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Effect of Suckling and Ovariectomy on the Control of Luteinizing Hormone Secretion During the Postpartum Period in Beef Cows[1]

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ABSTRACT

Twenty-two mature pluriparous beef cows were randomly assigned to one of six treatments in a 2 × 3 factorial experiment in order to study the role of suckling and ovarian factors on control of the tonic and episodic release of luteinizing hormone (LH). Twelve cows remained intact (INT) and 10 were ovariectomized (OVX) within 4 days following the day of parturition (Day 0). The suckling intensities were nonsuckled (0), suckled once daily for 30 min (1) and suckled ad libitum by two calves (2). Blood samples were collected at 15-min intervals for 6 h weekly, from Days 6 to 76 postpartum. The postpartum intervals to initiation of ovarian luteal function were 31 ± 3, 41 ± 4 and 67 ± 1 days ($\bar{X}$ ± SEM) for INT cows with 0, 1 and 2 suckling intensities, respectively. Mean LH concentrations and frequency of LH pulses increased as time of ovulation approached in INT cows. In OVX animals, both mean LH concentrations and frequency of LH pulses increased as time postovariectomy progressed. No differences were detected in mean LH concentrations or frequency of LH pulses between the two suckled OVX groups. Mean LH in the OVX-0 cows was greater on Days 13, 20 and 27 postpartum when compared to the respective days in suckled OVX cows. Frequency of LH pulses tended to be lower ($P<0.10$) in both suckled OVX groups when compared with OVX-0 cows from Day 6 to Day 55 postpartum. It is postulated that suckling and ovarian factors act together during the postpartum period to suppress LH levels and frequency of LH pulses in beef cows.

INTRODUCTION

Suckling increases the length of the postpartum interval to ovulation and first postpartum estrus (Casida et al., 1968; Casida, 1971). This increase is proportional to the number of calves suckled (Wetteman et al., 1978), the frequency of suckling (Reeves and Gaskins, 1981) and appears to be independent of nutritional factors (Wetteman et al., 1978). The general endocrine changes during the postpartum period in cows have been reviewed (Wagner and Oxenreider, 1971; Arije et al., 1974; Goodale et al., 1978; Wetteman, 1980; Edgerton, 1980; and Lamming et al., 1981). Walters et al. (1982a,b) found that suckling reduced the pulsatile release of luteinizing hormone (LH) and decreased the amplitude of LH pulses and mean circulating levels of LH in beef cows. Chang et al. (1981) reported no differences in LH baseline concentrations or frequency of LH pulses in suckled and nonsuckled young beef cows, however, suckled cows had LH pulses of lower amplitude.

A comparison of the response to ovariectomy in estrual and postpartum anestrous dairy cows indicated that mean LH concentrations increased earlier following ovariectomy in cows which had been exhibiting estrous cycles before ovariectomy than in postpartum cows which were anestrus before ovariectomy. No differences in LH secretion were detected 11 days after ovariectomy (Schallenberger and Peterson, 1982). Echternkamp (1978) reported that LH concentrations in ovariectomized (OVX) 2-yr-old cows that were nonsuckled, suckled twice daily, or suckled ad libitum were not different. These observations suggest a different effect of suckling in the presence and absence of ovaries on LH secretion. Therefore the present experiment was performed to study the combined effect of suckling and ovariectomy on the

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control of tonic and episodic release of LH during the postpartum period in beef cows.

MATERIALS AND METHODS

Animals

Parturition was induced in 22 pluriparous beef cows (Hereford and Hereford X Angus) within 10 days of the expected day of calving using an intramuscular injection of 25 mg of prostaglandin $F_{2\alpha}$ (Lutalyse, Upjohn Co., Kalamazoo, MI), plus 20 mg of estrone. At calving (Day 0) the cows were randomly assigned, in a 2 X 3 factorial experiment, to one of six treatments. Twelve cows remained intact (INT) and 10 were ovariectomized (OVX) via high lumbar laparotomy within the first 4 days after calving. These cows were allocated to three suckling intensities: nonsuckled (0), suckled once daily (1) or hypersuckled (2). Calves were removed from the nonsuckled cows within 48 h after birth. The cows suckled once daily were allowed to nurse one calf for 30 min daily beginning 48 h after parturition, while the hypersuckled cows were suckled ad libitum by two calves starting within 48 h after parturition. The initiation of the different suckling intensities by 48 h after parturition was done in order to allow the calves to receive colostrum from their natural mothers. The calves removed from cows in the nonsuckled group were fostered on cows in the hypersuckled treatment. These suckling regimens were maintained for the duration of the experiment and suckling was not interrupted during the period of intensive blood collection.

All animals were fed alfalfa hay ad libitum and were supplemented 1275 g·head·day of corn. Water and a commercial mineral mix containing calcium (12%), phosphate (12%), sodium chloride (12%) and iodine (<0.005%) were provided ad libitum.

Blood Collection

Blood samples were collected via jugular venipuncture in 10-ml vacutainer tubes three times a week to quantify serum progesterone concentrations in order to determine the time when ovarian luteal function was reestablished in intact cows. The postpartum initiation of corpora lutea function for an individual INT cow was assumed when a rise in progesterone concentration above 1 ng/ml persisted for more than 1 wk. Serial samples were collected at 15-min intervals for 6 h weekly from Day 6 to Day 76 postpartum. These samples were used to estimate mean LH concentrations and evaluate the patterns of LH release. All blood samples were allowed to clot at room temperature and then stored at 4°C. Blood was centrifuged at 1520 X *g* for 15 min at 4°C within 48 h of the time of collection. Serum was harvested and stored at −20°C until assayed for LH or progesterone.

Hormone Analyses

Serum LH concentrations were determined using the double antibody radioimmunoassay validated by Golter et al. (1973), using rabbit antiserum (1:40,000) for bovine LH (JJR-RABLH #5), highly purified ovine LH (LER-1056-C2) for iodination and NIH-LH-B7 as standard. The antisera to LH detected 0.015 LH units/mg of NIH-follicle-stimulating hormone (FSH)-S18 and the NIH-FSH-S18 contains 0.013 units of LH/mg. The LER-1056-C2 had a purity of 1.73 NIH-LH-S1 units/mg and contained 0.02 USP units/mg thyroid-stimulating hormone (TSH) and <0.016 NIH-FSH-S1 units/mg. The assay had an average sensitivity (2 standard deviations of the median variance ratio) of 228 pg/ml and intra- and interassay coefficients of variation of 4.4% and 15%, respectively. Progesterone concentrations were determined using the radioimmunoassay validated by Anthony et al. (1981). All samples were assayed in duplicate.

Analysis of the Data

Mean LH concentrations were calculated as the average of the 25 samples collected from each animal during serial sampling. Pulsatile release of LH was estimated using the criteria of Goodman and Karsch (1980). LH pulse frequency was calculated as the total number of pulses in 6 h. Amplitude of LH pulses was determined as the average amplitude of the total number of pulses detected in 6 h. Amplitude for an individual LH pulse was calculated using the criteria of Goodman and Karsch (1980).

Statistical analyses were performed using analysis of variance for a split-plot design with a factorial arrangement of treatments (Steel and Torrie, 1980), using suckling and the presence or absence of ovaries as the main factors and time as the subplot. Multivariate analysis of variance was performed to characterize the changes of LH secretion over time and to establish the relationships between the different variables in the experiment. Regression analysis was also performed to characterize the changes in the pattern of secretion of LH during the experiment (Draper and Smith, 1981). LH determinations after the onset of estrous cycles or from the first follicular phase prior to the first postpartum estrus in INT cows were excluded from all statistical analyses. Orthogonal contrasts were performed to determine differences among treatments.

RESULTS

Initiation of Luteal Function Following Parturition

Mean intervals to first systemic rise in progesterone indicative of the onset of corpora lutea function following parturition for INT cows were 31 ± 3, 41 ± 4 and 67 ± 1 days ($\bar{X}$ ± SEM) for INT-0, INT-1 and INT-2, respectively. No differences ($P > 0.05$) were detected between the postpartum interval to initiation of ovarian luteal function in INT-0 and INT-1; however, the postpartum interval of INT-2 cows was longer than that of INT-0 and INT-1 ($P < 0.05$). Two cows had placentae retained for more than 24 h postpartum but expulsion of the retained tissue in these two individuals occurred within 72 h postpartum. No apparent effect on hormone secretion occurred as a result of placental retention.

LH in Intact Cows

No differences in LH concentrations between the three suckling intensities in the INT cows were detected on Day 6 postpartum. Mean LH concentration in INT-0 cows ranged from 1.2 ± 0.4 ng/ml on Day 6 to 1.9 ± 0.4 ng/ml on Day 20 postpartum. Frequency of LH pulses ranged from 1.5 ± 0.9 on Day 6 to 3.2 ± 0.7 pulses/6 h on Day 13 postpartum. In INT-1 cows a linear increase ($P<0.05$) in mean serum LH concentration (Fig. 1) and frequency (Fig. 2) of LH pulses was observed between Days 6 and 27 postpartum. Mean LH concentration increased ($P<0.05$) from 0.6 ± 0.1 ng/ml on Day 6 to 2.1 ± 0.4 ng/ml on Day 27, while frequency of LH pulses changed ($P<0.05$) from 0.2 ± 0.2 pulses to 3.5 ± 0.6 pulses/6 h between Days 6 and 27.

Mean concentrations of LH in INT-2 cows remained unchanged between Days 6 and 34 postpartum, but on Day 41 increased ($P<0.05$) to 1.3 ± 0.2 ng/ml, then declined ($P<0.05$) on Day 48 to 0.8 ± 0.1 ng/ml and again increased ($P<0.05$) on Day 55 to 1.7 ± 0.5 ng/ml. The increase ($P<0.05$) observed on Day 41 was due to one cow which had a mean LH concentration of 3.1 ng/ml. No significant changes ($P>0.05$) in frequency of LH pulses was observed between Days 6 and 48 postpartum in the INT-2 cows. During this period the frequency of LH pulses stayed below 1.5 pulses/6 h. An increase in frequency of LH pulses (3.0 ± 0.6 pulses/6 h; $P<0.05$) was observed in this treatment at Day 55 postpartum, and progesterone concentrations indicative of the development of corpora lutea were detected in the cows in this treatment within 2 weeks (Figs. 1 and 2). Amplitude of LH pulses was low initially in all treatment groups, then increased in all groups and subsequently declined before the study was terminated (Table 1).

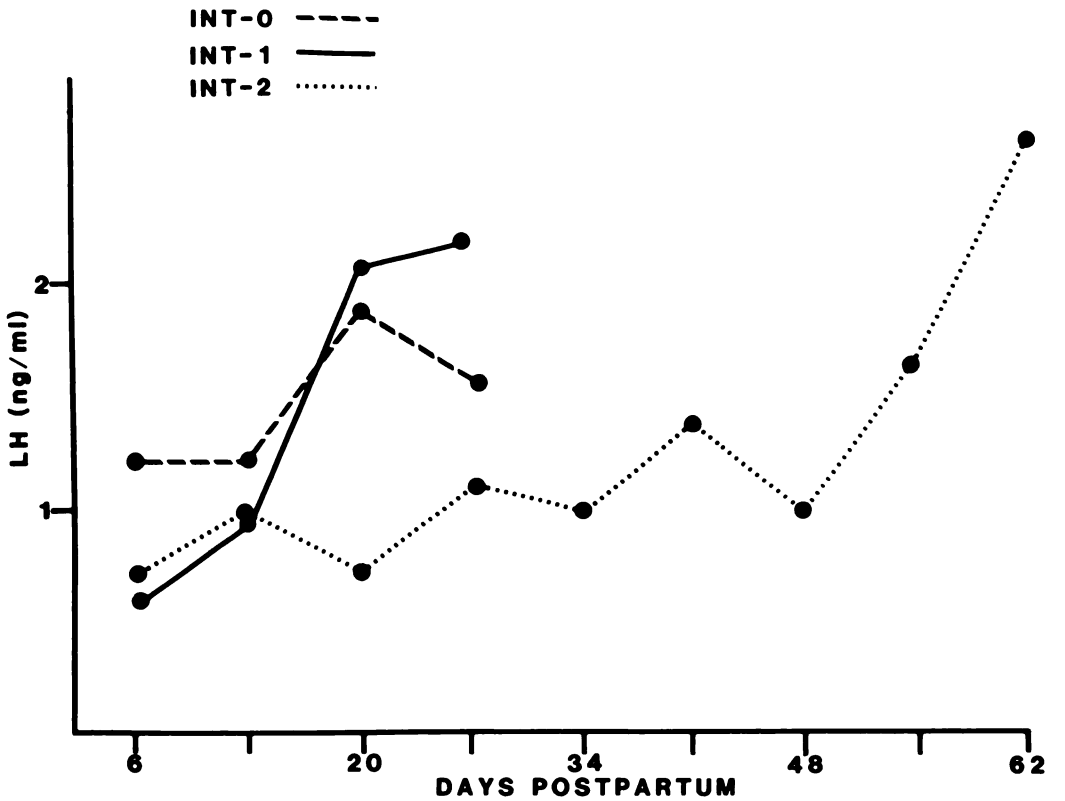

FIG. 1. Mean serum LH concentrationsin intact nonsuckled (*INT-0*), once daily suckled (*INT-1*) and hypersuckled (*INT-2*) cows.

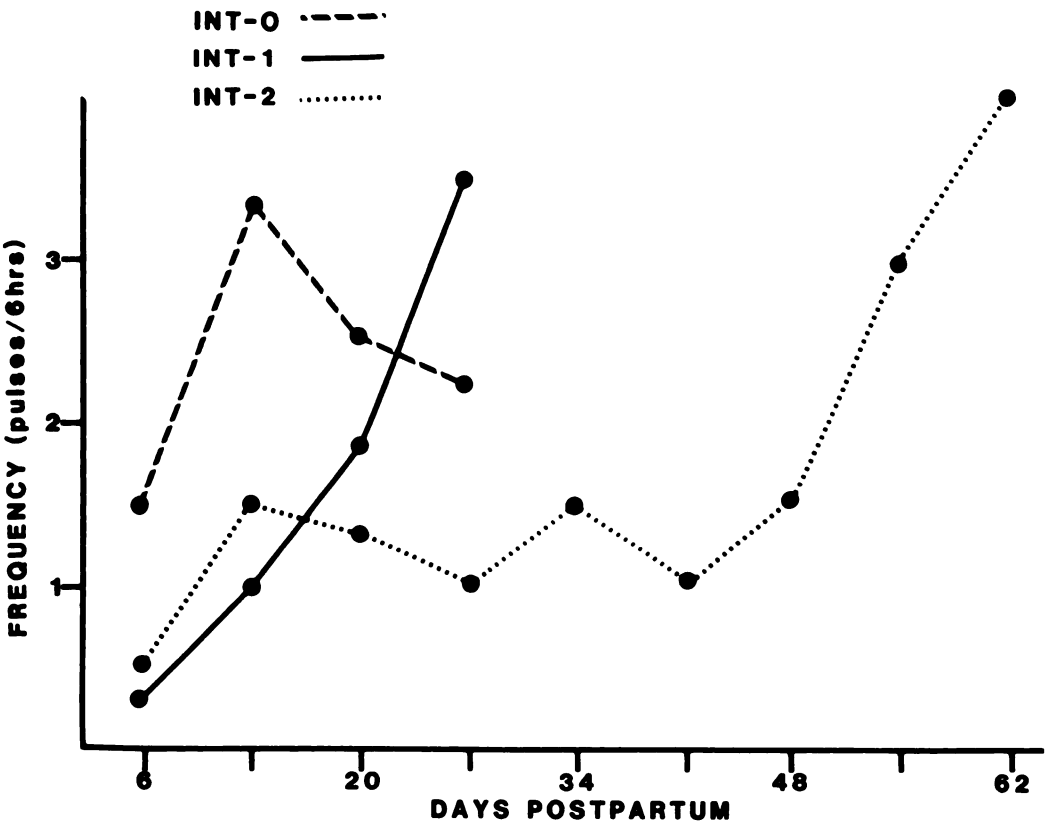

FIG. 2. Frequency of LH pulses in intact nonsuckled (*INT-0*), once daily suckled (*INT-1*) and hypersuckled (*INT-2*) cows.

LH in OVX Cows

No differences in mean LH concentrations (Fig. 3) were observed on Day 6 postpartum (2 days postovariectomy) between the three OVX groups. The OVX-0 cows had an increased ($P<0.05$) mean LH concentration between Days 6 (1.0 ± 0.1 ng/ml) and 27 (9.3 ± 1.9 ng/ml) postpartum. No further changes were detected at the time the study was terminated. Compared with the rapid increase in mean LH concentration, the changes in frequency (Fig. 4) of LH pulses in OVX-0 cows were more gradual, with a linear increase ($P<0.05$) between Days 6 and 55 postpartum (2.28 ± 0.5 to 8.75 ± 0.5 pulses/6 h). No further changes in frequency of LH pulses were observed for the remaining portion of the experiment (Fig. 4).

There were no differences in mean LH concentrations or frequency of LH pulses between the OVX-1 and OVX-2 cows with one exception: at Day 6 postpartum the OVX-2 cows had a lower ($P<0.05$) LH pulse frequency than OVX-1 cows. Mean LH concentrations of 0.91 ± 0.1 and 0.75 ± 0.1 ng/ml for OVX-1 and OVX-2 cows, respectively, were observed on Day 6 postpartum and by 27 days postpartum mean LH concentrations increased to 3.09 ± 1.4 and 4.68 ± 0.9 ng/ml in OVX-1 and OVX-2 cows, respectively. Frequency of LH pulses increased in a linear fashion ($P<0.05$) from Day 6 to Day 55 postpartum in OVX-1 and OVX-2 (from 2.30 ± 1.2 to 6.67 ± 0.9 pulses/6 h in OVX-1 and from 0 to 7.0 ± 0.6 pulses/6 h in OVX-2). The average of the frequency of LH pulses in both ovariectomized suckled groups tended to be lower ($P<0.10$) when compared with the OVX-0 cows, during the period from Day 6 to Day 55 postpartum. The mean LH concentrations of both suckled ovariectomized groups was lower than the mean LH concentration observed in the OVX-0 cows on Days 13, 20 and 27 postpartum ($P<0.05$), however, no differences were detected thereafter.

TABLE 1. Amplitude of LH pulses (ng/ml) in intact (*INT*) or ovariectomized (*OVX*) cows nursing, 0, 1 or 2 calves.[a]

Treatment	N	Days postpartum						
		6	13	20	27	34	41	55
INT-0	4	1.6(1.0)[b]	1.7(0.5)	4.9(1.0)	2.2(1.2)			
INT-1	4	0.6(0)	0.7(0.5)	9.1(2.3)	3.0(0.6)	0.8(0.4)		
INT-2	4	0.5(0.1)	0.3(0.1)	0.3(0.1)	0.6(0.3)	2.5(1.2)	7.4(1.4)	3.2(2.4)
OVX-0	4	0.7(0.1)	4.2(0.7)	13.4(3.0)	9.2(3.1)	4.3(1.2)	6.2(0.9)	6.7(1.7)
OVX-1	3	0.8(0.3)	3.1(2.8)	3.4(1.5)	9.6(4.7)	7.3(3.1)	7.1(2.8)	7.1(4.5)
OVX-2	3	0	1.6(1.3)	4.4(3.1)	24.1(0.1)	7.6(4.2)	9.8(0.8)	12.1(4.5)

[a]Amplitude of LH pulses determined by the methods of Goodman and Karsch (1980).

[b]Mean (SEM).

Significant interactions ($P<0.05$) between the presence or absence of ovaries and the different suckling intensities were observed for all criteria of LH secretion studied.

DISCUSSION

The intervals to the time of initiation of ovarian luteal function following parturition observed in INT cows in this study were similar to the intervals previously reported for non-suckled beef cows (La Voie and Moody, 1976; Radford et al., 1978), cows under limited suckling (Reeves and Gaskins, 1981) and for cows under continuous nursing (England et al., 1973; Radford et al., 1978; Wetteman et al., 1978). Increased mean LH concentrations and frequency of LH pulses as time of ovulation approached in postpartum INT cows have been previously reported in milked dairy cows (Goodale et al., 1978; Carruthers and Hafs, 1980), suckled dairy cows (Carruthers et al., 1980; Peters et al., 1981) and suckled beef cows (Humphrey et al., 1976; Rawlings et al., 1980; Walters et al., 1982a,b). All these observations suggest that as the time postpartum progresses the inhibitory effect of suckling on mean concentration of LH and/or frequency of LH pulses lessens, resulting in greater LH secretion. As a result of the increased gonadotropin secretion, ovulation is thought to result. The LH data from INT cows in the present study would also support this concept.

The increase in serum LH concentrations and frequency of LH pulses observed in OVX-0 cows indicates that the pituitary of postpartum cows is able, if both suckling stimuli and ovarian factors are removed, to secrete LH during the first few weeks after parturition. Similar results have been reported after ovariectomies performed during early postpartum (10 days postpartum) in beef cows (Echternkamp, 1978). The lack of differences in LH concentration in the OVX-1 and OVX-2 treatments during the course of this experiment cannot be explained at the present time; however, similar results were reported by Echternkamp (1978). Comparisons of mean LH concentrations of OVX suckled groups to LH concentrations in the OVX-0 cows indicate that suckling can partially suppress the postcastration rise in mean LH concentrations up to 27 days postpartum in the absence of the ovaries. The increase in serum LH that follows ovariectomy has been reported to be suppressed by suckling in beef cows ovariectomized 21 days after parturition

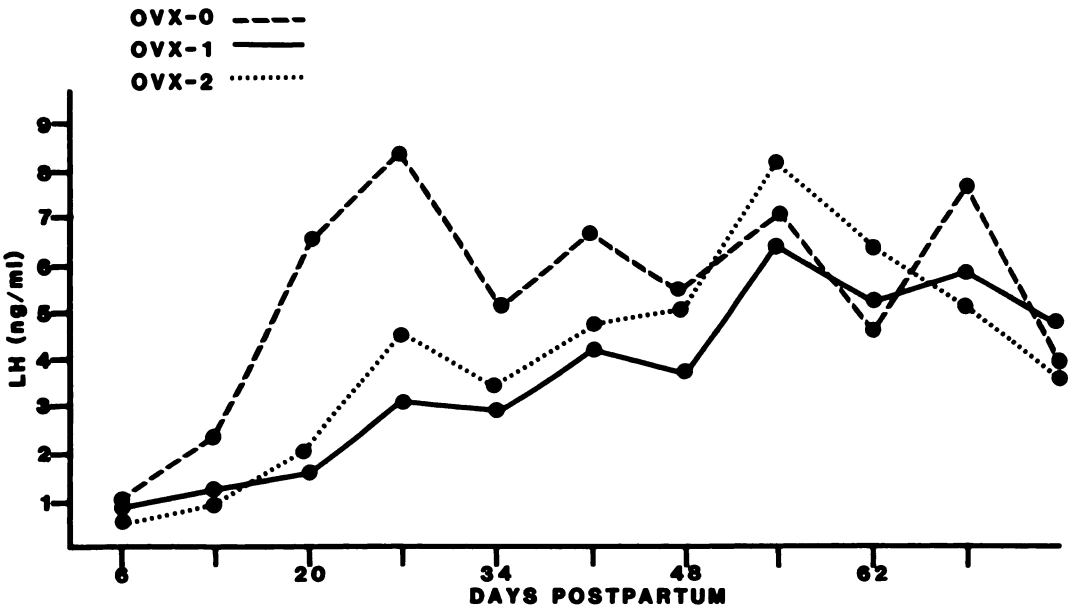

FIG. 3. Mean serum LH concentrations in ovariectomized nonsuckled (*OVX-0*), once daily suckled (*OVX-1*) and hypersuckled (*OVX-2*) cows.

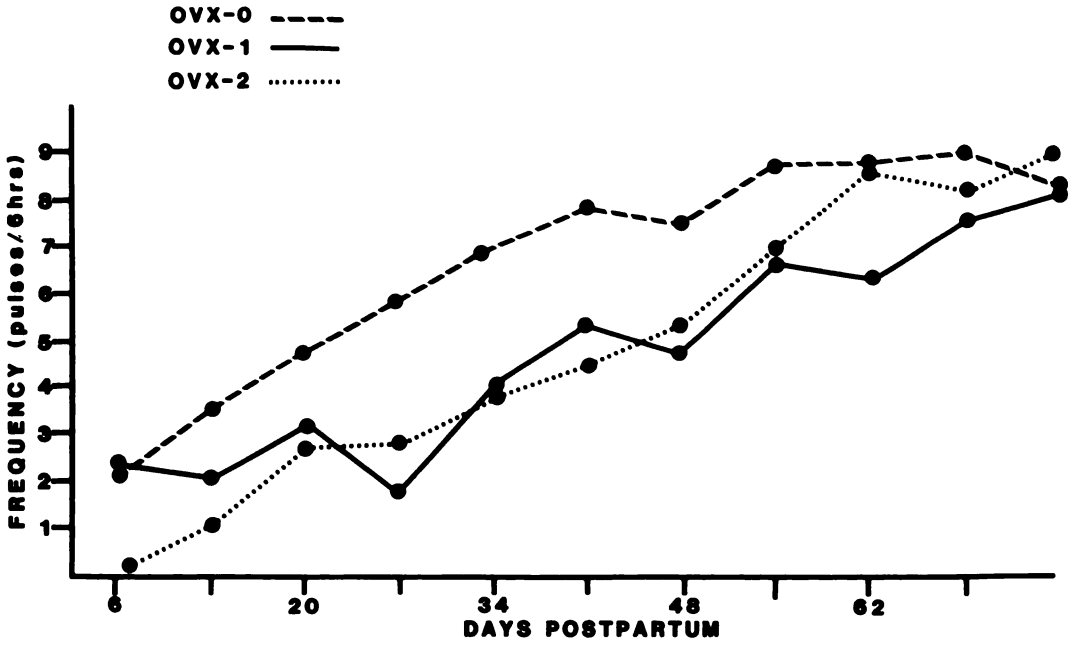

FIG. 4. Frequency of LH pulses in ovariectomized nonsuckled (*OVX-0*), once daily suckled (*OVX-1*) and hypersuckled (*OVX-2*) cows.

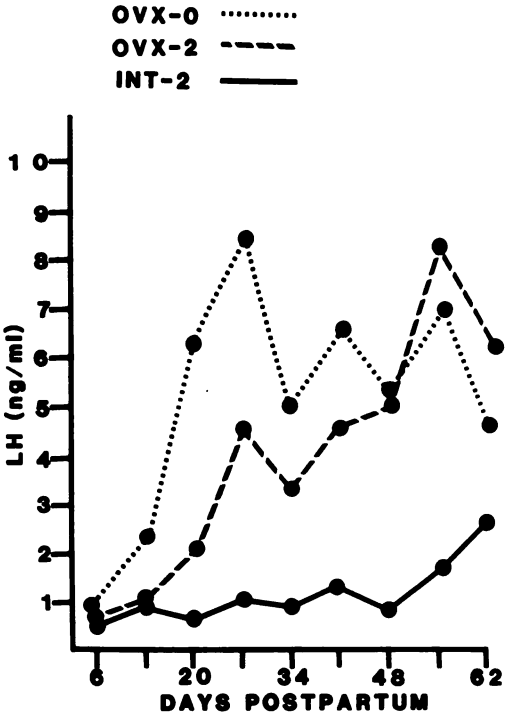

FIG. 5. Effect of suckling and ovarian factors on mean serum LH concentration during the postpartum period in beef cows. The difference between OVX-0 and OVX-2 is the mean LH reduction due to suckling, while the difference between OVX-0 and INT-2 represents the reduction caused by the interaction of suckling and ovarian factors.

(Walters et al., 1982a). Similar observations have been made in OVX postpartum monkeys that were being suckled (Weiss et al., 1976).

Suppression of frequency of LH pulses in OVX cows by suckling could indicate that, during the postpartum period, frequency of episodic release of LH is the endocrine parameter influenced to the largest degree by suckling. Suppression of episodic release of LH by suckling during the postpartum period has been reported previously by Carruthers and Hafs (1980), Carruthers et al. (1980) and Walters et al. (1982a). The increase in mean LH concentrations and frequency of LH pulses observed as time postpartum progresses in INT and OVX cows seems to confirm the hypothesis that the suckling stimulus becomes a less potent inhibitor as time postpartum progresses and that this allows the hypothalamo-hypophyseal axis to increase LH secretion. A similar concept has also been postulated to occur in postpartum lactating rats (Hammons et al., 1973; Smith and Neill, 1977).

The physiological significance of interactions between suckling and ovarian factors found in the present study remains unclear. These interactions could explain the low mean LH concentration and frequency of LH pulses observed in INT-2 cows during this experiment (Figs. 5 and 6), suggesting that during the postpartum period the suckling stimulus and some ovarian factor(s) might act together, to suppress the release of luteinizing hormone-releasing hormone from the hypothalamus, consequently delaying the initiation of estrous cycles in the postpartum suckled beef cow. This concept is reinforced by the fact that the suckling intensities in OVX cows were not able to maintain serum LH concentrations or frequency of LH pulses at levels observed in INT-2 cows. This concept is also supported by the fact that in the absence of suckling (INT-0) and where suckling was limited (INT-1) cows exhibited onset of ovarian activity earlier than INT-2 cows. The confirmation of this hypothesis and the elucidation of the mechanisms by which suckling and ovarian factors

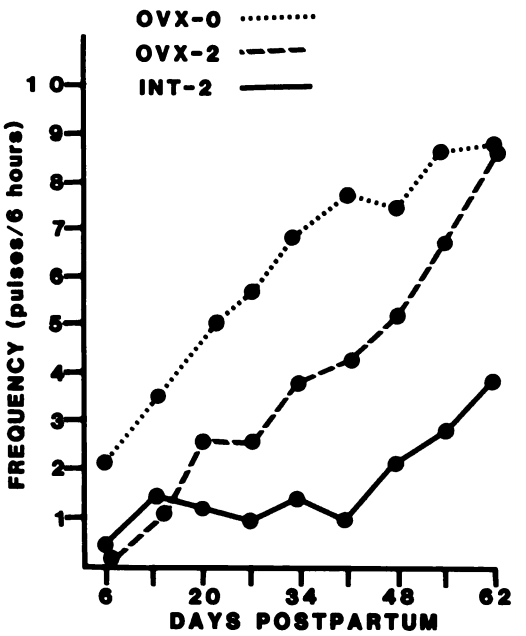

FIG. 6. Effect of sukling and ovarian factors on LH pulse frequency during the postpartum period in beef cows. The difference in pulse frequency between OVX-0 and OVX-2 is the reduction due to suckling, while the difference between OVX-0 and INT-2 represents the reduction caused by the interaction of suckling and ovarian factors.

interact during the postpartum period in intact cows should be the task of future research.

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