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Pattern of follicular growth and resumption of ovarian activity in post-partum beef suckler cows*

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Summary. The ovaries of 18 post-partum beef suckler cows were examined daily, using ultrasound, from Day 5 *post partum* until a normal oestrous cycle was completed. Periods of growth and regression of medium-sized (5–9 mm) follicles were identified before one medium follicle became dominant (single large follicle ≥ 10 mm). The mean (± s.e.m.) number of days from parturition to detection of the first post-partum dominant follicle was 10·2 ± 0·5. The first post-partum dominant follicle ovulated in 2/18 (11%) cows. The interval from calving to first ovulation (mean ± s.e.m. = 35·9 ± 3·3 days) was characterized by the growth and regression of a variable number (mean = 3·2 ± 0·2; range 1–6) of dominant follicles. The maximum diameter of the dominant follicle increased as the cows approached first ovulation ($P < 0·05$). Behavioural oestrus was not detected in 16/18 (89%) cows at first ovulation. Following first ovulation, the length of the subsequent cycle was short (mean = 9·7 ± 0·5 days; range 8–15 days) in 14/18 (78%) cows and was characterized by the development and ovulation of a single dominant follicle. During oestrous cycles of normal length (mean = 20·6 ± 0·5 days; range 18–23 days) one (N = 2), two (N = 7) or three (N = 8) dominant follicles were identified. The growth rate, maximum diameter or persistence of non-ovulatory dominant follicles before first ovulation or during oestrous cycles were not different ($P > 0·05$). These data show that, in beef suckler cows, follicular development and formation of a dominant follicle occur early after parturition and the incidence of ovulation of the first dominant follicle is low. The number of dominant follicles that develop before first ovulation is variable; first ovulation is rarely associated with oestrus and short cycles are common after first ovulation. It is concluded that prolonged anoestrus in post-partum beef suckler cows is due to lack of ovulation of a dominant follicle rather than delayed development of dominant follicles.

Keywords: follicle; *post partum*; beef suckler; cow; ultrasound

Introduction

The patterns of follicular development in the early post-partum period of beef cows that are nursing calves are not well understood, despite the fact that such cows have a prolonged interval from calving to first ovulation (Wiltbank & Cook, 1958; Casida *et al.*, 1968; Oxenreider, 1968). In dairy cows, follicular development resumes within 7–10 days after parturition and is characterized initially by the growth of small (≤4 mm) and medium (5–9 mm) follicles (Savio *et al.*, 1990a). Subsequently, one of these follicles is selected and becomes the dominant follicle. A dominant follicle is defined as the largest follicle which is present in the ovary and which can suppress the

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growth of other follicles. The first dominant follicle after calving ovulates in more than 70% of dairy cows, indicating that there is sufficient luteinizing hormone (LH) secretion to cause maturation and ovulation of the first post-partum dominant follicle (Murphy *et al.*, 1989; Savio *et al.*, 1990a). It is not clear whether the long post-partum interval to first ovulation in beef cows is due to failure of a dominant follicle to ovulate or to lack of development of dominant follicles.

Using real-time ultrasound scanning techniques in cattle, it is possible to monitor accurately, on a daily basis, the growth and regression of individual follicles greater than 5 mm in diameter (Pierson & Ginther, 1984; Quirk *et al.*, 1986; Savio *et al.*, 1988, 1990a, b; Sirois & Fortune, 1988; Knopf *et al.*, 1989). The objectives of this study were to use daily ultrasound scanning techniques to monitor follicular development in the ovaries of post-partum beef suckler cows and, in conjunction with concentrations of progesterone and oestradiol in blood, to determine (i) the pattern of resumption of follicular growth after parturition, (ii) if there were periods of sequential growth and regression of dominant follicles before first ovulation, and (iii) if the length of the first ovarian cycle was affected by the post-partum interval to first ovulation as has been proposed previously (Savio *et al.*, 1990b).

Materials and Methods

Animals

Eighteen Limousin × Friesian cows (second to fourth parity) that calved normally, between 26 April and 25 May, were used. The cows were at pasture for the duration of the study and nursed a single calf, with the exception of one cow that was nursing twins.

Experimental protocol

The ovaries were scanned daily from Day 5 *post partum* until each cow completed a normal (18–24 days) oestrous cycle. The ultrasound scanning equipment and methodology have been described previously (Savio *et al.*, 1988), but the following modifications were used: (i) the reproductive tract was not palpated before ultrasonography; (ii) a 7·5 MHz transducer probe was used to scan the ovaries; (iii) only follicles ≥ 5 mm in diameter were identified and recorded on a daily basis; and (iv) video-tape recordings were made of scanning events using a time-lapse video tape recorder (Panasonic, Livingston, West Lothian, UK). The tailhead region of all cows was painted once weekly and a virile steer was run with the cows to aid detection of oestrus. Confirmation of oestrus was based on visual observations of animals being mounted, removal of tail paint and associated signs of oestrus such as mucous discharge and increased activity.

Blood samples were collected daily by jugular venepuncture during the period of ovarian examination. The blood was stored at room temperature for 1 h and at +4°C for 24 h. After centrifugation at 700 ***g*** for 20 min the serum was decanted and stored at −20°C until assayed for progesterone (Ronayne & Hynes, 1990) and oestradiol concentrations (Korenman *et al.*, 1974). The inter- and intra-assay coefficients of variation for a pool of samples containing 0·1, 0·8 and 4·8 ng progesterone/ml were 18·0, 11·4 and 12·5% and 14·0, 4·4 and 10·4% respectively. The sensitivity of the progesterone assay was 0·03 ng/ml. The inter- and intra-assay coefficients of variation for a pool of samples containing 3, 7 and 14 pg oestradiol/ml were 10·3, 8·5 and 7·5% and 5·2, 9·0 and 7·0% respectively. The sensitivity of the oestradiol assay was 2 pg/ml. Each week the cows were weighed and body condition score was assessed (Lowman *et al.*, 1973).

Definitions used

The definitions used were similar to those used by Savio *et al.* (1988) with the following modifications.

Dominant follicle: the largest follicle present on the surface of the ovary in the absence of any other large (> 10 mm) follicle (Fig. 1).

Ovulation: the disappearance of a large follicle followed by the development of a corpus luteum in the position previously occupied by the ovulatory dominant follicle (Fig. 2).

Normal cycle: an oestrous cycle which was 18–24 days in duration.

Short cycle: an ovarian cycle which was ≤ 17 days in duration.

Ovarian cycle: a cycle initiated and terminated by an ovulation, the first of which was not associated with a detected oestrus.

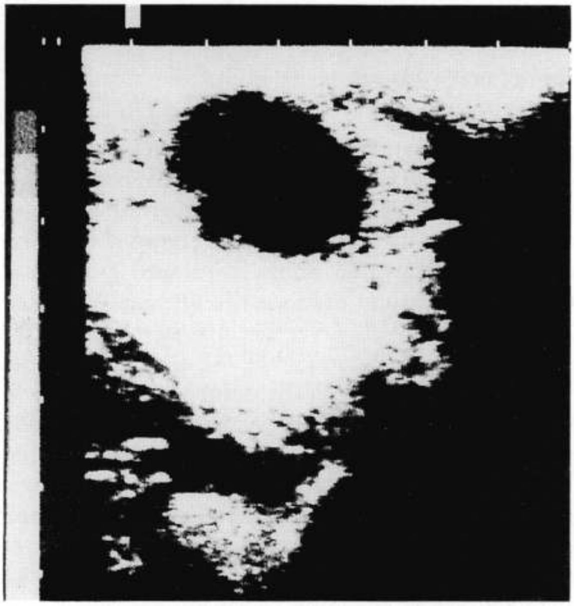

Fig. 1. Ultrasonic appearance of a dominant follicle in the ovary of a post-partum beef suckler cow.

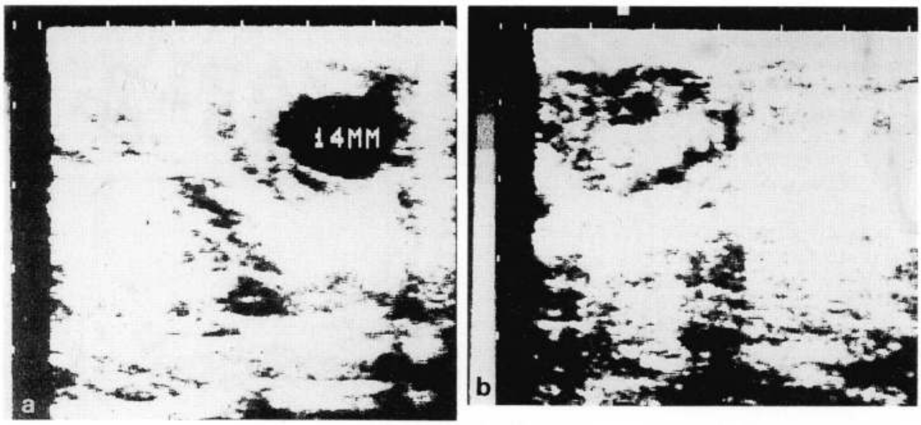

Fig. 2. Confirmation of ovulation of a dominant follicle at Day 60 *post partum*: (a) the dominant follicle on the day of oestrus (Day 0), and (b) the same ovary 1 day later showing echogenic changes characteristic of development of a corpus luteum at the site of ovulation of a dominant follicle.

Statistical analysis

Differences in maximum diameter, day of maximum diameter, growth rate, and persistence of dominant follicles were compared by one-way analysis of variance (SAS, 1985). Serum concentrations of progesterone and oestradiol were not statistically analysed, but were used to confirm ultrasonographic observations of the reproductive status of the cows.

Results

Follicular development before first ovulation

It was not possible to scan the ovaries of 8 cows at Day 5 *post partum* due to the anatomy of the involuting uterus (Savio *et al.*, 1990a). However, once ovaries were identified, it was possible to locate and scan them daily thereafter. Ovarian follicular dynamics before development of the first dominant follicle were characterized by the growth and regression of medium (5–9 mm) follicles (Fig. 3). The duration of detection of these follicles averaged 4 days (range 2–8 days). After a variable period of time, one medium-sized follicle continued growing while the other follicles regressed. This was the first post-partum dominant follicle and the interval from calving to its detection was 10·2 ± 2·2 days (range 7–18 days). The first post-partum dominant follicle ovulated in 2/18 cows (11%). In the remaining 16 cows 3·0 ± 0·1 dominant follicles were identified before first ovulation (range 2–6 dominant follicles). The number of dominant follicles identified before first ovulation and the day *post partum* when each ovulatory follicle was identified are presented in Table 1. The maximum diameter of the dominant follicle increased as the cows approached first ovulation ($P < 0.05$). The number of dominant follicles identified was correlated ($r = 0.87$, $P < 0.001$) with post-partum interval to first ovulation. Data from 2 representative cows showing the pattern of growth of non-ovulatory and ovulatory dominant follicles, between calving and first ovulation, are presented in Fig. 3. The growth rate of the dominant follicle, associated with each period of follicular growth before first ovulation, in general, was not different ($P > 0.05$; Table 2). However, the ovulatory follicle grew more rapidly ($P < 0.05$) and persisted for a shorter period ($P < 0.01$) compared to most of the non-ovulatory dominant follicles (Table 2).

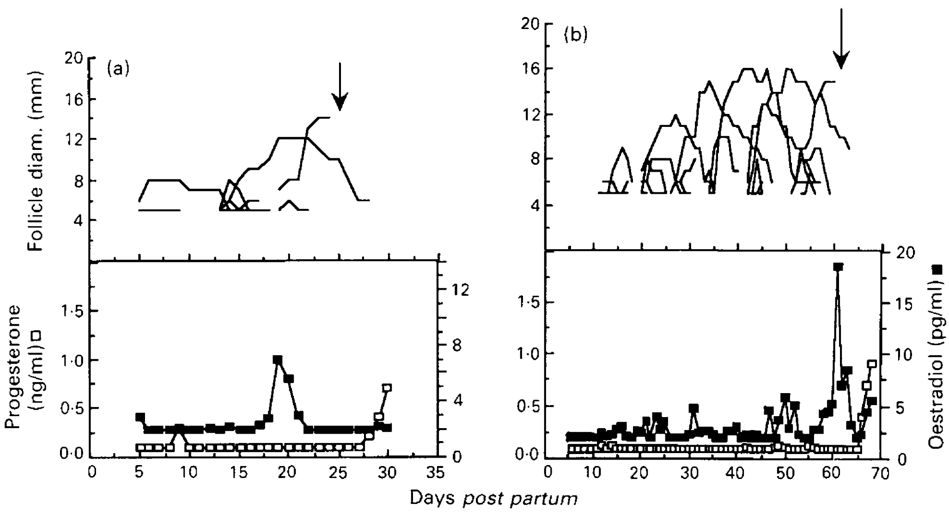

Fig. 3. Pattern of growth and regression of individual follicles that were detected before and after the development of the first dominant follicle in (a) a beef suckler cow with 2 dominant follicles before first ovulation, and (b) a beef suckler cow with 5 dominant follicles before first ovulation. Arrow indicates first ovulation.

Interval from calving to first ovulation and first oestrus

The interval from calving to first ovulation was 35·9 ± 3·3 days (range 20–61 days) based on determination of ovulation by ultrasound and confirmation by a subsequent sustained elevation in

Table 1. Number of dominant follicles before first ovulation, and the day *post partum* when each ovulatory dominant follicle was first detected, in 18 post-partum beef suckler cows

No. of dominant follicles before ovulation	No. of cows	Day *post partum*
1	2	13·0 ± 4·0
2	4	17·8 ± 2·8
3	7	23·0 ± 2·0
4	3	41·0 ± 4·2
5	1	48·0
6	1	53·0

Values are mean ± standard error of the mean (s.e.m.).

Table 2. Characteristics of follicular development and number of follicles, associated with each period of follicular growth before first ovulation, in 18 post-partum beef suckler cows, determined by daily ultrasound examination from 5 days after calving

Dominant follicles before ovulation*	Maximum diam. (mm)	Growth rate (mm/day)	Duration of persistence (days)	No. of follicles
Ovulatory (18)	$16·9^{a}$	$2·1^{a}$	$8·6^{c}$	4·1
First (16)	$16·3^{a}$	$1·5^{b}$	$24·4^{d}$	3·8
Second (12)	$14·0^{b}$	$1·9^{a}$	$19·7^{e}$	4·6
Third (5)	$13·7^{b}$	$1·6^{b}$	$18·4^{e}$	5·5
Fourth (2)	$13·5^{b}$	$1·9^{a}$	$17·5^{e}$	6·0
Fifth (1)	$14·0^{a}$	$1·4^{a}$	$24·0^{d}$	5·0
Pooled s.e.m.	0·3	0·1	0·5	0·3

*Values in parentheses indicate number of animals.
^{ab}Means in the same column with different superscripts are different ($P < 0·05$).
^{cde}Means in the same column with different superscripts are different ($P < 0·01$).

progesterone concentrations. Data from 2 representative cows showing the patterns of follicular growth and progesterone and oestradiol concentrations, after first ovulation, are presented in Figs 4 and 5. First ovulation was not associated with detection of oestrous behaviour in 16/18 (89%) cows. Within the constraints of the system used for detection of oestrus in this experiment, the interval from calving to first oestrus was 54·2 ± 3·2 days (range 19–92 days).

Duration of first post-partum ovarian cycles

The duration of the first post-partum ovarian cycle was 12·1 ± 1·2 days (range 7–23 days). In 14 of 18 cows the duration of the first post-partum ovarian cycle was 9·7 ± 0·5 days (range 7–15 days). The 4 remaining cows had a normal ovarian cycle of 20·4 ± 0·5 days (range 18–23 days), and 2 of these 4 cows ovulated on Day 20 *post partum*.

Follicular development during short cycles

All cows with a short ovarian cycle developed one dominant follicle during this cycle, which subsequently ovulated (Fig. 4). When the dominant follicle ovulated after Day 20 *post partum*, the

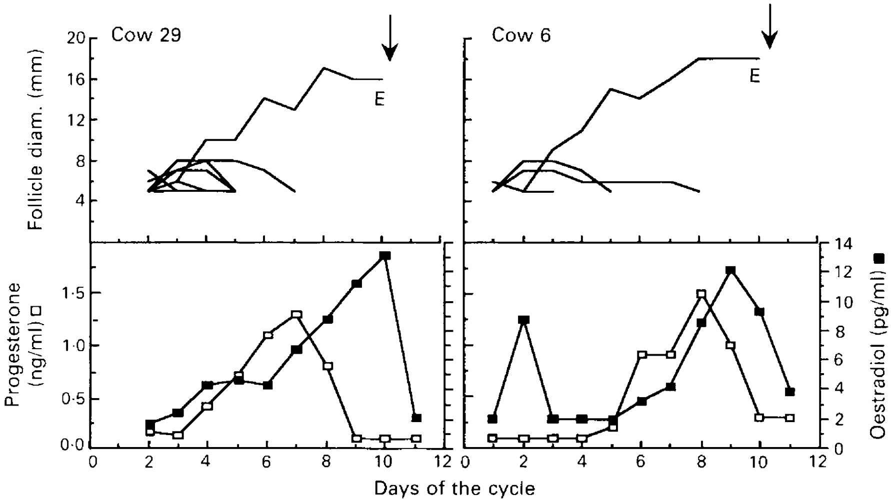

Fig. 4. Pattern of growth of individual follicles during short cycles (< 17 days) in 2 post-partum beef suckler cows. Arrow indicates ovulation. E = oestrus.

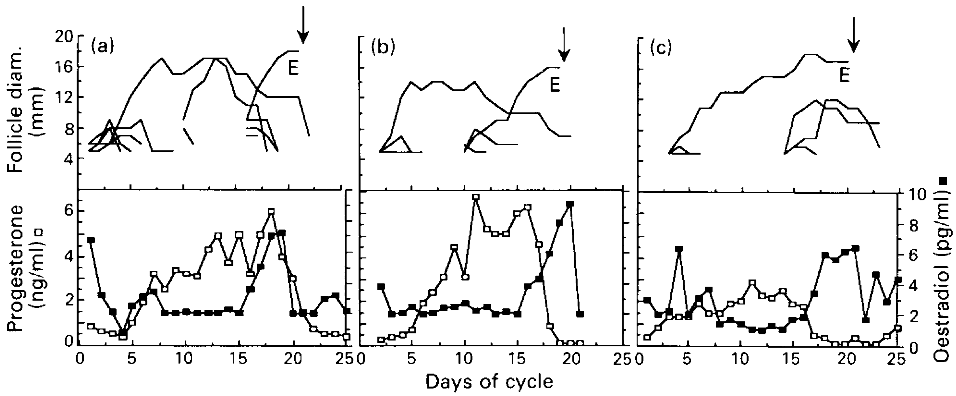

Fig. 5. Pattern of growth and regression of individual follicles during normal oestrous cycles of post-partum beef suckler cows with (a) 3, (b) 2 or (c) 1 dominant follicles. Arrow indicates ovulation. E = oestrus. The scale for progesterone values is different from that in Figs 3 and 4.

resultant cycle was short in 14/16 (87%) cows. The growth rate of the dominant follicle detected during the short ovarian cycle was 2·3 ± 0·1 mm/day and the maximum diameter was 19·1 ± 0·5 mm. There was no difference ($P > 0{\cdot}05$) in growth rate, persistence and maximum diameter between the first post-partum ovulatory follicle, the dominant follicle of the short cycle or the ovulatory follicle of oestrous cycles with 2 or 3 dominant follicles (Table 3). The growth rate ($P < 0{\cdot}01$) and persistence ($P < 0{\cdot}05$) of the dominant ovulatory follicle in cycles with a single dominant follicle was slower than for other ovulatory follicles.

Follicular development during normal oestrous cycles

The duration of oestrous cycles in the cows studied (N = 17) was 20·4 ± 0·5 days. Follicular development during oestrous cycles was characterized by one (N = 2), two (N = 7) or three (N =

Table 3. Characteristics of follicular development and number of follicles, associated with each period of follicular growth, determined by daily ultrasound examination in 18 post-partum beef suckler cows during short oestrous cycles and those of normal length

	Data relating to dominant follicles					
	No. of follicles	Maximum diam. (mm)	Growth rate (mm/day)	Day of appearance (day of cycle)	Day of maximum diam. (day of cycle)	Persistence of dominant follicles (days)
Short cycles (N = 14); length of cycle: 9·7 ± 0·5 days						
Ovulatory	4·9	$19·1^{a}$	$2·3^{c}$	$2·2^{e}$	$9·1^{a}$	$8·5^{a}$
Oestrous cycles with 3 periods of follicular growth (N = 8); length of cycle: 21·8 ± 0·5 days						
First	5·6	$16·9^{b}$	$1·9^{d}$	$1·4^{f}$	$8·8^{a}$	$22·1^{b}$
Second	3·9	$14·9^{b}$	$1·8^{d}$	$9·6^{g}$	$15·5^{b}$	$17·4^{b}$
Ovulatory	4·3	$17·3^{a}$	$2·3^{c}$	$16·4^{h}$	$21·1^{b}$	$7·5^{a}$
Oestrous cycles with 2 periods of follicular growth (N = 7); length of cycle: 19·4 ± 0·9 days						
First	5·1	$15·4^{b}$	$1·9^{a}$	$3·1^{e}$	$9·0^{a}$	$19·9^{b}$
Ovulatory	4·1	$17·7^{a}$	$2·2^{a}$	$12·1^{i}$	$18·9^{b}$	$8·4^{a}$
Oestrous cycles with 1 period of follicular growth (N = 2); length of cycle: 20·0 ± 1·0 days						
Ovulatory	7·5	$19·5^{a}$	$1·4^{b}$	$2·5^{e}$	$15·5^{a}$	$19·5^{b}$
Pooled s.e.m.	0·3	0·3	0·1	0·2	1·1	0·5

[ab]Means in the same column with different superscripts are different ($P < 0·05$).
[cd]Means in the same column with different superscripts are different ($P < 0·01$).
[efghi]Means in the same column with different superscripts are different ($P < 0·0001$).

8) dominant follicles. No data were available on the normal oestrous cycle of one cow which was removed from the study due to scanning difficulties.

Oestrous cycles with three periods of follicular growth. The patterns of follicular growth during oestrous cycles in which 3 dominant follicles were identified are shown in Fig. 5(a). A single dominant follicle developed in conjunction with a smaller number of non-dominant follicles. There was no difference in the growth rate or maximum diameter of the dominant follicle of the first and second periods of follicular growth ($P > 0·05$). The ovulatory follicle grew more rapidly ($P < 0·01$) and was larger ($P < 0·05$) than the dominant follicle of the first and second periods of follicular growth. The maximum diameter of the dominant follicle associated with the second period of follicular growth tended ($P = 0·06$) to be smaller than the ovulatory follicle. The persistence of the third dominant follicle was shorter than the first or second dominant follicle ($P < 0·05$). Non-dominant follicles were observed for an average of 5 days during each of the periods of follicular growth.

Oestrous cycles with two periods of follicular growth. The patterns of follicular growth during oestrous cycles in which 2 dominant follicles were identified are presented in Fig. 5(b). The growth rate of the second dominant follicle was not significantly different from the first dominant follicle ($P > 0·05$). The ovulatory follicle persisted for a shorter period than did the non-ovulatory follicle ($P < 0·05$). From data presented in Table 3 it can be seen that, with the exception of day of maximum diameter and day of appearance of the dominant follicle, there was no significant difference ($P > 0·05$) in the parameters examined.

Oestrous cycles with one period of follicular growth. Two oestrous cycles were identified in which a single dominant follicle was detected (Fig. 5c). In 1 animal (Cow 3), although only one dominant follicle was identified, a period of secondary follicular growth was identified (Fig. 5c) on the ovary opposite to that bearing the dominant follicle. However, this was not associated with the development of a dominant follicle.

The growth rate, maximum diameter and persistence of dominant non-ovulatory follicles before first ovulation and during normal length oestrous cycles were not different ($P > 0{\cdot}05$).

Discussion

The majority of post-partum beef suckler cows resumed follicular development early after calving. Initially, medium-sized follicles were identified and subsequently, a single dominant follicle developed which generally underwent atresia rather than ovulation. The number of first dominant follicles which ovulated in beef cows was lower than that reported for dairy cows (Savio *et al.*, 1990a). Recurrent growth and regression of dominant follicles occurred in those cows in which the first dominant follicle did not ovulate. The duration of the cycle after first ovulation was short in most post-partum beef suckler cows.

The resumption of follicular growth in cows after calving is affected by season (Peters & Riley, 1982; Savio *et al.*, 1990a), energy balance (Rutter & Manns, 1986; Butler & Smith, 1989), suckling (Oxenreider, 1968; Peters *et al.*, 1981) and infectious disorders (Chauhan *et al.*, 1984). The prerequisites for the re-establishment of follicular growth and ovarian cyclicity are uterine involution and escape from the suckling (or lactation)-induced inhibition of LH secretion (Malven, 1984; Butler & Smith, 1989). The pituitary content of LH and responsiveness to gonadotrophins increase rapidly after parturition (Malven, 1984; Schallenberger & Walters, 1985) and are estimated to be fully recovered by Day 10 *post partum* in lactating dairy cows (Moss *et al.*, 1985). The early establishment of pulsatile LH release required for first ovulation is inhibited by suckling (Lamming *et al.*, 1982).

The incidence of ovulation of the first post-partum dominant follicle (Murphy *et al.*, 1989; Savio *et al.*, 1990a) is high in dairy cows [28/33 (84%)] compared with only 2/18 (11%) in beef cows in this study. Data on follicular dynamics in the early post-partum period show that post-partum beef cows resume follicular growth and development of dominant follicles at a time (7–15 days) after parturition similar to that of dairy cows (Savio *et al.*, 1990a). Thus, although suckling increased the interval to first ovulation relative to the intervals reported for dairy cows (Eipper & Mains, 1980; Fonseca *et al.*, 1983; Savio *et al.*, 1990a), it did not delay resumption of follicular growth or development of dominant follicles in beef cows in this study. Our data show that, before first ovulation, there are recurrent periods of growth and regression of dominant follicles but that these dominant follicles fail to ovulate and consequently undergo atresia.

Functional studies of ovarian follicles, carried out before first ovulation in beef cows, which have evaluated LH and follicle-stimulating hormone (FSH) receptors in granulosa cells, LH receptors in thecal cells and concentrations of progesterone, oestradiol, androstenedione and testosterone in follicular fluid, suggest that follicles which develop during the post-partum anoestrous period are similar to those which develop during the luteal phase of oestrous cycles (Walters *et al.*, 1982; Spicer *et al.*, 1983; Braden *et al.*, 1986; Prado *et al.*, 1989). It appears, therefore, that ovarian follicular capacity is not a limiting factor in post-partum anoestrus. Data in the literature have shown that a more likely explanation for the suckling-induced inhibition of ovulation and oestrus in beef cows is reduced frequency of pulsatile LH release, reduced follicular LH receptor concentrations and thus decreased synthesis of androgens, which are the precursors for the pro-oestrus oestradiol rise. Removal of the suckling stimulus on Day 21 *post partum* increased pulsatile LH release and markedly increased follicular LH receptor concentrations (Walters *et al.*, 1982). The increased frequency of pulsatile LH release in weaned beef cows is similar to the pattern of pulsatile LH release that occurs before first oestrus and ovulation in beef suckler cows (Humphrey *et al.*, 1976) and in dairy cows (Webb *et al.*, 1980).

If a calving interval of 365 days is to be achieved in beef suckler production systems, then it is necessary to have early resumption of ovulation after calving and the re-establishment of oestrous cycles of normal duration. Short cycles (< 17 days) occur spontaneously before first oestrus in prepubertal heifers (Berardinelli *et al.*, 1979; Keisler *et al.*, 1983) and post-partum cows and ewes (Corah *et al.*, 1974; LaVoie *et al.*, 1981; Lamming *et al.*, 1981; Sharpe *et al.*, 1986). Corpora lutea with a short lifespan also occur after weaning of calves from anoestrous cows (Odde *et al.*, 1980; Copelin *et al.*, 1987). The physiological importance of short cycles is unknown. However, the transient increase in progesterone of the short cycle is followed by resumption of oestrous cycles of normal length in sheep and cattle (Lamming *et al.*, 1981; Ramirez-Godinez *et al.*, 1981; Southee *et al.*, 1988; Savio *et al.*, 1990b). Follicular development during short cycles is associated with the development and ovulation of a single dominant follicle (Savio *et al.*, 1990b). The occurrence of short cycles appears to be related to the post-partum interval to first ovulation (Savio *et al.*, 1990b). Dairy cows which ovulate between Days 20 and 40 *post partum* have a high incidence of short cycles (Savio *et al.*, 1990b). The pattern of follicular growth during short cycles in beef cows was identical to that described for dairy cows and, in 14/16 (88%) beef cows which ovulated after Day 20 *post partum*, the length of the subsequent cycle was short. The explanation for this observation is unknown. Perry *et al.* (1989) have shown by ultrasonic examination of ovaries in beef cows that the size of the first and second post-partum ovulatory follicles were similar but they suggest that the interval to first ovulation was not important in influencing cycle type after first ovulation. Savio *et al.* (1990b) proposed that, if dominant ovulatory follicles are exposed to the carry-over effect of progesterone from the previous pregnancy in the early post-partum period, this may explain the occurrence of short cycles in cows that ovulate after Day 20 *post partum*. It is also possible that the ovary can recognize, by an as yet unknown mechanism, a defective corpus luteum and eliminate it by the premature release of a uterine luteolysin, presumably prostaglandin F-2α (Savio *et al.*, 1990b). It is important to recognize the involvement of the uterus in the aetiology of short cycles. Short-lived corpora lutea do not have inherently short lifespans, rather the presence of the uterus results in premature luteolysis (Copelin *et al.*, 1987). Confirmation of the role of the uterus, specifically of PGF-2α, in the aetiology of short cycles has been reported by Copelin *et al.* (1989), who showed that active immunization of beef cows against PGF-2α *pre* and *post partum* prevented the development of corpora lutea with a short lifespan. They concluded that premature release of PGF-2α from the uterus was responsible for short cycles in post-partum beef cows.

The pattern of turnover of dominant follicles before first ovulation and during oestrous cycles of normal duration was similar, suggesting that the rate at which dominant follicles develop and undergo atresia is similar in the presence or absence of progesterone. This observation agrees with the pattern of follicular development described for dairy cows during early pregnancy (Savio *et al.*, 1990b) and in pre-pubertal heifers (Ronayne, 1990).

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References

Berardinelli, J.G., Dailey, R.A., Butcher, R.L. & Inskeep, E.K. (1979) Source of progesterone prior to puberty in beef heifers. *J. Anim. Sci.* **49**, 1276–1280.

Braden, T.D., Manns, J.G., Cermak, D.L., Nett, T.M. & Niswender, G.D. (1986) Follicular development following parturition and during the estrous cycle in beef cows. *Theriogenology* **25**, 833–843.

Butler, W.R. & Smith, R.D. (1989) Interrelationships between energy balance and postpartum reproductive function in dairy cattle. *J. Dairy Sci.* **72**, 767–783.

Casida, L.E., Graves, W.E., Hauser, E.R., Lauderdale, J.W., Reiser, J.W., Saiduddin, S. & Tyler, W.J. (1968) Studies on the post-partum cow. *Res. Bull. Agric. Exp. Stn, Univ. Wis.* No. **270**, 1–54.

Chauhan, F.S., Mgongo, F.O.K. & Kessy, B.M. (1984) Recent advances in hormonal therapy of bovine reproductive disorders: a review. *Vet. Bull.* **54**, 991–1009.

Copelin, J.P., Smith, M.F., Garverick, H.A. & Youngquist, R.S. (1987) Effect of uterus on subnormal luteal function in anestrous beef cows. *J. Anim. Sci.* **64**, 1505–1511.

Copelin, J.P., Smith, M.F., Keisler, D.H. & Garverick, H.A. (1989) Effect of active immunization of prepartum and post-partum cows against prostaglandin

F-2α on lifespan and progesterone secretion of short-lived corpora lutea. *J. Reprod. Fert.* **87,** 199–207.

Corah, L.R., Quealy, A.P., Dunn, T.G. & Kaltenbach, C.C. (1974) Prepartum and postpartum levels of progesterone and estradiol in beef heifers fed two levels of energy. *J. Anim. Sci.* **39,** 380–385.

Eipper, B.A. & Mains, R.E. (1980) Structure and biosynthesis of pro-ACTH/endorphin and related peptides. *Endocr. Rev.* **1,** 1–27.

Fonseca, F.A., Britt, J.H., McDaniel, B.T., Wilk, J.C. & Rakes, A.H. (1983) Reproductive traits of Holstein and Jerseys. Effects of age, milk yield and clinical abnormalities on involution of cervix and uterus, ovulation, estrous cycles, detection of estrus, conception rate and days open. *J. Dairy Sci.* **66,** 1128–1147.

Humphrey, W.D., Kortinik, D.R., Kaltenbach, C.C., Dunn, T.G. & Niswender, G.D. (1976) Progesterone and LH in postpartum suckled beef cows. *J. Anim. Sci.* **43,** 290, abstr.

Keisler, D.H., Inskeep, E.K. & Dailey, R.A. (1983) First luteal tissue in ewe lambs: influence on subsequent ovarian activity and response to hysterectomy. *J. Anim. Sci.* **57,** 150–156.

Knopf, L., Kastelic, J.P., Schallenberger, E. & Ginther, O.J. (1989) Ovarian follicular dynamics in heifers: test of two-wave hypothesis by ultrasonically monitoring individual follicles. *Dom. Anim. Endocr.* **6,** 111–119.

Korenman, S.G., Stevens, R.H., Carpenter, L.A., Robb, M., Niswender, G.D. & Sherman, B.M. (1974) Estradiol radioimmunoassay without chromatography: procedure, validation and normal values. *J. clin. Endocr. Metab.* **38,** 718–723.

Lamming, G.E., Wathes, D.C. & Peters, A.R. (1981) Endocrine patterns of the post-partum cow. *J. Reprod. Fert., Suppl.* **30,** 155–170.

Lamming, G.E., Peters, A.R., Riley, G.M. & Fisher, M.W. (1982) Endocrine regulation of postpartum function. *Curr. Top. Vet. Med. Anim. Sci.* **20,** 148–172.

LaVoie, V., Han, D.K., Foster, D.B. & Moody, E.L. (1981) Suckling effect on estrus and blood plasma progesterone in postpartum beef cows. *J. Anim. Sci.* **52,** 802–812.

Lowman, B.G., Scott, N. & Somerville, S. (1973) Condition scoring of cattle. *Bull. East of Scotland Coll. Agric.* No. 6.

Malven, P.V. (1984). Pathophysiology of the puerperium: definition of the problem. *Proc. 10th Int. Congr. Anim. Reprod. & AI,* Urbana, vol. 4; III 1–8.

Moss, G.E., Parfet, J.R., Marvin, C.A., Allrich, R.D. & Diekman, M.A. (1985) Pituitary concentrations of gonadotrophins and receptors for GnRH in suckled beef cows at various intervals after calving. *J. Anim. Sci.* **60,** 285–293.

Murphy, M.G., Boland, M.P. & Roche, J.F. (1989) The effect of a progesterone releasing intravaginal device on resumption of follicular activity and oestrus in autumn-calving Friesian dairy cows. In *Follicular Development and the Ovulatory Response*, p. 26, abstr. Eds N. A. Dekel & A. Tsafriri. Tiberias, Israel.

Odde, K.G., Ward, H.S., Kiracofe, G.H., McKee, R.M. & Kittok, R.J. (1980) Short estrous cycles and associated serum progesterone levels in beef cows. *Theriogenology* **14,** 105–112.

Oxenreider, S.C. (1968) Effects of suckling and ovarian function on post-partum reproductive activity in beef cows. *Am. J. vet. Res.* **29,** 2099–2107.

Perry, R.C., Corah, C.R., Kiracofe, G.H., Stevenson, J.S., Beal, W.E. & Brethour, J.R. (1989) Endocrine changes and ultrasonography of ovarian function in post-partum suckled beef cows. *J. Anim. Sci.* **67,** (Suppl. 1) 807, abstr.

Peters, A.R. & Riley, G.M. (1982) Milk progesterone profiles and factors affecting post-partum ovarian activity in beef cows. *Anim. Prod.* **34,** 145–153.

Peters, A.R., Lamming, G.E. & Fisher, M.W. (1981) A comparison of plasma LH concentrations in milked and suckling post-partum cows. *J. Reprod. Fert.* **62,** 567–573.

Pierson, R.A. & Ginther, O.J. (1984) Ultrasonography of the bovine ovary. *Theriogenology* **21,** 495–504.

Prado, R., Rhind, S.M., Wright, I.A., Russel, A.J.F., McMillen, S.M., Smith, A.I. & McNeilly, A.S. (1989) Ovarian follicular populations, steroidogenic capacity and physiological status in post-partum suckling beef cows in high and low body condition. *Anim. Prod.* **48,** 661, abstr.

Quirk, S.M., Hickey, G.J. & Fortune, J.E. (1986) Growth and regression of ovarian follicles during the follicular phase and during the oestrous cycle in heifers undergoing spontaneous and PGF-2α-induced luteolysis. *J. Reprod. Fert.* **77,** 211–219.

Ramirez-Godinez, J.A., Kiracofe, G.H., McKee, R.M., Schalles, R.R. & Kittok, R.J. (1981) Reducing the incidence of short estrous cycles in beef cows with norgestomet. *Theriogenology* **15,** 613–623.

Ronayne, E. (1990) *Manipulation of gonadal function in ruminants.* Ph.D. thesis, National University of Ireland.

Ronayne, E. & Hynes, N. (1990) Measurement of plasma progesterone by extraction and non-extraction radioimmunoassay. *Ir. J. Agric. Res.* (in press).

Rutter, L.M. & Manns, J.G. (1986) Hypoglycaemia alters pulsatile luteinising hormone secretion in the postpartum beef cow. *J. Anim. Sci.* **64,** 479–486.

SAS (1985) *SAS User's Guide: Statistics* (5th Edition). Statistical Analyis System Institute, Cary, North Carolina, USA.

Savio, J.D., Keenan, L., Boland, M.P. & Roche, J.F. (1988) Pattern of growth of dominant follicles during the oestrous cycle of heifers. *J. Reprod. Fert.* **83,** 663–671.

Savio, J.D., Boland, M.P., Hynes, N. & Roche, J.F. (1990a) Resumption of follicular activity in the early post-partum period of dairy cows. *J. Reprod. Fert.* **88,** 569–579.

Savio, J.D., Boland, M.P. & Roche, J.F. (1990b) Development of dominant follicles and length of ovarian cycles in post-partum dairy cows. *J. Reprod. Fert.* **88,** 581–591.

Schallenberger, E. & Walters, D.L. (1985) Endocrine mechanisms contributing to postpartum anoestrus in dairy and beef cattle. In *Endocrine Causes of Seasonal and Lactational Anoestrus in Farm Animals*, pp. 206–220. Eds F. Ellendorff & F. Elsaesser. Martinus Nijhoff, The Hague.

Sharpe, P.H., McKibbin, P.E., Murphy, B.D. & Manns, J.G. (1986) First postpartum ovulations and corpora lutea in ewes which lamb in the breeding season. *Anim. Reprod. Sci.* **10,** 61–74.

Sirois, J. & Fortune, J.E. (1988) Ovarian follicular dynamics during the estrous cycle in heifers monitored by real-time ultrasonography. *Biol. Reprod.* **39,** 308–317.

Southee, J.A., Hunter, M.G., Law, A.S. & Haresign, W. (1988) Effect of hysterectomy on the short life-cycle corpus luteum produced after GnRH-induced ovulation in the anoestrous ewe. *J. Reprod. Fert.* **84,** 149–155.

Spicer, L.J., Leung, K., Convey, E.M., Gunther, J., Tucker, H.A. & Short, R.E. (1983) Secretion of luteinising hormone (LH), follicle stimulating hormone (FSH) and prolactin (PRL), and changes in ovarian folliculogenesis and follicular fluid (FF) hormones during anestrus in beef cattle. *J. Anim. Sci.* **57** (Suppl. 1), 375, abstr.

Walters, D.L., Short, R.E., Convey, E.M., Staigmiller, R.B., Dunn, T.G. & Kaltenbach, C.C. (1982) Pituitary and ovarian function in postpartum beef cows. II. Endocrine changes prior to ovulation in suckled and nonsuckled postpartum cows compared to cycling cows. *Biol. Reprod.* **26,** 647–754.

Webb, R., Lamming, G.E., Haynes, N.B. & Foxcroft, G.R. (1980) Plasma progesterone and gonadotrophin concentrations and ovarian activity in post-partum dairy cows. *J. Reprod. Fert.* **59,** 133–143.

Wiltbank, J.N. & Cook, A.C. (1958) The comparative reproductive performance of nursed and milked cows. *J. Anim. Sci.* **17,** 640–648.

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