately including all variables of interest, and the fixed effect of farrowing season (spring – 1 March to 31 May; summer – 1 June to 31 August; autumn – 1 September to 30 November; and winter 1 December to 28 February) and the regression on parity number. Factors influencing ($p < 0.2$) the dependent variable and not showing collinearity ($r < 0.6$) were included in the final regression model, and significant effects ($p < 0.05$) were identified by backward stepwise elimination. The relationship between parity number and suckling behaviour was analysed with the MIXED procedure including the fixed effect of sow batch within parity number.

To explore the factors influencing the timing of lactational ovulations, the MIXED procedure was used, and statistical models for this purpose were constructed according to the procedure mentioned above.

Oestradiol values were log-transformed before analysis to improve distribution pattern and the MIXED model for oestradiol analysis included the fixed effects of parity number (4), lactation week (3–7) and occurrence of lactational oestrus.

To explore the relationship between oestradiol pattern during the group-housing period and occurrence of lactational oestrus, a model was constructed including only those sows showing lactational oestrus at the last week of lactation, and those not showing lactational oestrus at all. This model included the fixed effect of parity number, occurrence of lactational oestrus and week in lactation.

Weaning-to-oestrus interval was analysed, using log-transformed values, in a MIXED model including the fixed effect of season, parity number, occurrence of lactational ovulation, and the regression on litter size, sow weight and backfat thickness.

Results

Two gilts were excluded because of farrowing failure, and hence records were collected from 38 primiparous sows. Thirty-five of these sows farrowed a second time, 31 a third time and 26 a fourth time. Eight of the 14 excluded sows (57%) were slaughtered because of reproductive failure, including anoestrus (three), repeat breeding (three) and empty at farrowing (two). Five of these 14 sows had ovulated during the seventh week in their last lactation period, two were anoestrus during lactation and one sow had incomplete blood sampling records. Two sows (14%) were slaughtered because of locomotor disorders and four sows (28%) because of udder disorders including two cases of mastitis and two cases of traumatic injuries. Data on lactational ovulation are presented for the sows where a complete blood sampling record was obtained (37 of the first-parity sows, 33 of the second-parity sows, 28 of the third-parity sow and 26 of the fourth-parity sows).

Total litter size, number of stillborn piglets and number of weaned piglets per litter were on average 12.8 (± 3.7), 2.0 (± 1.9) and 9.5 (± 2.7), respectively. Sow weight was 233 (± 38) kg on day 14 of lactation and 231 (± 39) kg on the day of weaning. Average piglet weight was 2.2 (± 0.4) kg on day 4 of lactation and 18.5 (± 3.6) kg on the day of weaning.

Ovulation during lactation

The average progesterone concentration of the first sample collected during the luteal phase was 19.7 nmol/l (range 2.6–89.5). In 87% of these samples, progesterone levels were > 10 nmol/l, in 9% they were between 5 and 10 nmol/l, and in 4% they were lower but constituted a 2–10-fold increase when compared with the previous sample collected from the same sow.

Of 124 lactation periods totally recorded, one lactational ovulation was recorded in 52 of these periods, whereas two ovulations during the same lactation period was noted in eight periods. The total average lactational ovulation frequency was 47%. Parity number influenced occurrence of ovulation ($p < 0.001$), and ovulation frequency was 17%, 50%, 44% and 83% for the first, second, third and fourth parity sows, respectively. Ovulation frequency during winter, spring, summer and autumn was 76%^a, 57%^{ab}, 14%^c and 29%^{bc} respectively (no superscript in common indicates a statistical difference, $p < 0.05$).

Occurrence of lactational ovulation was also associated with a lower average duration of each suckling occasion recorded in week 4 ($p = 0.03$), a decrease in the number of piglets per suckling, between week 4 and 6 ($p = 0.03$), a higher total litter weight on day 14 ($p = 0.04$) of lactation and a higher average piglet weight gain between day 14 and weaning ($p = 0.04$).

The average suckling duration in weeks 4 and 6 seemed lower ($p < 0.07$) among three parity sows compared with the first parity sows, but no other age-related differences in suckling behaviour were detected. The proportion of sows that ovulated in each batch of

Table 2. The distribution of ovulation occurrences during group-housing, weeks 3–7 of lactation

	Week of lactation					Total
	3	4	5	6	7	
No. of ovulations	7	9	4	15	33	68
Percentage	10	13	6	22	49	100

sows is presented in Table 1. The distribution of ovulation occurrences during the group-housing period is presented in Table 2.

The week that preceded, a luteal-phase progesterone value was considered the week of ovulation. Almost half of the sows showing a lactational ovulation, ovulated during the seventh week of lactation. Weight loss during the group-housing period was similar ($p > 0.05$) among sows showing lactational ovulation (-0.2 ± 14.6 kg) and among those being anoestrus (-3.6 ± 13.5 kg). However, among the sows that showed lactational ovulation, high sow weight loss from grouping to weaning seemed ($p = 0.08$) associated with lactational ovulations occurring late during the lactation period, whereas litter size, litter weight change and suckling behaviour had no influence on timing of ovulation ($p > 0.05$).

Oestradiol-17 β patterns

Oestradiol-17 β levels were positively associated with lactation week, and a significant difference was noted between the primiparous sows and the older sows (Table 3). Among the sows that showed lactational ovulation, the average oestradiol level during the lactation period was higher (12.0 ± 1.0 pmol/l) compared with those being anoestrus (10.0 ± 1.0 pmol/l) ($p < 0.001$).

Compared with the sows that did not ovulate during lactation, oestradiol levels for those sows that ovulated the seventh week of lactation tended to be higher at week 5, and was significantly higher at week 6 of lactation, whereas no differences were noted before and after these occasions (Table 4).

Table 3. Average oestradiol-17 β levels during group housing weeks 3–7 of lactation, and in different parities [lsmeans (SEM)]

	Oestradiol-17 β (pmol/l)
Week in lactation	
3	9.5 (1.1) ^a
4	9.5 (1.0) ^a
5	10.8 (1.0) ^b
6	12.3 (1.1) ^c
7 (weaning)	13.2 (1.1) ^c
Parity number	
1	9.4 (1.0) ^a
2	11.3 (1.0) ^b
3	11.8 (1.0) ^b
4	11.5 (1.0) ^b

Values in each part table (Week in lactation and Parity number) with different superscript alphabet differ significantly ($p < 0.05$).

Table 4. Oestradiol-17 β levels (pmol/l) during group housing weeks 3–7 of lactation for the sows that showed lactational ovulation week 7 of lactation, and for those that were anoestrus during lactation, [lsmeans (SEM)]

Week of lactation	Ovulating week 7	Anoestrus during lactation	Between-group difference (p-value)
3	8.5 (1.0)	8.4 (1.0)	0.86
4	9.0 (1.1)	8.9 (1.0)	0.94
5	10.2 (1.0)	9.2 (1.0)	0.11
6	17.9 (1.1)	10.6 (1.1)	< 0.001
7 (weaning)	12.6 (1.1)	12.2 (1.1)	0.87

Oestrus signs during lactation

In only 50% of the sows that ovulated during lactation, standing oestrus was recorded, whereas in 24% of these ovulating sows only vulval signs were noted. The remaining 26% of the sows that ovulated did not show any oestrous signs at all. In 11% of all lactations, the sows showed vulval signs but no standing oestrus and no ovulation.

Weaning to oestrus interval and udder examination

None of the sows showed a total pre-weaning mammary gland atrophy, which would have indicated a complete cessation of milk production. Overall average weaning to oestrus interval (WOI) was 8.7 (± 8.5) days. WOI varied more (Fig. 1) and was also longer ($p < 0.001$) among sows showing lactational ovulation (12.6 ± 10.4) compared with those which were anoestrus (5.0 ± 3.8). WOI was shorter among older sows ($p < 0.001$) and tended ($p = 0.06$) to be longer among those losing more weight from grouping to weaning, whereas no association ($p > 0.05$) with backfat loss and litter size was noted.

Discussion

The results of the present study show that lactational ovulation is a common event in a group-housing system using a long lactation period although there is no boar contact and, furthermore, that the ovulations occur mainly during the end of the lactation period. In a similar indoor group-housing system, applying a 5-week-long lactation period, average lactation frequency was somewhat lower (28%), which could be explained by the distribution pattern for ovulation occurrences revealed in the present study. According to our results, after the fifth lactation week 33% of the sows had ovulated. Suckling intensity decreases continuously during the lactation period (Jensen and Recén 1989; Hultén et al. 2002) and the inhibition of the pituitary–gonad axis is thus gradually released (Quesnel and Prunier 1995). In previous studies where sows were kept in groups of four to six sows without boar contact during a 6- to 7-week-long lactation period, lactational oestrus frequencies between 0% and 30% were reported (Petchey et al. 1978; Rowlinson and Bryant 1982). The high ovulation frequency noted in our study could partly be due to the fact that occurrence of ovulation and not only oestrus signs were recorded here. As a result of social interactions, sows kept in groups may

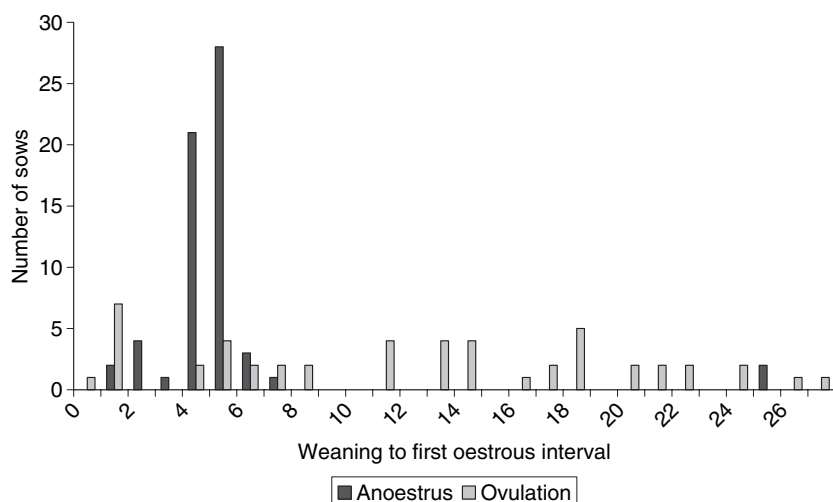


Fig. 1. The distribution of weaning to first oestrus interval among sows that ovulated during the group-housing period (weeks 3–7 of lactation), and among those that were anoestrus during the same period.

express oestrus signs less clearly. Furthermore, different strategies for boar contact during the lactation period were applied in previous studies, which also influence the occurrence of ovulation and oestrus signs (Kemp et al. 2005). To our knowledge, this is the first study exploring both occurrence of oestrus signs and ovulation, and a discrepancy between these measures was evident.

High frequency of lactational oestrus has been associated with boar contact, a high feeding level, maintained or increased body weight and backfat, and small litter size (Petchey and Jolly 1979; Rowlinson and Bryant 1982; Bryant et al. 1983), but the results from the present study and those of Hultén et al. (1995a) show that sow condition and litter size are of less importance (Hultén et al. 1995a). By contrast, our results demonstrate, in conclusion to a previous study on a similar group system (Hultén et al. 1995a) as well as studies on disrupted suckling (Smith 1961; Newton et al. 1987a,b), that parity has a strong influence on lactational ovulation. Newton et al. (1987b) revealed, in accordance to our results, higher oestradiol levels among multiparous sows, compared with primiparous sows. In addition, Palmer et al. (1965) and Kunavongkrit et al. (1982) showed that during lactation, follicle size is larger in second-parity sows compared with primiparous sows. These observations indicate a less inhibited pituitary–gonad axis among older sows, possibly caused by a less intensive mother–infant interaction among these sows.

In a group-housing system similar to the present, suckling seemed less intense among older sows compared with the younger ones (Hultén et al. 1995b). In the present study, an association between suckling behaviour and occurrence of lactational ovulation was evident by the fact that ovulation was more common in sows showing a low-average suckling duration week 4 of lactation and a more pronounced decrease in the number of piglets per suckling, between weeks 4 and 6. In addition, sows with a heavy litter day 14 of lactation and with piglets growing well from day 14 to weaning were more prone to show lactational ovulation. These findings may constitute indicators of a sow being well adopted to this housing system, in the sense that it feed its litter effectively, and possibly its litter started to

consume solids quite early, and thereby it is soon prepared for bringing up yet another litter. No clear relationship between suckling behavioural parameters and sow age was noted, thus the biological explanation for the influence of sow age is still unclear.

In conventional housing systems, oestradiol concentrations are generally low and do not show any time-related variation through lactation (Quesnel and Prunier 1995). However, manipulation of the suckling process through interrupted suckling or fractionated weaning leads to an immediate rise in oestradiol levels, or a more swift increase after final weaning (Rojkittikhun et al. 1991; Matte et al. 1992; Mota et al. 2002). In the present study, the continuous rise in oestradiol-17 β levels during the group-housing period and the higher levels noted among older sows, may reflect an age- and time-dependent influence on suckling intensity, although the causal relationship between these entities is unclear. The fact that in sows showing lactational ovulation, oestradiol levels were significantly higher only the week before ovulation but not before and after, suggests that the process leading to the occurrence of oestrus is sudden and not the result of a long-term stimulatory effect on the ovaries.

Previous results regarding the effect of group-housing on milk production, estimated by piglet growth rate, are not conclusive (Algers 1991; Schwarz and Klement 1992; Arey and Sancha 1996; Hultén et al. 1997; Rantzer et al. 1997). Although ovulation frequency was high in the present study, milk production did not cease completely during lactation in any sow. This is in contrast to a previous study where pre-weaning mammary gland atrophy occurred in 16% of the sows which showed lactational oestrus, although ovulation frequency was lower than reported in the present study (Hultén et al. 1995a). As both the inhibition of ovarian activity and the lactogenic hormone release are dependent on the suckling process (Algers 1991; Matte et al. 1992), a concerted effect on these two functions would be expected. The present results suggest that a certain level of suckling stimulation is sufficient to maintain lactation but not to inhibit the pituitary–ovarian axis, or these two entities may be controlled by different components of the suckling process.

The swine is considered to be a short-day breeder. Impaired reproductive functions are noted during the summer/autumn period in commercial units, and the wild boar breed during winter (Mauget 1982; Love et al. 1995; Peltoniemi et al. 2000). The fact that lactational ovulation frequency seemed highest during the winter period and lowest during summer could be due to a seasonal influence on the reproductive functions, and similar effects have previously been noted in group-housing systems (Petchey and Jolly 1979; Hultén et al. 1998a,b). However, as in the present study the group-housing system differed between autumn/winter and spring/summer, other factors such as light exposure and social interactions could also contribute to the differences noted between seasons.

In accordance with previous studies (Hultén et al. 1995a), lactational oestrus was associated to a delay in the weaning to first oestrus interval. Hence, the mating period is prolonged which is negative if batch-wise farrowing routines are applied and, moreover, it counteracts the efforts to maintain optimal mating routines. This is reflected by a higher repeat breeder frequency and a higher culling rate due to anoestrus in group-housing systems (Hultén et al. 1998a; Larsen and Kongsted 2001).

The present study shows that group-housing without boar during a 7-week-long lactation period is associated with a high incidence of lactational ovulations, but corresponding visible signs of oestrus is of a much lower magnitude. The ovulations are preceded by a short-lasting rise in blood oestradiol levels, and the ovulations occur mainly during the end of the lactation period. In addition, occurrence of ovulations is associated to parity number, season, suckling behaviour and litter weight gain. Lactational ovulation prolongs the mating period and thus counteracts efforts to maintain batch-wise farrowing routines.

References

- Algers B, 1991: Group-housing of Farrowing Sows – Health Aspects on a New System. VII Int Cong on Anim Hyg, Vol III, Leipzig, Germany, pp. 851–857.
- Arey DS, Sancha ES, 1996: Behaviour and productivity of sows and piglets in a family system and in farrowing crates. *Appl Anim Behav Sci* **50**, 135–145.
- Baldwin DM, Stabenfeldt G, 1975: Endocrine changes in the pig during late pregnancy, parturition and lactation. *Biol Reprod* **12**, 508–515.
- Bryant MJ, Palmer G, Petherick DJ, Rowlinson P, 1983: Lactational oestrus in the sow. 4. Variation in the incidence and timing of lactational oestrus in groups of sows. *Anim Prod* **36**, 453–460.
- Eliasson L, 1989: A study on puberty and oestrus in gilts. *J Vet Med A* **36**, 46–54.
- Hultén F, Dalin A-M, Lundeheim N, Einarsson S, 1995a: Ovulation frequency among sows group-housed during late lactation. *Anim Reprod Sci* **39**, 223–233.
- Hultén F, Lundeheim N, Dalin A-M, Einarsson S, 1995b: A field study on group housing of lactating sows with special reference to sow health at weaning. *Acta Vet Scand* **36**, 201–212.
- Hultén F, Lundeheim N, Dalin A-M, Einarsson S, 1997: Pre- and post-weaning piglet performance, sow food intake and change in backfat thickness in a group-housing system for lactating sows. *Acta Vet Scand* **38**, 119–133.
- Hultén F, Lundeheim N, Dalin A-M, Einarsson S, 1998a: Reproductive performance among sow group-housed during late lactation. *Acta Vet Scand* **39**, 237–250.
- Hultén F, Zhang BR, Forsberg M, Dalin A-M, 1998b: Applying a progesterone assay to faecal samples collected from sows during the oestrous cycle. *Reprod Dom Anim* **30**, 101–105.
- Hultén F, Zhang BR, Forsberg M, Dalin A-M, 1999: Determining ovulation frequency in individually penned lactating sows using a faecal 'progesterone' assay. *Reprod Dom Anim* **34**, 71–76.
- Hultén F, Valros A, Rundgren M, Einarsson S, 2002: Reproductive endocrinology and postweaning performance in the multiparous sow. Part 2. Influence of nursing behaviour. *Theriogenology* **58**, 1519–1530.
- Hultén F, Persson A, Eliasson-Selling L, Heldmer E, Lindberg M, Sjögren U, Kugelberg C, Ehlorsson C-J, 2003: Clinical characteristics, prevalence, influence on sow performance and assessment of sow-related risk factors for granulomatous mastitis in sows. *Am J Vet Res* **64**, 463–469.
- Jensen P, Recén B, 1989: When to wean – observation from free-ranging domestic pigs. *Appl Anim Behav Sci* **23**, 49–60.
- Kemp B, Soede NM, Langendijk P, 2005: Effects of boar contact and housing condition on estrus expression in sows. *Theriogenology* **63**, 643–656.
- Kuller WI, Soede NM, van Beers-Schreurs HMG, Langendijk P, Taverne MAM, Verheijden JHM, Kemp B, 2004: Intermittent suckling: effects on piglet and sow performance before and after weaning. *J Anim Sci* **82**, 405–413.
- Kunavongkrit A, Einarsson S, Settergren I, 1982: Follicular development in primiparous lactating sows. *Anim Reprod Sci* **5**, 47–56.
- Larsen VA, Jørgensen E, 2002: Reproductive performance of outdoor sow herds. *Livest Prod Sci* **78**, 233–243.
- Larsen VA, Kongsted AG, 2001: Frilandssohold. Produktion, foderforbrug, udsætningsårsager og graesdaekke. (Free Range Sows: Production, Feed Consumption, Causes of Culling and Level of Grass Cover). DJF rapport nr 30, Denmark.
- Love RJ, Klupiec C, Thornton EJ, Evans G, 1995: An interaction between feeding rate and season affects fertility of sows. *Anim Reprod Sci* **39**, 275–284.
- Matte JJ, Pomar C, Close WH, 1992: The effect of interrupted suckling and split-weaning on reproductive performance of sows: a review. *Livest Prod Sci* **30**, 195–212.
- Mauget R, 1982: Seasonality of reproduction in the wild boar. In: Cole DJA & Foxcroft GR (eds), *Control of Pig Reproduction*. Butterworth Scientific, London, pp. 509–526.
- Mota D, Alonso-Spilsbury M, Mayagoitia L, Trujillo ME, Valencia J, Ramírez-Necoechea R, 2002: Lactational estrus induction in the Mexican hairless sow. *Anim Reprod Sci* **72**, 115–124.
- Mwanza AM, Madej A, Kindahl H, Lundeheim N, Einarsson S, 2000: Plasma levels of cortisol, progesterone, oestradiol-17 β and prostaglandin F_{2 α} metabolite after ACTH (Synacthen® depot) administration in ovariectomized gilts. *J Vet Med A* **47**, 193–200.
- Newton EA, Stevenson J, Davies LD, 1987a: Influence of duration of litter separation and boar exposure on estrus expression of sows during and after lactation. *J Anim Sci* **65**, 1500–1506.
- Newton EA, Stevenson JS, Minton JE, Davis DL, 1987b: Endocrine changes before and after weaning in response to boar exposure and altered suckling in sows. *J Reprod Fert* **81**, 599–609.

- Palmer WH, Teague HS, Venzke WG, 1965: Macroscopic observations on the reproductive tract of the sow during lactation and early postweaning. *J Anim Sci* **24**, 541–545.
- Peltoniemi OAT, Tast A, Love RJ, 2000: Factors effecting reproduction in the pig: seasonal effects and restricted feeding of the pregnant gilt and sow. *Anim Reprod Sci* **60–61**, 173–184.
- Petchey AM, Jolly GM, 1979: Sow service in lactation: an analysis of data from one herd. *Anim Prod* **29**, 183–191.
- Petchey AM, Dodsworth TL, English PR, 1978: The performance of sows and litters penned individually or grouped in late lactation. *Anim Prod* **27**, 215–221.
- Quesnel H, Prunier A, 1995: Endocrine bases of lactational anoestrus in the sow. *Reprod Nutr Dev* **35**, 395–414.
- Quesnel H, Pasquier A, Mounier AM, Prunier A, 1998: Influence of feed restriction during lactation on gonadotropic hormones and ovarian development in primiparous sows. *J Anim Sci* **76**, 856–863.
- Rantzer D, Svendsen J, Weström B, 1997: Weaning of pigs in group housing and in conventional housing systems for lactating sows. *Swedish J Agric Res* **27**, 23–31.
- Razdan P, Mwanza AM, Kindahl H, Hultén F, Einarsson S, 2001: Impact of postovulatory food deprivation on the ova transport, hormonal profiles and metabolic changes in sows. *Acta Vet Scand* **42**, 45–55.
- Rojkittikhun T, Rojanasthien S, Einarsson S, Madej A, Lundeheim S, 1991: Effect of fractionated weaning on hormonal patterns and weaning to oestrus interval in primiparous sows. *Acta Vet Scand* **32**, 35–45.
- Rowlinson P, Bryant MJ, 1982: Lactational oestrus in sows. 2. The influence of group-housing, boar presence and feeding level upon the occurrence of oestrus in lactating sows. *Anim Prod* **34**, 283–290.
- Schwarz H-P, Klement G, 1992: Neueste Ergebnisse zur Gruppenhaltung von Sauen. *SUS* **40** (Heft 5), 140–142.
- Smith DM, 1961: The effect of daily separation of sows from their litters upon milk yield, creep intake and energetic efficiency. *N Z J Agric Res* **4**, 232–245.
- Zak LJ, Xu X, Hardin RT, Foxcroft GR, 1997: Impact of different patterns of feed intake during lactation in the primiparous sow on follicular development and oocyte maturation. *J Reprod Fert* **110**, 99–106.

Submitted: 6.12.2005

Author's address (for correspondence): Fredrik Hultén, Department of Clinical Sciences, Unit for Comparative Reproduction, Obstetrics and Udder Health, Swedish University of Agricultural Sciences, PO Box 7054, S-750 07 Uppsala, Sweden. E-mail: fredrik.hulten@kv.slu.se