Plasma concentrations of LH, prolactin, oestradiol-17 β and progesterone in sows weaned after lactation for 10 or 35 days

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Summary. Piglets were weaned from multiparous sows at 10 days (Group E; N = 7) or 35 days (Group C; N = 8) of lactation. Blood samples were collected at 8 h intervals from the day before weaning (Day – 1) until and including the day of first mating, then once daily until 10 days *post coitum*. Additionally, 5 sows in each group were sampled at 30 min intervals for 12 h on Days – 1, 0 and 1, then at 30 min intervals for 6 h daily until mating, finally at 30 min intervals for 2 h daily until 5 days *post coitum*. Group E sows had relatively longer weaning to remating intervals (8.3 ± 0.8 compared with 5.0 ± 0.7 days; $P < 0.01$) and tended, but not significantly, to produce smaller subsequent litters (10.2 ± 1.9 compared with 12.0 ± 0.6). Sows in group E had lower lactational and post-weaning plasma LH levels ($P < 0.001$). They also had greatly attenuated preovulatory LH rises and the area under the peak was reduced ($P < 0.01$ and $P < 0.001$, respectively). Prewaning plasma prolactin levels were higher at 9 days of lactation than at 34 days and levels in both groups dropped precipitously subsequent to piglet removal. Although peak levels of prolactin at oestrus did not differ between treatments, they tended to occur before the LH peak in sows of Group C and after the LH peak in Group E. No treatment differences were detected in plasma levels of oestradiol-17 β or progesterone. These results suggest that the poorer reproductive performance of sows after a very short lactation is due, at least in part, to a reduced release of LH at the first post-weaning oestrus.

Introduction

There is evidence that weaning piglets from the sow before the 21st day of lactation is characterized by a prolonged weaning to remating interval, reduced conception rates and increased embryo mortality (van der Heyde, 1972; Cole, Varley & Hughes, 1975; Varley & Cole, 1976). Varley, Atkinson & Ross (1981) found that, after short lactations, plasma oestrogen levels of sows were elevated in the immediate post-mating period, and offered this as a possible explanation for the reduced reproductive performance. However, information on the endocrine status during the weaning to remating interval of sows after very short lactations is sparse.

It has been demonstrated that pituitary LH responsiveness to GnRH or oestrogen is low immediately after parturition (Elsaesser & Parvizi, 1980; Bevers, Willemse, Kruip & van de Wiel, 1981) and also during lactation, although there appears to be a progressive escape from inhibition as lactation proceeds (Elsaesser & Parvizi, 1980; Stevenson & Britt, 1980; Bevers *et al.*, 1981). After lactations of 3–5 weeks small transient increases in plasma progesterone (Stevenson & Britt, 1980)

and LH (Edwards & Foxcroft, 1983) occur in the first 24 h after weaning. Hypothalamic stores of GnRH increase rapidly within 60 h of weaning (Cox & Britt, 1982). Serum levels of prolactin fall dramatically at weaning, reach low levels within 4 h of piglet removal (Bever, Willemse & Kruij, 1978; Stevenson & Britt, 1980), then remain at basal levels until oestrus. Plasma levels of oestradiol are reported to be low throughout lactation and after weaning, rise to a peak before the ovulatory surge of LH, then decline to basal levels once more (Ash & Heap, 1975).

Since the extent to which these hormonal changes occur when lactation is very short is not known, we have monitored the changes in plasma concentrations of LH, prolactin, oestradiol-17 β and progesterone in the period from 24 h before weaning until 10 days *post coitum* in sows weaned at 10 or 35 days of lactation. A note was also made of each sow's weaning to remating interval and litter size at the subsequent farrowing.

Materials and Methods

Animals and treatments

Fifteen multiparous Landrace $\times$ Large White sows were allocated at random to one of two treatments: in Group E, piglets were weaned at 10 days of age ($N = 7$) and in Group C at 35 days ($N = 8$). At least 48 h before piglet removal, all sows were anaesthetized with thiopentone (1.5 g i.v.) and maintained with halothane/oxygen. Indwelling Silastic (Dow Corning, Midland, Michigan, U.S.A.) cannulae were inserted into the vena cava by the method of Takken & Williams (1981). The free ends of the cannulae were suspended so that sows could be bled without disturbance. At weaning (08:10 h, Day 0) the sows were housed in individual stalls and fed 2 kg daily of a standard sow breeding diet. Sows were taken to the boar for 10 min daily for detection of oestrus and were mated on the 1st and 2nd days of oestrus.

Blood samples were taken from all sows from Day -1 until 10 days *post coitum*. Frequency of sampling was every 8 h up to and including the first day of mating and thereafter once daily. Additionally, 5 sows from each group were intensively sampled in that blood samples were taken at 30 min intervals for 12 h per day (08:00–20:00 h) on Days -1, 0 and 1; then for 6 h per day (11:00–17:00 h) until and including the first day of mating; and finally for a 2 h period (13:00–15:00 h) for the first 5 days *post coitum*. Blood samples were collected into heparinized tubes, centrifuged, and the plasma stored at -20°C until assayed.

Hormone assays

LH. Plasma concentrations of LH (all samples) were determined by the method of Niswender, Reichert & Zimmerman (1970) which had previously been validated in this laboratory (Flor Cruz & Lapwood, 1978). The assay utilized rabbit anti-porcine LH serum (pool No. 566 courtesy of Dr G. D. Niswender), porcine LH (LER 788/4, courtesy of Dr L. E. Reichert) for assay standards and highly purified porcine LH (LER 786/3 courtesy of Dr L. E. Reichert) for radioiodination. Mean assay sensitivity, defined as the minimum detectable LH concentration significantly different from zero was 0.43 ng/ml. Intra-assay coefficients of variation (CV) were 10.5, 10.0 and 7.9% and inter-assay CVs were 22.0, 12.3 and 7.7% for samples containing mean LH concentrations of 1.7, 3.5 and 12.1 ng/ml, respectively ($n = 9$).

Prolactin. Plasma prolactin concentrations (all samples) were measured by the heterologous double-antibody method of van Landeghem & van de Wiel (1978). This assay utilized rabbit anti-serum to ovine prolactin, which is highly specific for porcine prolactin (van Landeghem & van de Wiel, 1978) at a final dilution of 1:50 000. Porcine prolactin (AEW-SP-162C, prepared by Dr A. E. Wilhelmi and donated by Dr L. E. Reichert) was used for assay standards and highly purified porcine prolactin (LER-2073, courtesy of Dr L. E. Reichert) for radio-iodination. Mean assay sensitivity was 0.20 ng/ml. Intra-assay CVs were 9.7, 9.7 and 11.3% and inter-assay CVs were 6.2,

Text-fig. 1. Mean $\pm$ s.e.m. plasma prolactin levels in sows ($N = 4$) after i.v. administration of 50 μ g TRF.

5.0 and 6.4% for plasma samples containing mean prolactin concentrations of 6.3, 25.9 and 35.5 ng/ml, respectively ($n = 5$).

The assay was further validated in this laboratory by establishing plasma prolactin profiles in 4 sows receiving an intravenous injection of 50 μ g thyrotrophin-releasing factor (Roche, Basle, Switzerland). The results (Text-fig. 1) indicate a prolactin response profile very similar in magnitude and variability to those obtained by previous workers (van Landeghem & van de Wiel, 1978; Bevers & Willemse, 1982). Dilution response curves for four porcine plasma pools assayed neat or at dilutions of 1:1, 1:3 and 1:7 showed no evidence of non-parallelism. Data obtained were transformed to logarithms to remove a correlation between means and variance. The anti-logarithms of the logarithmic averages of all pools for dilutions of 1:0, 1:1, 1:3 and 1:7 were 17.1 ± 2.1 , 20.1 ± 2.0 , 18.9 ± 2.3 and 18.0 ± 2.2 ng/ml, respectively.

Progesterone. Determinations were made on 500 μ l samples from the daily 08:00 h blood collection. Samples were extracted with 5 ml toluene:hexane (1:2 v/v). The plasma was frozen overnight and solvent was then decanted into clean tubes, dried under air and redissolved in 500 μ l ethanol. Duplicate 100 μ l samples of ethanol extract were dispensed into plastic tubes and dried under air, as were duplicate 100 μ l samples of standard ethanolic solutions of progesterone (P-1030: Sigma Chemical Co., St Louis, Missouri, U.S.A.) with concentrations corresponding to plasma progesterone levels of 0.625–40 ng/ml. A mixture containing antiserum (courtesy of Dr J. T. France) at a final dilution of 1:18 000 (Tungsubutra & France, 1978); [1,2,6,7- 3 H]progesterone (TRK 413, Amersham, Bucks, U.K.) at 20 000 c.p.m./100 μ l; phosphate-buffered saline containing 0.02 M-EDTA and 0.1% gelatin (PBS-EG) in the ratio of 1:1:4 (by vol.) was added (600 μ l) to each tube and vortexed. After overnight incubation at 4°C, 600 μ l of 2.5% (W/V) charcoal (Norit A; A. H. Thomas Co., Philadelphia, U.S.A.) suspension in PBS-EG were added to the tubes, vortexed and then incubated at 4°C for 10 min. Tubes were then centrifuged at 3000 g for 10 min at 4°C. The supernatant was decanted into scintillation vials and 6 ml toluene–triton scintillation fluid added before counting for 2 min in a Beckman LS 7500 scintillation counter. Assay sensitivity was 0.05 ng/ml. Intra-assay CVs were 13.8, 8.2 and 8.2% and inter-assay CVs were 16.5, 11.1 and 9.2% for plasma pools containing mean progesterone concentrations of 1.4, 7.6 and 12.0 ng/ml, respectively ($N = 6$).

Oestradiol-17 β . The determinations were made on 500 μ l duplicate plasma samples from the

daily 08:00 h sample by the method of Smith, Drost, Fairclough, Peterson & Tervit (1976). To validate the accuracy of this assay for pig plasma, samples were compared with and without Sephadex LH-20 chromatographic purification of oestradiol-17 β extracts before assay. These samples consisted of four quality control plasma pools and also ovariectomized sow plasma to which had been added 0, 50 or 100 pg oestradiol-17 β /ml. A regression analysis of the results gave a correlation coefficient of 0.99 with a constant overestimation of 22 pg/ml by the direct assay. Accordingly, all results have been corrected for this error. Mean assay sensitivity was 10 pg/ml and the intra-assay and inter-assay CVs for oestradiol concentrations which inhibited specific binding by 50% relative to that of the zero standard were 6.1 and 16.3%, respectively ($n = 6$).

Statistical analysis

Analysis of all hormone data for animals, days and treatment differences was performed by a repeated measure multivariate profile analysis (Morrison, 1976).

Results

Sows with piglets weaned at 10 days *post partum* had a longer weaning to oestrus interval than did sows with young weaned at 35 days (8.3 ± 0.81 compared with 5.0 ± 0.71 days, $P < 0.01$) and subsequently gave birth to smaller litters (10.2 ± 1.93 compared with 12.0 ± 0.62), although the latter difference was not statistically significant.

Plasma profiles of LH and prolactin for animals in each treatment group were established by plotting the mean values obtained from the 08:00, 16:00 and 24:00 h samples. The overall patterns thus obtained were not found to be modified when data from all samples were included. As shown in Text-fig. 2, plasma LH levels were consistently higher in Group C than in Group E sows; daily means for all samples on Days -1, 0, 1 and 2 being 1.45 ± 0.08 , 1.43 ± 0.12 , 1.53 ± 0.08 , 1.40 ± 0.08 and 1.21 ± 0.18 , 1.14 ± 0.16 , 1.19 ± 0.06 , 1.16 ± 0.09 ng/ml for sows in Groups C and E respectively ($P < 0.001$). Also, the area under the LH peaks (166.2 ± 12.2 and 97.6 ± 8.7 ng/ml. h $^{-1}$; $P < 0.001$) and the peak LH values obtained (7.77 ± 0.93 and 3.63 ± 1.37 ng/ml; $P < 0.01$) were significantly reduced in Group E sows. There was no evidence of any prolonged LH surges before the preovulatory surge, nor was there any significant treatment effect on LH values recorded in the first 5 days *post coitum*.

Mean prolactin levels before weaning were consistently higher in Group E sows than in Group C sows (Text-fig. 2), but this difference was significant ($P < 0.01$) only for the 08:00 h samples. Prolactin values declined precipitously in both groups of sows after weaning. Between Day 1 and the peak observed about the time of oestrus, plasma prolactin levels fluctuated considerably, with occasional elevations of up to 7 ng/ml being recorded from sows of both groups. The mean peak values of plasma prolactin during oestrus were 6.98 ± 1.68 and 8.93 ± 2.33 ng/ml for Groups C and E, respectively. The peak values illustrated in Text-fig. 2 have been modified by the plasma prolactin values being centred on the time of peak LH rather than peak prolactin. No significant difference between treatments was found. Although the mean plasma prolactin values achieved at oestrus were not influenced by the length of the preceding lactation, this factor appeared to affect the timing of the prolactin peak in relation to the LH peak (Text-fig. 2). Group C sows showed a prolactin peak in the 24 h before the LH peak, whereas in Group E sows plasma prolactin was rising during this time and peaked within 24 h after the LH peak.

Daily mean plasma concentrations of oestradiol-17 β (Text-fig. 3) did not differ significantly between treatments. Mean values were initially very high, with particularly high levels (≥ 100 pg/ml) being found in 3 Group C and 4 Group E sows. Individual plasma levels of oestradiol were very variable during the weaning to remating interval, with levels occasionally approaching those seen immediately before the ovulatory release of LH (Text-fig. 4). Mean oestradiol levels were significantly elevated at oestrus ($P < 0.05$).

Text-fig. 2. Mean $\pm$ s.e.m. plasma LH and prolactin concentrations in sows from Days -1 to 2; 24 h either side of the ovulatory peak and for the first 5 days post coitum.

Text-fig. 3. Mean $\pm$ s.e.m. plasma oestradiol-17 β and progesterone concentrations in sows from Days -1 to 2 and 3 days before to 5 after the ovulatory peak of LH.

Text-fig. 4. Oestradiol profiles of 2 individual sows (Sows 3 and 14) over the entire sampling period. Arrows indicate position of LH peak and bars the period of mating.

Plasma progesterone levels (Text-fig. 3) in Group C and Group E sows rose from 0.9 and 1.4 ng/ml, respectively, on the day of the LH peak, to 4.3 and 4.7 ng/ml 2 days later, and continued to rise thereafter. At no time were any treatment differences in plasma progesterone concentration apparent.

Discussion

The present findings confirm that very early weaning of piglets from sows significantly prolongs the weaning to remating interval. Although these sows tended to produce smaller subsequent litters, the difference was not significant in this study. Further, the length of the preceding lactation is shown to influence the endocrine status of the sows, most notably at the post-weaning oestrus.

It has been reported that in sows plasma levels of LH (Stevenson & Britt, 1980; Stevenson, Cox & Britt, 1981) and pituitary responsiveness to GnRH stimulation (Bevers *et al.*, 1981) increased with length of lactation. Those results suggest a partial escape of the hypothalamic/pituitary axis from lactational inhibition, probably due at least in part to a reduced suckling intensity later in lactation. The results presented here agree with this conclusion in that plasma LH levels were significantly higher at 34 days of lactation, than at 9 days. A small transient increase in plasma LH has been noted to occur in the first 24 h after weaning (Edwards & Foxcroft, 1983). Such an increase could serve to trigger the preovulatory release of oestrogen, as has been shown to occur with male-induced puberty in mice (Bronson & Desjardins, 1974). However, in the present results there was no post-weaning elevation in basal LH before that seen at ovulation, which is in agreement with

results from other workers (Dyck, Palmer & Simaraks, 1979; Stevenson & Britt, 1980). The low lactational and post-weaning plasma LH levels observed in Group E sows is further reflected in a greatly attenuated ovulatory surge, as has been reported for sows after a 3-week lactation (Edwards & Foxcroft, 1983). This reduction in LH release following short lactations may reflect a lower pituitary level of LH and/or a reduced hypothalamic store of GnRH 8 days after weaning in Group E sows as compared to 5 days after weaning in Group C sows. Also, a reduced hypothalamic responsiveness to oestrogen stimulation cannot be ruled out. The consequences of an attenuated LH peak for subsequent reproductive performance are not known. Since a reduction in ovulation rate in early weaned sows is reported not to occur (Varley & Cole, 1976; Edwards & Foxcroft, 1983), it may be that ovarian steroid secretion is modified in some way. If this were so, an influence on the uterine environment (e.g. uterine protein secretion) could be postulated, with consequences for embryo survival.

Plasma prolactin levels were consistently higher during lactation in Group E than Group C sows probably resulting from a greater suckling intensity in Group E. After weaning of the piglets plasma prolactin values dropped precipitously in both groups. Bevers *et al.* (1978) and Stevenson *et al.* (1981) have reported that, after piglet removal, plasma prolactin reaches baseline levels within 4 h. Whilst this was true for Group C sows in the present work, sows in Group E did not achieve baseline levels before 8 h after weaning. This, however, may simply be a reflection of higher pre-weaning levels. It is therefore unlikely that hyperprolactinaemia is involved in the extension of the weaning to remating interval in early weaned sows, which is in agreement with conclusions from studies with sows weaned at 35 days (van de Wiel, van Landeghem, Willemse & Bevers, 1979; Benjaminsen, 1981). An increase in plasma levels of prolactin at the time of oestrus has been noted in this and other work (Bevers *et al.*, 1978). In the present study prolactin levels tended to peak in the 24 h before the ovulatory release of LH in Group C sows, but in the 24 h after in Group E sows. The reproducibility of these results is being investigated since conditions of rising prolactin, rather than prolactin level *per se*, inhibit LH release in rats (Wuttke, Dohler & Gelato, 1976; Lamberts, Hohn & Wuttke, 1979).

High initial plasma oestradiol levels seen in the present results are unlikely to be involved in the previously documented phenomenon of a non-ovulatory post-partum oestrus (Shearer, Purvis, Jenkin & Haynes, 1972), or a resumption of oestrous activity in late lactation, since at no time was such behaviour observed before weaning. Stevenson & Britt (1980) consider that the stress of cannulation may cause elevated plasma oestrogen levels. Whilst this is possible, in the present study cannulation was performed 2–6 days before sampling with no apparent relationship between the length of the interval and initial plasma oestrogen level. Individual oestradiol profiles between weaning and oestrus were variable, with some animals showing peaks of a magnitude similar to those that subsequently induced the preovulatory LH surge. Since these 'non-oestrus' oestradiol peaks failed to release LH, it may be that they have a role in priming the pituitary for the subsequent ovulatory release of LH. Whilst changes in mean daily levels of oestradiol were muted by the individual sow variations, the overall pattern is similar to the results of Ash & Heap (1975) and Edwards & Foxcroft (1983). The significant prolongation of the oestradiol surge at oestrus in very early weaned sows reported by Varley *et al.* (1981) was not evident in this study.

Also in contrast to the results of Varley *et al.* (1981), no treatment differences were apparent for progesterone secretion, and plasma levels were similar to those reported by van de Wiel, Erkens, Koops, Vos & van Landeghem (1981).

In conclusion, the present findings have not demonstrated any difference in steroid secretion between sows lactating for 10 or 35 days. The prolonged weaning to remating interval experienced after short lactations may be due to a slower recovery of the hypothalamic/pituitary unit in terms of GnRH and LH stores and/or to a lower sensitivity/responsiveness of the unit.

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