Relationships between LH, FSH and prolactin secretion and reproductive activity in the weaned sow

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Summary. Blood samples were collected from primiparous sows via indwelling jugular cannulae at 15-min intervals for 12 h before and for 24 h (2 sows) or 48 h (10 sows) after weaning and then every 4 h until behavioural oestrus. Weaning to oestrus intervals ranged from 3 to 10 days and 2 sows showed no signs of oestrus and had not ovulated by Days 11 and 16 after weaning.

Prolactin concentrations in plasma decreased significantly \( (P < 0.001) \) and reached basal levels 1–2 h after weaning in all sows whilst plasma progesterone concentrations remained basal until \( \sim 30 \) h after the preovulatory LH surge in sows that ovulated. Elevated concentrations of prolactin or progesterone during the post-weaning period were, therefore, not responsible for delayed restoration of cyclicity.

Overall, mean LH concentrations rose significantly \( (P < 0.001) \) from 0.22 ± 0.02 during the 12-h period before weaning to 0.38 ± 0.03 ng/ml during the 12-h post-weaning period. After weaning, pulsatile and basal LH secretions were markedly increased for sows that showed an early return to oestrus (\( \leq 4 \) days) compared with sows showing a longer weaning to oestrus interval but a correlation did not exist between either of these LH characteristics and the time taken to resume cyclicity. Mean LH concentrations before weaning were, however, inversely related \( (r = -0.649; \ P < 0.05) \) to the weaning to oestrus interval.

Overall, mean FSH concentrations rose significantly \( (P < 0.001) \) from 151.1 ± 6.2 (s.e.m.) ng/ml in the 12-h period immediately before weaning to 187.7 ± 9.7 ng/ml in the subsequent 12-h period but there was no correlation between FSH concentrations, before or after weaning, and the interval from weaning to oestrus. However, a significant correlation was apparent between ovulation rate and peak concentrations of the rise in FSH after weaning \( (r = 0.746; \ P < 0.05) \) and overall mean FSH values \( (r = 0.645; \ P < 0.05) \).

It is concluded that both LH and FSH concentrations in peripheral blood rose in response to removal of the suckling stimulus at weaning. The increase in LH pulse frequency associated with weaning was not directly related to the weaning to oestrus interval although a specific pattern of LH secretion was observed in sows showing an early return to oestrus (\( \leq 4 \) days). It is proposed that the characteristics of LH secretion after weaning may reflect the ovarian status at the time of weaning and that this may, in part, be dependent on steroid feedback. The weaning-associated rise in FSH may be involved in the determination of ovulation rate.

Introduction

Changes in LH, FSH, prolactin and steroid secretion at the post-weaning oestrus in sows have been studied extensively (Ash & Heap, 1975; Aherne, Christopherson, Thompson & Hardin, 1976;
Parvizi, Elsaesser, Smidt & Ellendorff, 1976; van Landeghem & van de Wiel, 1978; Bevers, Willemsen & Kruip, 1978; Stevenson & Britt, 1980; Stevenson, Cox & Britt, 1981; Edwards & Foxcroft, 1983; Kirkwood, Lapwood, Smith & Anderson, 1984) but there is little information available on the precise endocrine changes immediately before and after weaning. Aherne et al. (1976) and Edwards & Foxcroft (1983) showed that FSH concentrations in peripheral blood rose inconsistently after weaning and hence the functional significance of this FSH rise is unknown (Edwards & Foxcroft, 1983). By contrast, early investigations, in which daily changes in plasma LH concentrations were measured, showed that LH remained low at and immediately after weaning but increased abruptly on the day before oestrus, i.e. Days 4–8 after weaning (Aherne et al., 1976; Parvizi et al., 1976; Stevenson & Britt, 1980). Edwards & Foxcroft (1983) found that a significant increase in LH secretion consistently accompanied weaning but the inadequate blood sampling frequency prevented demonstration that the transient increase in basal LH secretion (occurring within 24 h of weaning) was associated with an increase in LH pulsatile release. It has been suggested that high-frequency LH pulses in sheep and cows may be a prerequisite for final follicular growth and maturation (Baird, Swanston & Scaramuzzi, 1976; Baird, Swanston & McNeilly, 1981; Peters, Lamming & Fisher, 1981; McLeod, Haresign & Lamming, 1982; Haresign, Foxcroft & Lamming, 1983). A detailed knowledge of the patterns of hormone secretion at weaning may, therefore, provide an understanding of the mechanisms involved in follicular development in sows.

Materials and Methods

Experimental procedures

The 12 primiparous Landrace × (Landrace × Large White) or Landrace × Large White sows were nursing litters ranging from 6 to 10 (mean ± s.d. = 8 ± 1·5) piglets/sow at allocation to the experiment which took place over a 4-month period from March to June 1981. Sows were group penned during gestation and then transferred to individual farrowing crates 1 week before parturition where they remained throughout lactation. Sows were fed a standard sow ration according to accepted husbandry practice and were exposed to natural light through windows, although additional light provided from infra-red creep lamps was constantly present throughout lactation. During the intensive bleeding programme after weaning an attempt was made to minimize disruption of the natural photoperiod by using red lighting for night-time sampling.

Indwelling jugular cannulae were inserted surgically 3 days before weaning at about 21 (mean ± s.d. = 22 ± 2·4) days post partum. Sows were anaesthetized with 5% solution of metomidate (Hynodil: Janssen Pharmaceutica, Belgium) administered intravenously, via an ear vein, at a dose of 3·3 ml/50 kg. To evaluate the overall pattern of endocrine changes blood samples were collected every 4 h from the start of the experiment until 2 days after behavioural oestrus was observed and were assayed for plasma progesterone, LH, FSH and prolactin: the detailed changes in gonadotrophin and prolactin secretion immediately before and after weaning were analysed in a series of blood samples taken at 15-min intervals for 12 h before and for 24 h (2 sows) or 48 h (10 sows) after weaning. From Day 3 after weaning, sows were checked for oestrus daily between 09:00 and 10:00 h with an intact or vasectomized boar. At slaughter (8–16 days after weaning) the reproductive tracts were removed and the ovaries were examined to determine ovulation rate and to confirm the reproductive activity of each sow as indicated by behavioural and hormonal data.

Hormone assays

LH. Plasma concentrations were determined by the double-antibody radioimmunoassay (RIA) of Foxcroft, Pomerantz & Nalbandov (1975) with some modifications. Porcine LH (Instituut Voor Veeteeltkundig Onderzoek, IVO, Zeist, The Netherlands; biopotency 0·77 × NIH-LH-S1) was
used as reference standard preparation and ovine LH (LER-1374 A) for radioiodination; to increase assay sensitivity the antiserum (GDN No. 15) was used at an initial dilution of 1:80 000. Intra- and inter-assay coefficients of variation (CV) were 3-8, 9-0 and 10-7% and 9-9, 8-2 and 10-8%, respectively for samples containing mean LH concentrations of 97, 194 and 291 pg/tube (6 assays). Mean assay sensitivity, taken as 85% of total bound radioactivity, was 0:15 ng/ml.

**FSH.** Plasma FSH concentrations were measured by the method of Foxcroft, Elsaesser, Stickney, Haynes & Back (1984) using porcine FSH (NIH-FSH-P2) as assay standard. Intra- and inter-assay CVs were 6-2, 5-9 and 14-7% and 4-0, 13-3 and 15-3%, respectively for plasma samples containing mean FSH concentrations of 9, 18 and 36 ng/tube (6 assays). Mean assay sensitivity, taken as 88% of total bound radioactivity, was 18-6 ng/ml.

**Prolactin.** Plasma prolactin concentrations were quantified by an homologous double-antibody RIA utilizing goat antiserum to porcine prolactin (Research Products International Corporation, Elk Grove Village, IL 60007, U.S.A.); purified porcine prolactin (potency 30 i.u./mg; coded KK and kindly supplied by Dr K. Kochman) was used as reference standard and for radioiodination by the chloramine T method of Greenwood, Hunter & Glover (1963). For each iodination 2-5 µg prolactin in 10 µl 0-05 M-phosphate-buffered saline (PBS) was mixed with 1 mCi Na\(^{125}\)I in 50 µl 0-5 M-PBS (pH 7-2) and 30 µg chloramine T (1-5 µg/µl 0-05 M-PBS) for 10–12 sec. The reaction was stopped with the addition of 60 µg sodium metabisulphite (0-6 µg/µl 0-05 M-PBS) and the mixture diluted with 200 µl 0-1% potassium iodide and 100 µl assay diluent (0-05 M-PBS containing 2-7 mM-EDTA and 1% bovine serum albumin (BSA)). Free \(^{125}\)I was separated from \(^{125}\)I-labelled prolactin on a 20 x 1 cm Sephadex G100 column washed with 5% egg albumin and equilibrated with 0-05 M-PBS. Maximal binding of label was observed in the fractions representing the final portion of the protein-bound peak and these were pooled and stored at 4°C for subsequent use in the assay.

For the assay, 400 µl assay diluent, 100 µl plasma sample or standard (0-2, 0-3, 0-6, 1-0, 2-0, 3-0, 6-0, 10-0, 20-0 ng prolactin), 100 µl goat antiporcine prolactin (at an initial dilution of 1:50 000 in PBS containing 1:600 normal goat serum (NGS/PBS)) and 100 µl \(^{125}\)I-labelled pig prolactin (diluted in assay diluent to give 15–20 000 c.p.m.) were used as appropriate. All tubes were incubated at 4°C for 24 h before the addition of 200 µl of a 1:15 dilution of donkey anti-goat gamma globulin, and incubated at 4°C for a further 24 h. To separate bound and free \(^{125}\)I-labelled prolactin the tubes were centrifuged at 2000 g for 30 min, the supernatant was aspirated and the radioactivity in the pellet was counted.

The specificity of the antiserum has previously been investigated by Kraeling, Rampacek, Cox & Kiser (1982) who found that cross-reaction with large quantities (2–2000 ng) of FSH (NIH-FSH-P2), LH (LER-778-4) and growth hormone (NIH-GH-P-5268) were all < 1%. The dilution of first antibody used bound 20–30% of \(^{125}\)I-labelled prolactin in the absence of unlabelled hormone. Three volumes (100, 200 and 300 µl) of a pooled plasma sample included in each assay to test for parallelism to the standard curve gave mean values of 1-4, 2-7 and 4-3 ng/tube and a significant correlation existed between volume of plasma and mass of hormone (y = 0-014x – 0-03; r = 0-997; P < 0-05; linear regression analysis). Accuracy, estimated as the recovery of prolactin at known concentrations from pig plasma, gave values ranging from 88 to 105%. The intra- and inter-assay CVs were 4-4 and 11-4%, respectively, and the mean assay sensitivity was 4-4 ng/ml.

**Progesterone.** Plasma progesterone concentration was assayed by the method of Haresign, Foster, Haynes, Crighton & Lamming (1975) using the antiseraum 711/12 at a dilution of 1:6000. The specificity of this antiseraum was determined using 11α-hydroxyprogesterone, 11β-hydroxyprogesterone, 17α-hydroxyprogesterone, 3β-pregn-3,20-dione and corticosterone. The cross-reactions of these steroids were 130, 224, 11-8, 9-0 and < 1-0%, respectively. Ether blanks measured in each assay contained levels of progesterone which were below the sensitivity of the assay, estimated to be 0-26 ng/ml. The mean recovery of radioactivity after extraction over 11...
assays was 81.3%. However, the percentage recovery from each individual assay was used as a correction factor to estimate potencies within that assay. Intra- and inter-assay CVs were 5.3 and 4.9% and 8.1 and 10.5%, respectively, for plasma pools containing progesterone concentrations of 0.175 and 0.35 ng/tube.

Analyses of results

The sows were divided into three groups on the basis of the weaning to oestrus interval: Group 1, early (4 sows; interval 3–4 days); Group 2, intermediate (5 sows; interval 5–9 days); Group 3, late/anoestrous (3 sows; interval ≥ 10 days). The mean interval from weaning to oestrus for the University's herd was 5 days. Therefore, all sows that returned to oestrus within 4 days were designated to Group 1. Sows displaying oestrus or failing to do so by day 10 were classified as late or anoestrous sows in accordance with the definition of Meredith (1979). Data from the 60-h frequent sampling period were analysed as 5 separate 12-h time blocks (Periods 1–5) by split-plot analysis of variance appropriate for repeated measurements in individual animals (Gill & Hafs, 1971). Regression correlations were used to determine the relationships between hormone levels and restoration of cyclicity; Student's t test was used to make any other comparisons involving only two means.

Determination of the characteristics of LH secretion

With the aid of a computer programme maximum and minimum LH levels were estimated by means of an '8-value sliding window' technique. The highest and lowest points of the first 8 values of any one 12-h time block were extracted and a one-sample (or 15 min) shift was then made along the time axis before further extraction of the highest and lowest values from the next set of 8 samples. A total of 40 maximum and minimum values were obtained for each time block from which the maximum and minimum LH levels were calculated. Eight values were selected to allow for total clearance of LH after a typical LH pulse. The difference between the mean maximum and minimum levels derived for any one 12-h period was taken as an estimate of LH pulse amplitude during that time. This method of analysis is only suitable when applied to LH profiles containing pulses of consistent amplitude.

For the purpose of determining LH pulse frequency a pulse was defined as (i) any increase in the concentration of LH that exceeded the 95% confidence limits for the baseline and the peak samples and was completed within two sampling intervals; (ii) this rise was then followed by a decline in concentration that exceeded the 95% confidence limits, which had at least two sample points between the peak value and succeeding trough or baseline and occurred at a rate no greater than the known half-life of the hormone. The number of pulses in a profile were then counted and analysed using the procedure for analysis of deviance as described by Nelder & Wedderburn (1972) and Martin, Scaramuzzi & Henstridge (1983).

Results

Table 1 shows that the litter size, sow weights, lactation lengths and ovulation rates were not different between groups selected for analysis on the basis of different weaning to oestrus intervals.

LH concentrations

All sows showed a change in the pattern of LH secretion in response to weaning and overall mean LH concentrations rose significantly \(P < 0.001, N = 12\) from 0.22 ± 0.02 (s.e.m) ng/ml during the 12-h period before weaning to 0.38 ± 0.03 ng/ml in the 12-h period after weaning. Mean
Hormonal control of reproduction in weaned sows

Table 1. Comparison of sow and litter characteristics for each group selected on the basis of weaning to oestrus intervals (see text)

<table>
<thead>
<tr>
<th>Group</th>
<th>No. of sows</th>
<th>Litter size* (piglets/sow)</th>
<th>Sow weights* (kg)</th>
<th>Duration of lactation (days)</th>
<th>Ovulation rate</th>
<th>Weaning to oestrus interval (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4</td>
<td>7·3 ± 0·8</td>
<td>141·3 ± 4·2</td>
<td>22·3 ± 1·4</td>
<td>13·8 ± 1·5</td>
<td>3·8 ± 0·3</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>8·2 ± 0·8</td>
<td>132·9 ± 3·8</td>
<td>22·6 ± 1·2</td>
<td>14·7 ± 0·9</td>
<td>5·8 ± 0·4</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>8·7 ± 0·3</td>
<td>136·3 ± 3·8</td>
<td>20·7 ± 0·3</td>
<td>16 (N = 1)</td>
<td>10 (N = 1)</td>
</tr>
</tbody>
</table>

*Values taken at weaning.

LH concentration for sows in Groups 1, 2 and 3 for each of the five 12-h time blocks (Periods 1–5) are presented in Text-fig. 1. The preovulatory LH surge in Sow K in Group 1 had begun during the last 12 h of the frequent sampling period (Text-fig. 2) and these values were therefore excluded from statistical analysis; however, episodic release of LH persisted throughout the onset of the LH preovulatory surge in this animal. There was no significant difference in mean LH concentrations between groups of sows within time blocks. A significant reciprocal correlation (P < 0·05) did exist, however, between mean LH levels before weaning and the intervals from weaning to oestrus (r = −0·649) but this relationship was not apparent for LH concentrations in any of the post-weaning periods. Text-figure 1 also shows the mean maximum and minimum LH concentrations for each of the sow group categories and time blocks. The mean minimum LH values for Group 1 were significantly greater than those for both Groups 2 and 3 in the three 12-h periods immediately after weaning (P < 0·05, Periods 2 and 4; P < 0·01, Period 3) and reflects the elevated LH baseline seen in this group of animals. A significant correlation was found between minimum LH values and LH pulse frequency for all groups over each period (r = 0·63; P < 0·05). Maximum LH concentrations for sows in Group 2 were greater than those for the other two groups between 24 and 48 h after weaning but were only significantly elevated during the last 12 h (Group 1, P < 0·01; Group 3, P < 0·05); this increase in maximum LH was associated with the occurrence of high-amplitude LH pulses.

Representative examples of LH profiles for one sow from each of Groups 1, 2 and 3 are shown in Text-fig. 3. During lactation LH was released in distinct pulses with an overall mean ± s.e.m. LH pulse frequency of 3·2 ± 0·46 pulses/12 h which increased significantly (P < 0·001) to 7·8 ± 1·18 pulses/12 h for the period immediately after weaning and remained elevated thereafter; all but one sow (from Group 2) contributed to this rise in pulse frequency and even in this animal a marked increase in frequency occurred from 36 h after weaning. As shown in Table 2, LH pulse frequency increased significantly in the 12-h period after weaning in those sows showing both an early (Group 1) and late (Group 3) return to oestrus.

Mean pulse amplitude was significantly greater (P < 0·05) during the 12-h period immediately after weaning compared with the preceding period for Groups 2 and 3 (Table 2). Amplitude was further increased over the subsequent 36 h for sows in Group 2 but began to decline from 12 h after weaning for those in Group 3. A progressive decrease in pulse amplitude was also apparent for sows in Group 1 from 12 to 48 h after weaning (Table 2; see Text-fig. 3).

FSH concentrations

All but 2 sows responded to weaning with a rise in FSH values. Although the onset of these elevations varied from 1 to 19 h after weaning, they occurred within the first 12 h after weaning in 8 of the sows. Plasma FSH remained elevated between 8 and 32 h after weaning and the mean maximal level achieved was 286·2 ± 26·5 ng/ml with a range of 124 to 445 ng/ml. Representative
Text-fig. 1. Changes in maximum, minimum and mean LH concentrations for sows in Groups 1 (□), 2 (■), and 3 (■) (see text) during the 12-h period before (Period 1) and the four consecutive 12-h periods after (Periods 2–5) weaning. Bars represent the mean ± s.e.m. a Maximum values for Group 2 significantly different from Group 1 (P < 0.01) and b from Group 3 (P < 0.05). c,d Minimum values for Group 1 significantly different from Groups 2 and 3, P < 0.05 and P < 0.01, respectively.

Text-fig. 2. Episodic LH release in a sow (Sow K) during the onset of an LH surge immediately after weaning at ~21 days post partum. The peak of the LH surge occurred 55 h after weaning.

Examples of FSH profiles for one sow from each of Groups 1, 2 and 3 are shown in Text-fig. 3. Overall, FSH secretion rose significantly (P < 0.001) from 149.2 ± 8.9 (s.e.m.) ng/ml in the 12-h period immediately before weaning to 187.5 ± 5.6 ng/ml in the subsequent 12-h period. There was no difference in FSH concentrations in the 3 groups for the 12-h periods before or after weaning.
Text-fig. 3. Plasma LH, FSH and prolactin concentrations in 3 sows weaned at ~21 days post partum and with a subsequent weaning to oestrus interval of (a) 4 days (Sow B, Group 1), (b) 6 days (Sow E, Group 2), and (c) > 11 days (Sow C, Group 3). Samples were obtained at 15-min intervals.
Table 2. Comparison of LH pulse frequency, amplitude and plasma FSH concentrations for each group of sows before (Period 1) and after (Periods 2–5) weaning

<table>
<thead>
<tr>
<th>Group</th>
<th>Period 1</th>
<th>Period 2</th>
<th>Period 3</th>
<th>Period 4</th>
<th>Period 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LH pulse freq.</td>
<td>4.8 ± 0.75</td>
<td><strong>11.8 ± 0.63</strong></td>
<td>6.0 ± 2.00</td>
<td>5.0</td>
<td>6.0</td>
</tr>
<tr>
<td>LH pulse ampl.</td>
<td>0.4 ± 0.12</td>
<td>0.4 ± 0.03</td>
<td>0.4 ± 0.10</td>
<td>0.3</td>
<td>††0.3</td>
</tr>
<tr>
<td>FSH (ng/ml)</td>
<td>135.0 ± 11.2</td>
<td>176.4 ± 23.6</td>
<td>159.2 ± 22.0</td>
<td>110.9</td>
<td>128.8</td>
</tr>
</tbody>
</table>

| 2     |          |          |          |          |          |
| LH pulse freq. | 2.6 ± 0.40 | 3.4 ± 0.93 | 4.4 ± 1.30 | 4.4 ± 0.80 | 7.0 ± 1.1 |
| LH pulse ampl. | 0.4 ± 0.06 | *0.6 ± 0.04 | 0.6 ± 0.12 | 0.8 ± 0.15 | 0.8 ± 0.05 |
| FSH (ng/ml) | 165.8 ± 8.10 | 194.2 ± 13.6 | 169.3 ± 17.6 | **174.2 ± 29.2** | †176.9 ± 22.2 |

| 3     |          |          |          |          |          |
| LH pulse freq. | 2.3 ± 0.88 | *8.3 ± 0.66 | 5.0 ± 0.60 | 5.0 ± 1.00 | 6.3 ± 0.90 |
| LH pulse ampl. | 0.3 ± 0.08 | *0.6 ± 0.09 | 0.4 ± 0.09 | 0.5 ± 0.13 | †0.5 ± 0.12 |
| FSH (ng/ml) | 146.9 ± 5.9 | 191.9 ± 13.7 | 184.4 ± 1.70 | **153.9 ± 17.3** | †186.9 ± 25.9 |

Values are mean ± s.e.m. for the no. of sows indicated in parentheses.

*P < 0.05; **P < 0.01 compared with values for Period 1.
†P < 0.05 compared with values for Group 1.
‡P < 0.05; ††P < 0.01 compared with values for Group 2.

Table 3. Changes in overall mean (± s.e.m.) plasma prolactin concentrations and means for each group of sows during the 12-h periods immediately before and after weaning

<table>
<thead>
<tr>
<th>Prolactin conc. (ng/ml)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Group</td>
<td>No. of sows</td>
<td>12 h before weaning</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>37.8 ± 6.3</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>26.5 ± 5.3</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>27.7 ± 0.7</td>
</tr>
<tr>
<td>Overall</td>
<td>3</td>
<td>30.7 ± 3.6</td>
</tr>
</tbody>
</table>

*Significantly (P < 0.001) lower than values before weaning.

However, mean FSH concentrations of sows in Groups 2 and 3 between 36 and 48 h after weaning (Periods 4 and 5) were significantly greater (P < 0.05) than those for sows showing an early return to oestrus (Table 2).

A significant correlation existed between ovulation rate and both overall mean FSH concentrations (r = 0.645; P < 0.05) and peak concentrations of the weaning associated rise in FSH (r = 0.746; P < 0.05). There was no relationship between the weaning to oestrus interval and FSH secretion either before or after weaning but the time to resume cyclicity was correlated with the ratio of FSH to LH (calculated from mean values for each animal) for the entire sampling period (r = 0.595; P < 0.05).

Prolactin concentrations

A significant (P < 0.001) decline in prolactin concentrations occurred in all but one sow within 1–2 h of weaning and represented a 30–40% reduction in plasma prolactin values. The mean
plasma prolactin concentrations for sows in Groups 1, 2 and 3 for the 12-h periods before and after weaning were similar (Table 3).

**Progesterone concentrations**

Progesterone values were below the sensitivity of the assay for 12 h before and 48 h after weaning but began to rise about 30 h after the preovulatory LH surge.

**Discussion**

Contrary to the data of van de Wiel, van Landeghem, Willemse & Bevers (1979), LH episodic release was observed on Days 20 to 21 of lactation. It is uncertain, however, whether LH pulse activity was absent during the early stages of lactation as in the milked or suckling cow in which a pulsatile pattern was not apparent until Days 13 and 20 post partum, respectively (Peters et al., 1981; Riley, Peters & Lamming, 1981). A gradual increase in LH secretion has been reported throughout lactation for the sow (Stevenson et al., 1981) and this has been attributed to a progressive 'escape' from the inhibitory effects of the preceding pregnancy and to the decrease in suckling intensity in later lactation. The elevation in LH and FSH secretion observed immediately after weaning in the present study may therefore be due to the sudden removal of the inhibitory effects on gonadotrophin secretion imposed by suckling. The rise in mean LH concentrations at weaning was associated with an increase in LH pulse frequency which resulted in an elevated baseline in those sows in which pulsatility reached a frequency of 1 pulse/h; indeed this latter effect may occur entirely as a result of insufficient time between pulses for LH concentrations to decline to basal levels. The positive correlation between pulse frequency and minimum LH values in this study indicates that an assessment of LH minima may be a useful criterion on which to base LH activity during the follicular phase.

It seems reasonable to assume that any variation in the LH response to weaning may be related to the interval to post-weaning oestrus, since it has been suggested for sheep that the development of, or increase in, pulsatile LH release is a prerequisite for final follicular growth and maturation (Baird et al., 1976; Baird, 1978; Haresign et al., 1983). It is not certain, however, whether LH pulsatility per se is an absolute requirement since follicular growth and the preovulatory oestradiol rise can be elicited in ewes by constant or episodic delivery of LH (Goodman, Bittman, Foster & Karsch, 1981; McNatty, Gibb, Dobson & Thurley, 1981; McNeilly, O'Connell & Baird, 1982) or GnRH (McLeod et al., 1982, 1983). The pulse frequency and mean minimum concentrations of LH were greater for sows showing overt oestrus within 4 days of weaning, but for all animals investigated neither episodic LH frequency nor mean, minimum or maximum LH values in the post-weaning periods were correlated with the time taken to resume cyclicity. However, mean LH concentrations during the 12-h period before weaning were inversely related to the interval from weaning to oestrus, indicating that events occurring during lactation may have determined the response to weaning. Since the latency between activation of the oestrogen positive-feedback mechanism and the preovulatory LH surge in the pig is estimated to be 50–55 h (Edwards & Foxcroft, 1983), the temporal relationship between weaning and oestrus in at least one animal in Group 1 (i.e. Sow K which had an LH surge 55 h after weaning; see Text-fig. 2) suggests that this sow was secreting oestrogen at the time of weaning. Although oestrogens were not measured in this study one hypothesis to explain the varied patterns of LH secretion in sows after weaning is that the state of ovarian activity at weaning may determine the gonadotrophic response of the sow, such that oestrogen secretion acts to enhance LH pulse frequency, with a consequent increase in mean and basal LH levels. Sows possessing ovarian follicles in a less advanced state (i.e. those in Group 2) may not have had sufficiently elevated plasma oestradiol concentrations to augment the weaning-associated rise in LH. Although it is generally assumed that oestriadiol exerts negative-
feedback on tonic LH secretion, Karsch, Foster, Bittman & Goodman (1983) have demonstrated that administration of oestradiol to ewes ovariectomized in the late luteal phase increases LH pulse frequency and that this effect could not be solely attributed to a withdrawal of progesterone. The effect of oestradiol on LH pulse frequency may be coupled to the positive-feedback effect on the preovulatory LH surge because LH pulsatility persisted in Sow K during the start of the LH surge as has previously been reported for a number of other species (Rahe, Owens, Fleeger, Newton, Harms, 1980; Gallo, 1981; Marut et al., 1981; Karsch et al., 1983). However, the precise mechanisms involved in the functional separation of these two feedback actions of oestradiol has yet to be determined. It has been suggested that the negative-feedback effect of oestrogen on tonic LH secretion is augmented during lactation in women (Baird, McNeilly, Sawers & Sharpe, 1979) and ewes (Wright, Geytenbeek, Clarke & Findlay, 1981). An alternative hypothesis, therefore, to explain the inverse relationship between LH concentrations during the later stages of lactation and the weaning to oestrus interval is that the hypothalamic–hypophyseal axis of some sows ‘escaped’ the negative-feedback effects of oestrogen earlier than others.

Since FSH concentrations were in the ‘normal’ range of the follicular phase before weaning it seems likely that these concentrations were sufficient to activate or maintain ovarian function during lactation provided the ovary was capable of responding to FSH, although the post-weaning rise in FSH in the majority of sows would suggest that, in general, lactation must exert a degree of inhibition on FSH secretion. A gradual elevation in FSH concentrations throughout lactation has been reported for the sow (Stevenson et al., 1981) and this would appear to be accompanied by a progressive increase in the number of large, healthy follicles (Kunavongkrit, Einarsson & Settergren, 1982), although ovulation is rarely attained until after weaning (see Edwards, 1982). However, the concentrations of FSH before and after weaning were unrelated to the interval from weaning to oestrus. In addition the weaning-associated rise in FSH did not appear to be a prerequisite for follicular growth and subsequent ovulation since 2 sows, that displayed oestrus and had ovulated by Days 3 and 6 after weaning, both failed to respond to weaning with an elevation in FSH values. Nevertheless, a positive correlation was established between the mean FSH:LH ratio and sow group categories for all periods; since there is reason to believe that FSH and LH may operate synergistically to control gonadal activity, this observation may be of considerable physiological significance. Certainly, FSH:LH ratios were shown to decrease in women 2 days before they were induced to ovulate with hCG at a time when oestradiol was rising (Yuen, Sy & Cannon, 1981). This observation may be due to the differential feedback effects of oestradiol on gonadotrophin secretion. An alternative explanation for a change in the relative proportion of LH and FSH concentrations in peripheral circulation observed just before ovulation may be a result of increasing GnRH stimulation. Wildt et al. (1981) reported that increasing GnRH pulse frequency caused a decrease in the FSH:LH ratio in rhesus monkeys. These findings are consistent with the lower FSH:LH ratios observed for sows in Group 1 compared with those in Groups 2 and 3. Furthermore, a relationship was apparent between ovulation rate and both peak levels of the weaning-associated rise in FSH and overall mean FSH concentrations. A similar relationship between FSH and follicular growth has been observed for hamsters (Greenwald, 1973), mice (Murr, Geschwind & Bradford, 1973) and sheep (Cahill et al., 1981). It is uncertain, however, whether the interval between the weaning-associated rise in FSH and ovulation is sufficient to recruit the ovarioly follicles. Follicular growth and ovulation have been reported to occur in the sow within 6–7 days after withdrawal of methallibre, an inhibitor of gonadotrophin secretion (Daguet, 1979). Therefore, after complete suppression of circulating gonadotrophins a rise in FSH (and/or LH) may be capable of recruiting and stimulating the early growth of follicles that ovulate about 1 week later and this may also be the case for the sow after weaning. FSH has been implicated in the prevention of atresia (Henderson, 1979) and this may be an alternative mechanism by which FSH acts to increase ovulation rate.

The possible inhibitory effects of prolactin and/or progesterone on gonadotrophin secretion or ovarian activity as a cause of delayed restoration of cyclicity in the post-weaning period seems
unlikely; as has previously been reported for weaned sows (Bevers et al., 1978; van Landeghem & van de Wiel, 1978; van de Wiel et al., 1979), prolactin decreased in all animals within 1–2 h after weaning. Similarly, progesterone levels were basal throughout lactation and the post-weaning period until about 30 h after the preovulatory LH surge, indicating that raised plasma progesterone values were not responsible for the prolonged interval to oestrus. These endocrine data, together with the absence of corpora lutea in ovaries examined at slaughter on Days 11 and 16 after weaning, show that sows that failed to display behavioural oestrus by this time had not experienced ‘silent heats’ as reported in other studies of primiparous sows (Love, 1979; Stork, 1979; Benjaminsen & Karlberg, 1981).

The present results would therefore suggest that although the majority of sows showed an elevation in both LH and FSH secretion after weaning the resumption of cyclicity is not solely dependent on the gonadotrophic response to weaning. Nevertheless, a specific pattern of LH secretion occurred in all sows showing an early return to oestrus (≤ 4 days) and may therefore be causally related to the timing of oestrus whilst the role of FSH in post-weaning fertility appears to be in the selection of the ovulatory follicles and in determining ovulation rate.

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