Hormonal and ovarian responses to a 5-day progesterone treatment in anoestrous dairy cows in the third week post-partum

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Abstract

Primiparous cows with low body condition at calving have an extended anovulatory period. Induction of ovulation and oestrus is possible with progesterone treatment but the response to this treatment differs between Friesian and Jersey breeds. The objective of this study was to describe changes in pulsatile LH secretion and the synchrony of developing ovarian follicles that occur during a progesterone treatment period of 5 days in primiparous anovulatory cows. The experimental model compared the progesterone treatment with spontaneous post-partum changes as well as a breed comparison in a factorial design.

Thirty-six cows (Jersey n = 19 and Friesian n = 17) were managed to calve with a low body condition score (BCS < 4.5). Daily changes in ovarian follicle size were observed with transrectal ultrasonography in each cow from 8 days post-partum. Thirty of these cows were diagnosed to be anovulatory at 12–18 days post-partum (day 0) and allocated to a treatment (n = 16) or a control group (n = 14), balanced for breed. Each treated cow had a progesterone-releasing controlled internal drug-releasing (CIDR) device inserted vaginally for 5 days while control cows were left untreated. Changes in plasma LH concentrations were measured with intensive blood sampling over 8 h on days 1, 1, and 4. Blood samples were also collected daily (06:00 h) for determination of plasma progesterone as well as oestradiol concentrations on days 6 and 8.

Treatment with progesterone was associated with a transient initial decrease day 1 in both LH pulse frequency and mean LH concentrations after device insertion, but both had returned to pre-treatment levels by day 4. Jersey cows had a greater pulse frequency, but there was no breed

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difference in mean LH concentrations. Patterns of ovarian follicle growth were affected by progesterone treatment with an increase in diameter of the dominant follicle (DF) identified after treatment initiation. This followed an earlier emergence of a new DF after device insertion. Follicular response to progesterone was dependent on the diameter of the DF present at treatment initiation. Those follicles ≥ 9 mm were replaced by a new DF during treatment such that the DF observed at the time of device removal was large (≥ 9 mm) and growing in 13/16 cases.

Progesterone was not effective for the induction of an LH surge, ovulation and oestrus in anovulatory cows with a low BCS. However, treatment was associated with synchronous development of a DF so that it was large and growing at the end of the treatment period in most cases. This synchronous development may be due to the transient suppression of LH and the presence of an LH-dependent DF.

Keywords: Cattle endocrinology; Progesterone; Ovarian follicles; LH; Oestradiol; Anoestrus

1. Introduction

It is common for cows in New Zealand to be anovulatory for at least the first 3 weeks post-partum (Fielden et al., 1973; McDougall et al., 1995a). The anovulatory period is extended for cows with a low body condition score (BCS) at calving and in primiparous cows (Grainger et al., 1982; McDougall et al., 1995a). Treatment of anovulatory cows to induce ovulation and oestrus at the start of the breeding period increases the proportion of the herd that is submitted for insemination (Macmillan, 1997). Currently recommended therapy involves the use of progesterone in a continuous dosage regimen for 5–8 days using a controlled internal drug-releasing (CIDR) device (Macmillan and Peterson, 1993).

Frequency of pulsatile secretion of LH increased with the use of continuous progesterone treatment for 5 days in the post-partum period (Macmillan et al., 1995). A spontaneous increase in LH pulse frequency had been observed during this period by Carruthers and Hafs (1980) and this was not taken into account in the study of Macmillan et al. (1995). The effect of progesterone on LH pulse frequency relative to spontaneous post-partum changes has not been measured.

Jersey and Friesian are the two most common dairy breeds in New Zealand. They differ in their interval from calving to first ovulation and oestrus, with the Jersey breed having the shorter intervals (McDougall, 1994). This has been associated with a greater LH pulse frequency in the post-partum period (Macmillan et al., 1995).

The hypothesis of this study was that the treatment of anovulatory cows with a progesterone treatment for 5 days would increase the mean concentration and frequency of pulsatile LH secretion relative to spontaneous changes in the corresponding post-partum period. In addition, there would be a greater increase in LH secretion in Jersey cows compared with Friesian cows. A second hypothesis was that the treatment of anovulatory cows with progesterone for 5 days would synchronise the follicle wave pattern, resulting in a large dominant follicle (DF) at the end of treatment. The effect of progesterone on follicle growth would be affected neither by the size of the DF at the start of treatment nor by breed. Consequently, there would be a greater incidence of ovulation after progesterone treatment than would occur spontaneously in untreated.
contemporaries. The cows, which did not ovulate after treatment, were also characterised according to LH pulse frequency and plasma oestradiol concentrations.

2. Materials and methods

2.1. Animals

Primiparous cows (17 Friesian, F; and 19 Jersey, J) calved in July and August, 1995 (mean calving date: 20 July ± 2 days) at 2 years of age were used. The cows used in the trial were anovulatory and did not have detectable pathology of the reproductive tract. The pre-partum ration was solely pasture with feed intake managed by regulating the area of grazing. Liveweight was measured weekly and BCS assessed to manage the feed intake so as the cows calved with a BCS of ≤ 4.5 (Macdonald and Macmillan, 1993). The serum copper, magnesium and selenium levels of each animal were monitored (Alpha Scientific, Hamilton, New Zealand). Those with marginal levels were treated at least 8 weeks pre-partum with sustained release rumen capsules. Experimental use of animals was approved by the Animal Ethics Committees of both AgResearch, Ruakura, and the University of Waikato, Hamilton, New Zealand.

2.2. Ultrasonography

The ovaries of each cow were observed daily by trans-rectal ultrasonography with a 7.5 MHz transducer. These observations were commenced from 8 to 10 days post-partum so as to characterise the growth pattern of large ovarian follicles. The description of all follicles by their size and location, and the definitions of a DF were as described by McDougall et al. (1995a). If ultrasonographic examination commenced after emergence of the first DF post-partum (DF1), the largest follicle present (that was ≥ 7 mm in diameter and at least 2 mm larger than the second largest follicle) was defined as the DF1. Subsequent DFs were described as the second DF post-partum (DF2), and the third DF post-partum (DF3) if they emerged before the first post-partum ovulation.

Cows were diagnosed as anovulatory at the commencement of treatment (day 0) if a new corpus luteum (CL) could not be identified. This definition incorporated the need to monitor the regressing CL of pregnancy. Daily ultrasonography continued until ovulation was confirmed by the presence of a newly formed CL, or until the identification of a recently emerged DF (> 7 mm) after the completion of the treatment period.

2.3. Experimental design

This study had a factorial design with main effects of breed (J and F) and progesterone treatment. Half the cows, within breed, were treated (T; day 0) with an intravaginal progesterone-releasing device (CIDR-B™, InterAg, Hamilton, New Zealand) for 5 days commencing 12–18 days post-partum. The remaining cows served as untreated controls (C). A jugular vein was cannulated on day −2 to facilitate regular blood sampling. Changes in LH secretion were measured in samples taken at 15-min
intervals for 8 h during the day before progesterone treatment (day −1), the day after insertion of the progesterone device (day 1), and the day before removal of the progesterone device (day 4). Blood samples were centrifuged at 1500 × g for 15 min and plasma stored at −20°C. Daily blood samples were collected at the time of ultrasonography (at 06:00 h) to determine plasma progesterone concentrations. A single blood sample was collected on days 6 and 8 to measure plasma oestradiol concentrations. Additional samples were collected from T-group cows at 4-h intervals from 16 to 84 h after device removal to detect a possible pre-ovulatory surge in LH secretion. Every control cow was blood-sampled daily at 06:00 h.

Tailpaint and a contrasting aerosol spray-paint were applied to the tailhead on days 0 and 5, respectively (as described by Macmillan et al., 1988) to aid the detection of oestrus. Changes in the coverage of paint were noted every 4 h from 06:00 h on day 6 to 18:00 h on day 9.

2.4. Hormone assay

A commercial kit (Coat-a-count, DPC, CA, USA) was used to measure progesterone directly in a solid phase, $^{125}$I-labelled radioimmunoassay as previously validated in our laboratory (McDougall et al., 1995b). Intra- and interassay coefficients of variance in standards of 0.4, 2.0 and 4.4 ng/ml were 11%, 8% and 6%, and 15%, 11% and 12%, respectively. The sensitivity of the assay was 0.08 ng/ml.

Concentrations of LH were measured in duplicate plasma samples by direct heterologous RIA using a second antibody precipitation technique (McDougall et al., 1995b). The assay measured ovine LH concentrations with a primary antibody raised in rabbits against ovine LH (R#2 antisera, AgResearch, Invermay, NZ) and a secondary antibody of sheep against rabbit gammaglobulins (AgResearch, Ruakura). Ovine LH for standards and iodination was given by NIH (NIH Lot No. AFP-7071B). Intra- and interassay coefficients of variance in standards of 0.3, 0.9, 2.8 and 10.6 ng/ml were 17%, 7%, 8% and 8%, and 19%, 9%, 9% and 9%, respectively. The sensitivity of the assay was 0.14 ng/ml.

Plasma oestradiol-17β (PE$_2$) concentrations were determined by a modified commercial kit RIA (Estradiol MAIA, Biodata Diagnostics, Rome, Italy). The kit utilised a double antibody magnetic separation technique where rabbit antisera were raised against oestradiol-17β as a primary antibody; and a secondary antibody consisted of goat antisera raised against rabbit gammaglobulins coupled to magnetic particles. Freeze-dried $^{125}$I-labelled oestradiol-17β and oestradiol-17β standards were also provided. The modified assay involved a similar protocol to Mann et al. (1995) and Prendiville et al. (1995). Intra- and interassay coefficients of variance in standards of 1.3, 5.7 and 16.0 pg/ml were 22%, 18% and 8%, and 24%, 23% and 10%, respectively. The sensitivity of the assay was 0.35 pg/ml.

2.5. Statistical analysis

LH data from serial sampling on days −1, 1 and 4 were analysed for pulsatile characteristics of mean and pulse frequency using a specialised software package.
Pulster, Objective Software, Sydney, Australia. This package used the pulsar algorithm described by Merriment and Wachter (1982). The ‘‘G parameters’’ were set as $G_1 = 3.8$, $G_2 = 2.6$, $G_3 = 1.9$, $G_4 = 1.5$, $G_5 = 1.2$. The precision profile was optimised with the coefficient of variation (CV) option as $\text{LH(CV)} = 19.4\pm 18.9$ LH (Mean).

Breed differences in liveweight and BSC at calving were analysed by Student’s t-test. Categorical data were analysed by chi-square methods, both in an Excel spreadsheet (Microsoft, USA) and by the SAS CATMOD procedure (SAS Institute, Cary, USA). Continuous data were analysed by the general linear model (GLM) option of SAS v6.10 (SAS Institute, Cary, USA), or Minitab v10.51Xtra (Minitab, PA, USA). If measurements were repeated over time, a split plot GLM was used. Each result is presented as mean ± SEM, unless stated.

3. Results

3.1. Animals

The F cows were heavier at calving ($340 \pm 11$ vs. $298 \pm 9$ kg; F vs. J; $p < 0.01$) and had a greater BCS ($4.6 \pm 0.07$ vs. $4.4 \pm 0.05$; F vs. J; $p < 0.05$). One cow was diagnosed with metritis and excluded from the trial. Four J cows were also excluded as they ovulated their first DF before treatment allocation. An additional J cow allocated to the control group ovulated on day 2. No F cows ovulated before or during the treatment period. With these exclusions, there were eight treated and eight control F cows, and eight treated and six control J cows. These numbers were the effective $n$ for all variables tested.

3.2. Plasma progesterone concentrations

Progesterone was not detected in any samples obtained before insertion of a CIDR device on day 0 and control cows had low plasma progesterone ($<0.08$ ng/ml) throughout the entire sampling period. Concentrations increased rapidly after device insertion, reaching a plateau of $2.8 \pm 0.15$ ng/ml by 45 min and with no further increase in the next 5 h. The mean daily plasma progesterone concentrations were greatest on day 1 ($4.0 \pm 0.07$ ng/ml; $p < 0.05$), then decreased on day 4 ($2.6 \pm 0.1$ ng/ml; $p < 0.01$), with no difference between days 4 and 5 ($2.6 \pm 0.14$ vs. $2.5 \pm 0.14$ ng/ml). Concentrations had returned to baseline ($0.13 \pm 0.07$ ng/ml) within 4 h after device removal. There was no breed effect on mean plasma progesterone concentrations during device insertion ($3.3 \pm 0.15$ vs. $3.0 \pm 0.18$ ng/ml; J vs. F).

3.3. Pulsatile LH concentrations

Representative profiles of LH concentrations on days −1, 1, and 4 are presented for J cows (Fig. 1) and F cows (Fig. 2). Analysis of pulsatile LH data showed a significant effect of breed and treatment on LH pulse frequency ($p < 0.05$), but only a treatment effect on mean concentrations ($p < 0.05$). The breed by treatment interaction was not
significant for either LH mean or frequency. Data presented are for the main effects only.

Overall frequency of pulsatile LH secretion was greater for J (2.5 ± 0.3 pulses/8 h) than F cows (1.4 ± 0.3 pulses/8 h; \( p < 0.05 \)). Pulse frequency was reduced in both breeds on day 1 compared with days −1 and 4 (Table 1). Mean LH concentrations were
Fig. 2. Typical profiles of LH concentrations for (a) a Friesian heifer (#3780) in the control group and (b) a Friesian heifer (#3805) in the treated group.

not affected by breed (0.27 ± 0.02 vs. 0.24 ± 0.02 ng/ml; J vs. F). Treatment significantly decreased mean LH concentrations on day 1 (0.18 vs. 0.27; SED 0.01; p < 0.05) compared with days −1 (0.27 vs. 0.27; SED 0.01) and 4 (0.26 vs. 0.28; SED 0.01).

3.4. Ovarian follicle dynamics

Observations of ovarian follicles before 12 days post-partum were incomplete in some cows due to the difficulty in locating ovaries with the uterus still enlarged. Many
Table 1
The effect of breed and progesterone treatment on the frequency of LH pulses (mean pulses/8 h) on the day before progesterone treatment (day 1), the day after the insertion of the progesterone device (day 1) and the day before removal of the progesterone device (day 4)

<table>
<thead>
<tr>
<th>Day</th>
<th>Control</th>
<th>Treated</th>
<th>J</th>
<th>F</th>
<th>J+F</th>
<th>J</th>
<th>F</th>
<th>J+F</th>
</tr>
</thead>
<tbody>
<tr>
<td>-1</td>
<td>3.0 a</td>
<td>1.0 b</td>
<td>2.0 d</td>
<td>3.1 a</td>
<td>1.5 b</td>
<td>2.3 d</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>2.8 a</td>
<td>1.5 b</td>
<td>2.2 d</td>
<td>0.6 c</td>
<td>0.5 c</td>
<td>0.6 e</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>2.5 a</td>
<td>1.9 b</td>
<td>2.2 d</td>
<td>2.9 a</td>
<td>2.0 b</td>
<td>2.4 d</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SEM</td>
<td>0.57</td>
<td>0.49</td>
<td>0.38</td>
<td>0.49</td>
<td>0.49</td>
<td>0.35</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a, b, c, d, and e refer to differences within treatment where \( p < 0.05 \).

DF1 were already large and in a plateau stage of development. Subsequent post-partum DFs (DF2 and DF3) were observed from emergence.

3.4.1. Breed effect on post-partum follicle development
The pattern of follicular development differed between breeds for the DF1 and DF2. The DF1 was larger at 8 days post-partum for J cows (9.1 ± 0.68 vs. 6.8 ± 0.68 mm; J vs. F; \( p < 0.02 \)) and reached its maximum diameter earlier (10.5 ± 0.8 vs. 12.6 ± 0.7 days post-partum; J vs. F; \( p < 0.05 \)). Thus, the post-partum follicle development was earlier in the Jersey breed than the Friesian breed.

Maximum diameter of DF1 was not different among breeds or treatment groups (Table 2; \( p > 0.1 \)). The DF2 emerged earlier in J cows (10.4 ± 0.68 vs. 13.1 ± 0.62 days post-partum; J vs. F; \( p < 0.02 \)) resulting in a larger mean DF2 diameter from 11 to 18 days post-partum for the J cows. The increase in maximum diameter between DF2 and DF1 was greater in the J cows (\( p < 0.05 \); Table 2).

3.4.2. Breed effect on the DF at the start of progesterone treatment
As the emergence of DF2 was earlier for the J breed, there was a predominance of DF2 compared with DF1 on the first day of progesterone treatment for the J cows, compared with a similar distribution of DF2 and DF1 for the F cows (12 vs. 2 and 9 vs. 7, respectively; \( p < 0.02 \)). To account for the variation of the DF at the time of

Table 2
The effect of breed and treatment on the mean maximum size of DF1 and DF2, and the difference (increase) in the size of the successive DF

<table>
<thead>
<tr>
<th>Breed</th>
<th>Control</th>
<th>Treated</th>
<th>Combined</th>
<th>Control</th>
<th>Treated</th>
<th>Combined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jersey</td>
<td>11.2 (1.3)</td>
<td>10.3 (1.1)</td>
<td>10.7 (0.8)</td>
<td>12.4 (1.1)</td>
<td>12.9 (1.1)</td>
<td>12.6 (0.8)</td>
</tr>
<tr>
<td>Friesian</td>
<td>13.2 (1.1)</td>
<td>14.1 (0.9)</td>
<td>13.6 (0.7)</td>
<td>12.8 (0.9)</td>
<td>13.9 (0.9)</td>
<td>13.3 (0.6)</td>
</tr>
<tr>
<td>Difference</td>
<td>2.0</td>
<td>3.8</td>
<td>2.9 (0.8)</td>
<td>0.4</td>
<td>1.0</td>
<td>0.7 (0.8)</td>
</tr>
</tbody>
</table>

a and b refer to significant differences within each row (\( p < 0.05 \)).
treatment, two DFs were identified. The DF observed at the time of treatment (day 0)
was identified as DF₀, and the DF observed after treatment (day 6) as DF₆.

3.4.3. Follicle development relative to the time of treatment
The size of the DF₀ on day 0 was a significant indicator of subsequent follicle
dynamics. If the DF₀ on day 0 was at least 9 mm, then a new DF was observed by the
time of device removal in every one of the nine T cows compared with 4/9 C cows
(\( p < 0.01 \)). If the DF₀ on day 0 was at < 9 mm, then a new DF was observed by the
time of device removal in only 1/7 T cows compared with 2/5 C cows. Associated
with the consistent loss of dominance of a large DF₀ in T cows was the earlier
emergence of DF₆ (day 0.7 ± 0.54 vs. day 3.7 ± 0.56; T vs. C; \( p < 0.01 \)). The DF₆ was
≥ 9 mm for at least 40 h after device removal in 13/16 T cows (solid line plots)
compared with 2/14 C cows (dashed plots; \( p < 0.05 \)).

The three T cows that did not have a large follicle were Friesian. They did not have a
single pulse of LH in the 8-h sampling period on days 1 and 4. Two of these cows had a
large DF at the time of device insertion, but a new DF did not emerge until days 3 and 4
resulting in a smaller, growing DF at device removal. The third cow did not have a
follicle > 9 mm throughout the entire experimental period.

3.5. PE₂ concentrations
PE₂ concentrations did not differ on days 6 and 8 (Table 3). A difference in PE₂
between breeds was observed (\( p < 0.01 \)), but there was no treatment effect, nor a breed
by treatment interaction. Regression analyses of the PE₂ on day 6 showed an increase
with a larger-diameter DF₆ (\( p < 0.05 \)), and a greater plasma concentration in the J cows
than F cows; but there was no treatment effect. The revised regression model (\( R² =
39.5\% \); \( p < 0.05 \)) is plotted in Fig. 3. The regression equation was (PE₂ on day
6) = 1.10 + 0.0813 (DF₆ on day 6) − 0.705(Breed), where Jersey = 0 and Friesian = 1.

3.6. Response to treatment
A surge in LH concentration, ovulation and oestrus was observed in only two treated
J cows and one control J cow. Cows that ovulated tended to have a greater pulse

<table>
<thead>
<tr>
<th>Day</th>
<th>Jersey Control</th>
<th>Jersey Treatment</th>
<th>Jersey Mean</th>
<th>Friesian Control</th>
<th>Friesian Treatment</th>
<th>Friesian Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>1.7 (0.3)</td>
<td>2.3 (0.3)</td>
<td>2.1 (0.2)*</td>
<td>1.1 (0.4)</td>
<td>1.2 (0.4)</td>
<td>1.2 (0.3)*</td>
</tr>
<tr>
<td>8</td>
<td>2.2 (0.3)</td>
<td>1.8 (0.3)</td>
<td>2.0 (0.2)*</td>
<td>1.1 (0.4)</td>
<td>1.3 (0.4)</td>
<td>1.2 (0.3)*</td>
</tr>
<tr>
<td>Mean</td>
<td>2.0 (0.3)</td>
<td>2.0 (0.2)</td>
<td>2.0 (0.2)*</td>
<td>1.1 (0.2)</td>
<td>1.3 (0.2)</td>
<td>1.2 (0.2)*</td>
</tr>
</tbody>
</table>
Fig. 3. The relationship between DF diameter and plasma oestradiol concentration on day 6. The fitted regression model: \( y = 1.10 + 0.0813x - 0.705\text{Breed} \), where Jersey = 0 and Friesian = 1 \( (R^2 = 39.5\%; \ p < 0.05) \).

frequency on day 1 (1.8 ± 0.28 vs. 3.5 ± 1.01 pulses/8 h; \( p < 0.15 \)). An LH surge was not detected for cows that did not ovulate.

4. Discussion

This study is the first to demonstrate the transient suppression of LH during progesterone treatment in anovulatory cows. This transient suppression was consistent in two breeds that had differing frequencies of LH secretion and was associated with the loss of dominance of all DF \( \geq 9 \) mm present at treatment initiation. This resulted in a synchronous emergence of a DF that was observed to be \( > 9 \) mm at the end of progesterone treatment in most cases.

The transient suppression of LH measured on day 1 was similar to observations in ovariectomised cattle by Burke et al. (1996). They showed a transient suppression of LH with exogenous progesterone treatment, but a prolonged LH suppression with a combined progesterone and oestradiol treatment. The numbers of oestradiol receptors in the hypothalamus were reduced after progesterone treatment in pre-pubertal anoestrous heifers (Day and Anderson, 1998).

The time post-partum had no effect on LH secretion patterns in the control cows. Although LH pulse frequency has been observed to increase with time post-partum (Carruthers and Hafs, 1980), the present study may differ as the cows were of low body condition with a low initial LH pulse frequency. Also the difference was only measured over a 5-day period.

Follicle growth patterns were altered resulting in a large pre-ovulatory follicle in most treated cows after device removal. Large follicles \( (\geq 9 \) mm) lost dominance after
treatment, which was associated with the transient decrease in LH secretion at this time. The change in LH secretion after device insertion did not affect the dominance of small follicles (< 9 mm). Treatment may have extended the life of the DF2, as they were larger between 20 and 21 days post-partum, and the emergence of DF3 tended to be later. The combination of earlier emergence of a new DF after device insertion and the larger size of follicles that did not regress resulted in the increase in large follicles after device removal.

This study supports the theory that follicles ≥ 9 mm are dependent on LH for further growth and development (Ginther et al., 1996; Gong et al., 1996). This relationship is remarkable in the present study, as many of the anoestrous heifers (particularly of Friesian breed) continued to develop a DF > 9 mm in an environment where there was only one pulse of LH in an 8-h sampling period, but follicles > 9 mm lost dominance at the start of progesterone treatment.

The current study has also demonstrated an increase in plasma oestradiol concentrations in the Jersey breed compared with the Friesian breed after a 5-day progesterone treatment in the post-partum period (Table 3). This observation concurs with the hypothesis that the transition from anoestrus to regular oestrous cycles is associated with a decline in negative feedback of oestradiol on GnRH and consequently LH secretion (Roche et al., 1981; Kinder et al., 1987). These endocrine differences may be associated with the breed differences observed in the interval from calving to first ovulation and first oestrus (McDougall, 1994). This variation in endocrine environment was also associated with differences in follicle populations, with an earlier day of maximum size of the DF1 and DF2 for the Jersey breed, the earlier day of emergence of the DF2, and a greater increase in the maximum size of the DF2 compared with DF1. A breed difference has also been observed in the post-partum interval where the distribution of DF favours the side opposite that of the preceding pregnancy (Nation et al., 1999).

The increase in the occurrence of large DFs after progesterone treatment did not result in a corresponding increase in post-treatment plasma oestradiol concentrations. This is in contrast to what might be expected in the follicular phase of a spontaneous oestrous cycle (Chenault et al., 1975; Glencross et al., 1981; Zelinski et al., 1982). Without elevated oestradiol concentrations, positive feedback on LH secretion did not eventuate in most cows; thus, a surge in LH secretion and ovulation did not occur.

A surge in LH secretion can be induced during the post-partum period with exogenous GnRH, indicating that the pituitary should be responsive in a pro-oestrus environment (McDougall et al., 1995b). Exogenous oestradiol can also induce a surge in LH secretion associated with ovulation (Radford et al., 1978). While exogenous oestradiol successfully induces ovulation, the lack of endogenous oestradiol secretion from the large follicles that were observed in this study might reflect the abnormal maturation of the oocyte and subsequent lack of fertility if ovulation is induced.

Progestosterone treatment alone was not effective in the induction of an LH surge, ovulation and oestrus. This treatment response has emphasised the need for a combination treatment that induces ovulation and oestrus with the resumption of regular oestrous cycles. The predominance of large DF after progesterone treatment as has been observed to occur in most cases in this study may be a key requirement for the success of a subsequent induction of ovulation.
Progesterone treatment alone was insufficient in restoring the reproductive endocrine axis of anoestrous cows to that of cycling cows. In addition to the treatment effects, there were also breed effects with Jersey cows having a greater LH pulse frequency, earlier follicle development of DF1 and DF2, and greater plasma oestradiol concentrations after treatment.

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