Some endocrine changes associated with the post-partum period of the suckling beef cow

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Summary. Seven Hereford cows with single calves were bled by jugular venepuncture, daily from parturition until 63–79 days *post partum*; 6 of the cows were also bled through jugular cannulae every 15 min for 8 h every 10 days. The average post-partum interval to first oestrus was 59.8 ± 3.7 days for 5 of the cows. In cows returning to oestrus, plasma concentrations of progesterone were low until 55.5 ± 3.0 days *post partum*, rose to exceed 0.5 ng/ml plasma for 4.0 ± 0.4 days, declined for 5.0 ± 0.5 days and then rose again to normal luteal-phase levels. First oestrus preceded the initial rise in progesterone in 1 cow and followed it in 4. Ovarian palpation revealed considerable follicular development before the initial rise in progesterone, but no clearly discernable corpus luteum until normal luteal-phase progesterone levels were detected. Plasma concentrations of oestradiol-17 β fell after parturition and, although very variable, showed no apparent trend thereafter. Plasma concentrations of LH varied in an episodic manner, with an apparent increase in frequency and magnitude of peaks up to 10–33 days before the first elevation in plasma progesterone. Subsequently there was little change, except for a decline in peak LH concentrations after the initial elevation in plasma progesterone.

Introduction

Following parturition in the cow there is a significant period of anoestrus, of variable length (Morrow, Roberts & McEntee, 1969). This period of reproductive inactivity is longer in the suckling or intensively milked animal (Morrow *et al.*, 1969; Short, Bellows, Moody & Howland, 1972). In the suckling beef cow post-partum anoestrus can be <50 days or >90 days (Morrow *et al.*, 1969), and an excessively long anoestrus creates managerial problems if a calf crop per year is expected. Follicular development is apparently depressed in the post-partum cow and recovers at a variable rate, again being slowest in the suckling cow (Wagner & Oxenreider, 1971), and ovulation can often occur initially without any external manifestations of oestrus (Saiduddin, Riesen, Tyler & Casida, 1968). Post-partum anoestrus is not a result of the maintenance of the corpus luteum of pregnancy (Labhsetwar, Collins, Tyler & Casida, 1964) and uterine involution, although difficult to assess, would appear to occur rapidly after parturition (Wagner & Hansel, 1969).

The endocrinology of the post-partum anoestrus is not well understood; pituitary follicle-stimulating hormone (FSH) concentrations appear to be highest at calving and then decline (Labhsetwar *et al.*, 1964), whereas pituitary LH concentrations tend to rise (Saiduddin *et al.*, 1968). Arije, Wiltbank & Hopwood (1974) investigated the temporal pattern of concentrations of several hormones in jugular plasma in post-partum suckling beef cows. Progesterone concentrations were low *post partum* and LH concentrations, although low

initially, showed periodic fluctuations, culminating eventually in a preovulatory surge. Other workers have shown for dairy and beef cattle that serum concentrations of oestrogen are low after parturition (Smith, Edgerton, Hafs & Convey, 1973; Corah, Quealy, Dunn & Kaltenbach, 1974) and that progesterone concentrations may in fact rise before first oestrus (Pope, Gupta & Munro, 1969; Donaldson, Bassett & Thorburn, 1970; Lamming & Bulman, 1976; Webb, Lamming, Haynes, Hafs & Manns, 1977; Schams *et al.*, 1978). Recent evidence suggests that plasma concentrations of LH *post partum* may vary in an episodic pattern with increasing frequency of elevations of LH concentration as first ovulation approaches (Stevenson & Britt, 1979).

The purpose of the present study was to correlate the recovery of ovarian activity, the occurrence of first oestrus and the temporal patterns of plasma concentrations of LH, oestradiol-17 β and progesterone during the post-partum period in the suckling beef cow.

Materials and Methods

Seven Hereford cows, each suckling a single calf, were bled daily by jugular venepuncture for 63–79 days, starting on the day of parturition. At approximately 10-day intervals, blood samples were taken every 15 min for 8 h (08:30–16:30 h) from 6 of the 7 cows, using indwelling jugular cannulae. Ovarian palpation *per rectum* was performed every 2–5 days, starting at approximately 25 days *post partum*. The cattle were kept at pasture during the study and were weighed every 2 weeks; the calves accompanied the cows at all times. The first occurrence of oestrus was detected by the exposure of a Kamar heat mount detector by a bull.

Assays

All blood samples were centrifuged immediately and heparinized plasma was stored at -15°C until assayed. Plasma samples were analysed by established radioimmunoassays (Rawlings, Kennedy, Chang, Hill & Henricks, 1977) for LH, progesterone and oestradiol-17 β .

LH was measured in a double-antibody assay, established for bovine and ovine LH, that utilized an anti-ovine LH serum that cross-reacts with bovine LH (GDN-15; Niswender, Reichert, Midgley & Nalbandov, 1969). Highly purified bovine LH (LER-1716-2) was iodinated by the method of Greenwood, Hunter & Glover (1963) and NIH-LH-B7 was used as the bovine LH reference preparation. Duplicate determinations were made for all samples using 200 μl plasma. The assay standard curve ran from 0.08 to 20 ng per assay tube, giving a sensitivity of 0.40 ng/ml plasma, i.e. the lowest concentration of unlabelled LH that significantly displaced labelled LH ($P < 0.05$). The inter-assay coefficient of variation was 16% ($n = 17$).

Progesterone was extracted from plasma with petroleum ether and the extracts were assayed directly using an antiserum specific for progesterone (HD-RC-4/10/73; Rawlings *et al.*, 1977). Duplicate determinations were made for all samples using 200 μl plasma and all determinations were corrected for procedural losses. The assay standard curve ran from 31 to 500 pg per assay tube and assay sensitivity was thus 155 pg/ml plasma. The average extraction efficiency was $90 \pm 1.9\%$ (s.e.m., $n = 23$), the assay blank was 24.4 ± 9.2 pg ($n = 5$)/tube and the inter-assay coefficient of variation was 8.5% ($n = 21$).

Oestradiol-17 β was extracted from plasma with diethyl ether and the extracts were assayed directly using an antiserum that had a 9% cross-reaction with oestrone, but $<0.01\%$ with oestriol, oestradiol-17 α and all other steroids tested (NCR-8145; Rawlings *et al.*, 1977). Duplicate determinations were made for all samples using 1 ml plasma and all estimations were corrected for procedural losses. The assay standard curve ran from 2.50 pg to 40 pg per assay tube, giving a sensitivity of 2.50 pg/ml plasma. The average extraction efficiency was $82 \pm 1.5\%$ ($n = 33$), the assay blank was 0.6 ± 0.33 pg ($n = 21$)/tube and the inter-assay coefficient of variation was 21.5% ($n = 12$).

Text-fig. 1. Peripheral plasma concentrations of LH (—), oestradiol-17 β (· · ·) and progesterone (—) for 6 suckling cows. Day 0 is the 2nd day of the first period when plasma progesterone exceeded 0.5 ng/ml for 3 consecutive days. Arrows indicate days of intensive bleeding; O indicates first oestrus.

Analyses

All data summaries are expressed as means with s.e.m. Analysis of variance and Duncan's multiple range test, both modified if appropriate for unequal numbers (Steele & Torrie, 1960) were used to examine the results statistically. To examine the apparent episodic nature of LH secretion, peaks in concentration of LH in plasma were defined as values greater than the mean plus twice the standard error of the mean.

Results

The average body weights for the 7 cows studied were 480 ± 11 kg when weighed within 1 week before calving, 432 ± 8 kg within 3 days after calving, 423 ± 8 kg at 11–28 days after calving

Table 1. The number and height of peaks of LH over 10-day intervals in 6 cows returning to oestrus after parturition

	Days –50 to –40	Days –39 to –30	Days –29 to –20	Days –19 to –10	Days –9 to –10	Days 1 to 10
Peak height (ng/ml)	4.8 ± 2.8	5.9 ± 1.55	14.9 ± 7.24	7.4 ± 1.09	9.8 ± 1.18	7.9 ± 1.15
No. of peaks	0.3 ± 0.21	1.0 ± 0.37	1.0 ± 0.63	$3.3 \pm 0.72^*$	4.3 ± 0.92	3.5 ± 0.67

Values are mean $\pm$ s.e.m.

The data are centered around the first period when serum concentrations of progesterone exceeded 0.5 ng/ml for 3 consecutive days; Day 0 is the 2nd day of such a period.

* Significantly different from each of the previous 3 observations.

Table 2. Structures detected by palpation *per rectum* in the right (R) and left (L) ovaries of suckling beef cows

Days*	Cow 119		Cow 120		Cow 108		Cow 132		Cow 149		Cow 163	
	L	R	L	R	L	R	L	R	R	L	R	L
–40 to –35	Fs	Fs	Fs	Fs	Fs	Fs	Fs		—†	—†	—†	—†
–35 to –30			Fm						—†	—†	—†	—†
–30 to –25	Fm				Fs	Fm		Fm	Fm			
–25 to –20			Fm			Fl			Fm		Fvl	
–20 to –15				Fm		Fm					Fl	
–15 to –10		Fl		Fm	Fvl	Fvl			Fvl			
–10 to –4				Fvl	Fvl	Fm	Fm	Fm	Fm		Fvl	Fl
–5 to 0	Fm		Fm§		Fs	Fl		Fl	Fvl		Fl	
0 to +5	Fs	Fs	CLm		§	Fl		Fl	Fvl§		Fm	Fm
+5 to 10	Fs§	Fl	CLm		Fl		Fl		CLs		§	
+10 to +15		CLI	CLI		—†	—†	—†	—†	CLvl		CLm	Fl

CL = corpus luteum; F = follicle; s $\leq$ 0.2 cm, m $\leq$ 0.6 cm, l $\leq$ 1.0 cm, vl $\leq$ 2.0 cm diameter.

* Day 0 = 2nd day of first 3 days of progesterone > 0.5 ng/ml.

† Not palpated.

§ Time of first oestrus.

Table 3. The number and height of peaks of LH during periods of intensive bleeding occurring during the periods indicated for 5 cows returning to oestrus after parturition

	Days -53 to -49	Days -43 to -38	Days -33 to -28	Days -23 to -18	Days -12 to -7	Days -3 to 2
Peak height (ng/ml)	3.0 ± 0.44	3.8 ± 0.58	6.2 ± 0.60*†	6.8 ± 0.61	6.1 ± 0.78	2.3 ± 0.17*
No. of peaks	4.5 ± 1.19	5.8 ± 1.00	9.2 ± 0.37*	7.2 ± 0.80	8.2 ± 1.02	8.8 ± 1.75

Day 0 = 2nd day of first 3 days when progesterone > 0.5 ng/ml.

* Significantly different from the previous observation.

† Significantly different from the value at Days -53 to -49.

Text-fig. 2. Peripheral plasma concentrations of LH (---), oestradiol-17β (....) and progesterone (—) for one representative cow (No. 149) bled every 15 min for 8 h on the days indicated. Day 0 is the 2nd day of the first rise in plasma progesterone by > 0.5 ng/ml.

and 429 ± 21 kg at 32–49 days after calving. Five cows were detected in oestrus, with an average post-partum interval to first oestrus of 59.8 ± 3.7 days. Cow 132 lost her Kamar detector just before an apparent oestrus and Cow 134 was not detected in oestrus by 77 days *post partum*. The concentrations of LH, progesterone and oestradiol-17 β for 6 of the cows are shown in Text-fig. 1. In the 6 cows that returned to oestrus, plasma concentrations of progesterone were low until 55.5 ± 3.0 days *post partum*, rose to exceed 0.5 ng/ml plasma for 4.0 ± 0.4 days, declined for 5.0 ± 0.5 days and rose again to normal luteal-phase levels. Progesterone levels remained low in Cow 134, that failed to return to oestrus. In the 5 cows in which the time of first oestrus was accurately determined, the initial elevation in plasma concentration of progesterone preceded first oestrus in 4 and followed it in 1. As the initial increase in plasma concentration of progesterone was such a consistent finding, and as the concomitant return to reproductive cyclicity was the event of primary interest, the data in Text-fig. 1 have been centered (Day 0) around the second consecutive day of the first period in which plasma concentrations of progesterone exceeded 0.5 ng/ml for at least 3 days.

Plasma concentrations of oestradiol-17 β declined after parturition and were subsequently quite variable in all cows studied, no apparent trend could be detected. Plasma concentrations of LH changed significantly during the period of the study ($P < 0.005$) and an episodic mode of secretion seemed likely. Taking the average values over periods of 10 days for the 6 cows that returned to oestrus, the pattern shown in Table 1 emerged.

Table 2 shows the ovarian structures palpable *per rectum* for the 6 cows that returned to oestrus during the study. Although variable, the data indicated an increased production of medium-sized and large follicles as the first oestrus and return to reproductive cyclicity approached. No correlation of follicular patterns and the concentration of oestradiol-17 β in plasma was apparent. No corpora lutea were detected with any assurance until after first oestrus, when plasma concentrations of progesterone rose to normal luteal phase levels. However, prior to first oestrus and during the first phase of elevated plasma concentrations of progesterone, the presence of an early corpus luteum was suspected in Cows 108, 149 and 163.

Of the 6 cows that were bled intensively every 10 days *post partum*, Cows 108, 119, 120, 132 and 149 returned to oestrus during the study: the results for Cow 149 are shown in Text-fig. 2 as representative. Plasma concentrations of progesterone were low and stable during all periods of intensive blood sampling, except those that coincided with the periods of elevated plasma concentrations of progesterone described in Text-fig. 1. Plasma concentrations of oestradiol-17 β were quite variable within and between the periods of intensive bleeding, but no significant trend could be detected. The pattern of plasma concentrations of LH suggested an episodic mode of secretion (Table 3).

Discussion

The decline in plasma concentrations of oestradiol-17 β following parturition and the subsequent levels of oestradiol-17 β resemble previous observations (Henricks, Dickey, Hill & Johnston, 1972; Hoffmann *et al.*, 1973; Smith *et al.*, 1973; Arije *et al.*, 1974; Corah *et al.*, 1974). The variability of plasma concentrations of oestradiol-17 β in samples taken daily and more intensively may well be due to the increasing, but variable, follicular growth observed *post partum*. However, no significant relationship emerged between the pattern of palpable ovarian follicles and plasma concentrations of oestradiol-17 β . A variable pattern of follicular growth and atresia (Morrow *et al.*, 1969) and plasma concentrations of oestradiol (Echternkamp & Hansel, 1973) have been previously reported in the post-partum cow. As has been previously reported (Donaldson *et al.*, 1970; Arije *et al.*, 1974; Corah *et al.*, 1974; Lamming & Bulman, 1976; Webb *et al.*, 1977; Schams *et al.*, 1978), plasma concentrations of progesterone were low after parturition, but the transient rise in progesterone concentration that has been previously

suggested to occur before the first normal luteal phase was very clearly confirmed in the present study. All 6 of our cows returning to oestrus exhibited this early elevation of plasma progesterone and oestrus followed it in 4 of 5 cows. The consistency of this elevation of progesterone in terms of length, magnitude and occurrence with respect to first oestrus and the first normal luteal phase is striking. Palpation of the ovaries did not clearly indicate the occurrence of ovulation and the formation of a corpus luteum until the time that plasma progesterone levels resembled those of a normal luteal phase. There were apparently many large follicles present at the time of the early elevation of progesterone and it is possible that luteinized follicles (Corah *et al.*, 1974) were the source of progesterone, or that ovulation took place and that an abnormal, short-lived and sub-functional corpus luteum developed.

Plasma LH concentrations clearly increased over the post-partum period and although some variability in pattern was observed the increase was due to a modulation of the number and magnitude of the LH peaks. Maximum magnitude and frequency of LH peaks occurred about 33–10 days before the initial elevation of plasma progesterone, i.e. when there was a marked development of large follicles and large variations of oestradiol-17 β . During the period from the early progesterone elevation through first oestrus and the onset of the first normal luteal phase, the average peak concentrations of LH in plasma tended to decline. In the dairy cow and the suckling beef cow an increase in episodic secretion of LH before first ovulation has been reported (Arije *et al.*, 1974; Stevenson & Britt, 1979), but is not consistently noted (Schams *et al.*, 1978). Pituitary LH stores appear to increase *post partum* (Saiduddin *et al.*, 1968) and FSH stores decline (Labhsetwar *et al.*, 1964). In dairy cattle plasma FSH concentrations have been reported to rise initially *post partum*, declining to first oestrus (Dobson, 1978), or to exhibit no change (Schams *et al.*, 1978). If an extrapolation from the dairy cow to the longer post-partum period of the suckling beef cow can be made, it would appear that plasma FSH concentrations may behave in a similar pattern to those of LH observed in the present study (Dobson, 1978). It is apparent that lactation, and especially suckling with lactation, prolong post-partum anoestrus (Short *et al.*, 1972). In the rat lactation suppresses LH and FSH secretion (Smith & Neill, 1977). Therefore, following parturition and under the suppressive effect of lactation, gonadotrophin secretion appears to recover gradually in suckling beef cows, culminating in the luteinization of large ovarian follicles, or possibly in ovulation and the formation of subnormal, short-lived corpora lutea.

The exact endocrine mechanisms that are needed to permit ovulation are unclear. After the initial rise in plasma progesterone and with the recurrence of cyclicity in the suckling beef cow, plasma LH concentrations appear to decline and resemble more closely the basal values of the cyclic cow (Henricks, Dickey & Niswender, 1970). Plasma concentrations of oestradiol-17 β do not clearly change at this time, indicating that progesterone may have an organizing effect on gonadotrophin secretion, as it appears to do in the cyclic ewe (Hauger, Karsch & Foster, 1977), and may also be necessary to programme the resumption of behavioural oestrus (Lindsay, 1966). In the ewe, changes in the negative feedback effects of oestradiol-17 β on LH secretion may be important in controlling the seasonality of breeding activity. However, in the lactating post-partum ewe changes in this interaction are not observed (Legan, Karsch & Foster, 1977; Foster, 1979). In cattle, the source of the early elevation of plasma concentrations of progesterone is unclear, and the exact mechanism that stimulates and controls the duration of its secretion is also unknown. This transient rise in plasma progesterone concentration may be critical in reorganizing the ovarian-pituitary-hypothalamic axis after parturition (Webb *et al.*, 1977).

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