Postpartum interval to estrus and patterns of luteinizing hormone (LH) concentrations in first-calf suckled beef cows exposed to mature bulls
by Edward Earl Custer

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal Science
Montana State University

Abstract:
The objectives of this study were to determine if: 1) exposure to mature bulls, initiated during the early postpartum period, hastens the onset of estrus and uterine involution in first-calf suckled beef cows; 2) patterns of IH secretion in first-calf suckled beef cows were altered due to presence of mature bulls throughout the postpartum period; and 3) other factors associated with postpartum cows, such as calving difficulty, weight change, condition score change and progesterone concentrations may be associated with the influence of bulls on postpartum reproductive activity of cows.

Fifty-two Angus x Hereford cows were assigned randomly, in a pairwise manner, by calving date to one of two treatments: exposure to mature bulls (BE; n = 25) or isolated from bulls (NE; n = 24). Male to female ratio was maintained at 1:13 throughout the study. Eight cows from each treatment were fitted with indwelling jugular catheters 5 to 9 d postpartum and blood samples were collected for assay of IH at 15-min intervals for 6 h beginning on D 10 postpartum and at weekly intervals until a cow exhibited estrus. Blood samples for progesterone were collected at weekly intervals from each cow and ovaries of each cow were examined for the presence of a corpus luteum. Cows were observed for estrus twice daily (am:pm) beginning 10 d postpartum. Postpartum weight change, dystocia score, condition score change and time to uterine involution did not differ (P>.10) between treatments. A greater percentage (P<.05) of BE cows exhibited estrus by 60 and 90 d postpartum compared to NE cows (44 and 88 % for BE cows and 25 and 46 % for NE cows). However, there was no interaction between percent of cows exhibiting estrus and days postpartum. Interval to estrus was shorter (P<.05) for BE cows (62 ± 3.7 d) compared to NE cows (77 ± 3.8 d). Changes in mean and baseline IH concentrations, amplitude, frequency and duration of IH pulses throughout the postpartum period were not altered (P>.10) by bull exposure. In addition, mean and baseline IH concentrations, amplitude, frequency and duration of IH pulses during the six weeks before estrus were not altered (P>.10) by bull exposure. There was no difference (P>.10) between treatments in the proportion of cows that showed an increase in progesterone prior to first estrus. In conclusion, exposure of first-calf suckled beef cows to mature bulls throughout the postpartum period hastens the resumption of ovarian cycling activity. However, the mechanism by which bulls cause this response does not appear to involve alterations in postpartum patterns of IH secretion.

POSTPARTUM INTERVAL TO ESTRUS AND PATTERNS OF LUTEINIZING HORMONE (LH) CONCENTRATIONS IN FIRST-CALF SUCKLED BEEF COWS EXPOSED TO MATURE BULLS

by

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliography, and consistency, and is ready for submission to the College of Graduate Studies.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The objectives of this study were to determine if: 1) exposure to mature bulls, initiated during the early postpartum period, hastens the onset of estrus and uterine involution in first-calf suckled beef cows; 2) patterns of LH secretion in first-calf suckled beef cows were altered due to presence of mature bulls throughout the postpartum period; and 3) other factors associated with postpartum cows, such as calving difficulty, weight change, condition score change and progesterone concentrations may be associated with the influence of bulls on postpartum reproductive activity of cows.

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INTRODUCTION

A major goal in beef cattle production is to increase the number of calves produced each year. To accomplish this goal and maximize profits, producers must have an understanding of reproductive processes of the bovine.

Reproductive efficiency in farm animals, especially beef cattle, can be increased by decreasing the interval from parturition to conception. It is well known that failure of females to display estrus early in the breeding season is a primary cause of decreased reproductive performance in beef cattle (Wiltbank, 1970). Furthermore, it is generally accepted that in order to produce a calf each year a cow should conceive and maintain pregnancy by Day 85 postpartum. Therefore it is essential to have at least one normal ovulation before this time. A "normal" postpartum cow has been defined as one which resumes ovarian activity by Day 50 postpartum (Lamming et al., 1981). Thus, it is necessary to understand the physiological mechanisms involved in the restoration of ovarian activity in postpartum cows so this knowledge can be applied to beef cattle production.

Genetic and environmental factors can influence the prepartum and postpartum cow to alter resumption of ovarian activity after parturition. Some of these factors are: breed, age, nutritional and(or) metabolic status, lactation and social interactions. One or a combination of these factors may result in extending the postpartum interval to estrus in beef cows.

The following review identifies and discusses factors which affect the postpartum interval in cattle with emphasis on effects of suckling, nutrition and social interaction.

REVIEW OF LITERATURE

Factors Influencing Postpartum Reproduction

Breeds

Wettemann (1980) stated that interval from parturition until onset of luteal activity is usually longer in beef cattle than in dairy cattle. Postpartum anestrous periods, intervals from parturition to behavioral estrus, range from 30 to 72 d in dairy cows (Graves et al., 1968) and from 46 to 104 d in beef cows (Lauderdale et al., 1968). Similarly, Casida (1968) and Marion and Gier (1968) reported that average interval from calving until first ovulation ranged from 14 to 45 d in dairy cows and from 36 to 71 d in beef cows. Postpartum interval can also be influenced by breed within beef cattle: Angus cows exhibited estrus earlier after calving than Brahman-cross cows (Reynolds et al., 1967) and Hereford and Shorthorn cows (Wiltbank et al., 1961).

Parity

Parity and(or) age may play a role in determining length of postpartum intervals in cattle. Wiltbank (1970) concluded that older cows have shorter postpartum anestrous intervals than younger cows. He reported that average postpartum intervals were 53.4 d for 5-year-old cows, 69.2 d for 4-year-old cows, 66.8 d for 3-year-old cows and 91.6 d for 2-year-old cows. In agreement with Wiltbank (1970), Bellows et al. (1982) reported that cows demonstrated better postpartum reproductive performance than heifers bred to calve at 2 years of age, as measured by: day of the year when first estrus occurred (154.1 and 181.1 d, respectively), postpartum interval to estrus (59.1 and 88.9 d, respectively) and percentage in estrus by the beginning of the breeding season (90.6 and 31.6 %, respectively). Izaike et al. (1984) showed a relationship between the number of calvings and postpartum interval in which they reported as parity increased, postpartum interval decreased in Japanese black cows. In contrast to these studies, Smith and Vincent (1972) failed to show any affect of age on the postpartum interval to estrus in cows, while Stevenson and Britt (1979) reported that the interval to first ovulation tended to be longer for pluriparous than for primiparous dairy cows (18.7 and 16.3 d, respectively), but interval to estrus (26.1 and 27.7 d, respectively) was not different between parities.

Dystocia

Several researchers have shown that dystocia (calving difficulty) increases postpartum interval to estrus and lowers subsequent fertility in beef cows (Wiltbank et al., 1961; Brinks et al., 1973; Laster et al., 1973).

Sex of Calf

Bellows et al. (1982) reported that sex of calf can influence time to estrus in postpartum beef heifers and cows. The authors concluded that dams nursing bull calves returned to estrus more slowly than dams nursing heifer calves, as measured by day of the year when first estrus occurred, (171.5 and 164.4 d for dams nursing bull and heifer calves, respectively). However, there was no difference in postpartum intervals of dams nursing bull calves and dams nursing heifer calves (77.8 and 70.1 d, respectively). It would appear that the influence of sex of calf on postpartum reproductive activity in beef cows requires further investigation before any generalizations can be made.

Uterine Involution

The uterus is usually considered involuted when it has returned to its normal, non-pregnant position and when both horns are similar in diameter and show normal consistency and tone (Casida, 1968).

Several factors influence the time to uterine involution in the cow. Suckling has been reported to hasten time to uterine involution in cows (Casida, 1968; Izaike et al., 1985; Izaike et al. 1986). Bastidas et al. (1984) reported that uterine involution was influenced by age in Brahman cows and Izaike et al. (1986) found that the time required for uterine involution increased with increasing parity in Japanese Black cows. Contrary to these studies Tennant et al. (1967) and El-Fouly et al. (1976) reported that age or parity had no effect on time to uterine involution in beef and dairy cows or Egyptian buffaloes.

Dunn and Kaltenbach (1980) stated that uteri of cows fed high energy diets after calving involuted three days sooner than cows fed moderate energy diets. However, Kiracofe et al. (1969) found no difference in uterine involution rates in cows fed high or low levels of energy or protein. Based on these studies one can conclude that energy and(or) protein in the diet has minimal effects on time to uterine involution in cows.

Numerous studies have found no relationship between uterine involution and interval from calving to first estrus of normal cows (Perkins and Kidder, 1963; Tennant and Peddicord, 1968). Therefore, based on the data presented in these studies it would seem that time to uterine involution is not a limiting factor in determining duration of postpartum anestrous in cattle.

Suckling Stimulus

In cattle, as in other domestic livestock, postnatal support of existing offspring via lactation is in a large degree inhibitory to further procreation (Edgerton, 1980). Clapp (1937) first reported the inhibitory effect of suckling on reproductive function in cows. Since then numerous investigators have reported that postpartum intervals of non-suckled cows are shorter than those of suckled cows (Saiduddin et al., 1968; Oxenreider and Wagner, 1971; Short et al., 1972; Bellows et al., 1974; Carruthers and Hafs, 1980; Lavoie et al., 1981; Acosta et al., 1983; Garcia-Winder et al., 1984; Dunn et al., 1985; Faltys, 1985). Graves et al. (1968) reported postpartum intervals for five studies with a total of 87 suckled cows and 88 cows which were neither suckled nor milked. Mean intervals to first estrus in these studies ranged from 18 to 41 d in the non-lactating cows and 53 to 93 d for suckled cows. Oxenreider and Wagner (1971) found that either twice daily milking or suckling by two calves doubled the postpartum interval to ovulation of Holstein cows. Wettemann et al. (1976) demonstrated that suckling intensity influenced the length of the postpartum interval of range cows. Cows nursing one calf had a shorter interval from parturition to first estrus than cows nursing two calves (67 and 94 d, respectively).

Several investigators have attempted to reduce postpartum interval to estrus in anestrous cows suckling calves by manipulating the suckling stimulus. Bellows et al. (1974) reported that weaning calves at three days of age resulted in an average postpartum interval of 19.6 d compared with 39.1 d in dams nursing calves to Day 35 postpartum, which suggest that weaning, initiated during the early postpartum period, is an effective method to hasten the onset of estrus in postpartum cows. Also, it was reported that early weaning resulted in a shortened postpartum interval to estrus in dams that gave birth to one or more calves. Laster et al. (1973) demonstrated that weaning calves at an average of 55 d after calving had a much greater effect on increasing the number of cows exhibiting estrus from calving to the end of the breeding season in 2-and 3-year-olds (29 and 27 %, respectively) compared to mature cows (16.3 %). Reeves and Gaskins (1981) reported that Angus cows suckling calves once daily for 30 min, beginning either 21 or 30 d postpartum, exhibited estrus 20 d earlier than suckled cows. Similarly, Randel (1981) reported that Brahman x Hereford first-calf heifers suckled once daily for 30 min beginning 30 d after calving reduced postpartum intervals from 168 to 68.9 d, without affecting calf weights at weaning. In agreement with these data, several researchers have reported that short-term calf removal reduced the time from calving to first estrus in postpartum beef cows (Beck et al., 1979; Smith et al., 1979; Odde et al., 1982).

Short et al. (1972) reported that first estrus cycles of cows induced by weaning was of shorter duration than subsequent cycles. More recently, Reeves and Gaskins (1981) reported that more Angus cows that were nursed once daily for 30 min had shorter first estrous cycles (< 11 d in length) than did normally nursed cows. Ramirez-Godinez et al. (1982) reported that all of the Hereford cows that had their calves weaned at approximately 35 d postpartum exhibited first estrous cycles of less than 10 d. In agreement with these studies, Ramirez-Godinez et al. (1981), Ward et al. (1979) and Odde et al. (1980) reported that approximately 80 % of postpartum anestrous cows that exhibited estrus within 10 d after weaning calves had estrous cycles of 7 to 12 d in length. Short-term calf removal, early weaning and once daily suckling are effective in reducing the postpartum interval to estrus without having any detrimental effects on calf performance. However, using such manipulation dramatically increased the incidence of short estrous cycles and there was no reduction in postpartum interval to conception. These aforementioned observations have led investigators to examine mechanisms involved in the inhibitory role of suckling on postpartum interval to estrous.

Short et al. (1972) examined the influence of the udder on postpartum interval to estrus and found that the interval from calving to first estrus was longer for suckled and nonsuckled cows (65 and 25 d, respectively) than for mastectomized cows (12 d), however treatments had no effect on the interval from calving to conception. Therefore the presence of the udder seems to enhance the inhibitory effect of suckling on postpartum interval to estrus in beef cows. In a followup study, Short et al. (1976) reported that mammary denervation failed to decrease the interval from calving to estrus in fall-calving suckled beef cows, which indicates that something unique to the calf, other than the stimulus of suckling alone, acts to inhibit the onset of estrus in postpartum cows. What the stimulus(i) might be is unknown, however, Williams et al. (1984) examined the effect of chronic manual teat stimulation in ovariectomized non-lactating beef cows on the release patterns of LH and found that neither concentration nor pulse frequency of LH were affected by treatment. These results were unexpected, since it has been reported that suckling acts to extend the postpartum interval in beef cows by inhibiting the pulsatile release of LH. Although mechanical teat stimulation was not effective in altering the release patterns of LH this does not imply that a suckling calf or some component associated with a suckling calf does not affect gonadotropin secretion in the cow. In a more recent study, Williams et al. (1987) attempted to show that chronic milking and(or) the physical presence of the calf would have an effect on the postweaning rise of tonic LH secretion in postpartum cows. They found that physical presence of a calf or milking eight times daily did not prevent the postweaning rise in LH from occurring in nonsuckled beef cows, and both factors together did not combine to simulate the physiological state of a suckled cow. The authors suggested that neural input, unique to the calf and transmitted from the level of the teat, seems to be required for the suckling effect to manifest itself in the form of suppressed LH release. The evidence presented in these studies supports the theory that suckling prolongs the postpartum interval of the cow, and it would seem that a combination of factors including the somatosensory stimulus by the calf at the level of the teat and the physical presence of the calf act to inhibit the onset of reproductive activity in the postpartum beef cow.

Nutrition and Body Condition

Several studies have shown that reproductive performance in beef cattle is influenced by nutrition (Dunn and Kaltenbach., 1980). One of the major areas of research emphasis has been on the effect of pre-calving nutrition on subsequent postpartum reproduction in beef and dairy cattle. Falk et al. (1975) reported that interval from parturition to first estrus in Hereford heifers assigned to three energy intakes of 100, 85 and 75 % of the National Research Council (NRC) requirement for beef cattle, approximately 150 d prepartum, were 63, 67 and 78 d for the 100, 85 and 75 % intakes, respectively. Bellows and Short (1978) reported that heifers receiving high feed levels 90 d prior to calving (6.3 or 6.4 kg of total digestible nutrients, TDN) had shorter postpartum intervals and, a greater number of heifers exhibited estrus before the breeding season compared with heifers fed a low level of feed (3.2 or 3.4 kg TDN) for 90 d prior to calving. In a more recent study, Henricks et al. (1986) reported that the number of heifers ovulating before Day 70 postpartum was higher if they were fed to gain 1 kg per day prepartum and postpartum than if they were fed to gain .4 kg per day prepartum and 0 kg per day postpartum. In agreement with these studies, several investigators have reported that low levels of prepartum nutrition prolonged the postpartum interval in beef cattle (Dunn et al., 1969; Clemente et al., 1978; Echternkamp et al., 1982; Ducker et al., 1985). Contrary to these studies, Doornbos et al. (1984) reported no effect of precalving feed level on the interval from parturition to first observed estrus. The contradictory results in this study could be a result of the moderate and high prepartum feed levels of 110 and 135 % of the NRC (1976) requirements for TDN, which is considerably higher than levels used in the previous studies. Based on these studies one can conclude that prepartum level of nutrition, especially low energy intake, has a significant influence on the postpartum interval to estrus of beef cattle.

It has been well established that the postpartum interval can also be influenced by postcalving level of nutrition. Wiltbank (1970) reported that the proportion of cows exhibiting estrus by 100 d postpartum was greater for cows fed a high (22 lb) or medium (13 lb) level of TDN postcalving than cows fed a low level (7 lb) of TDN postcalving (98, 97 and 81 %, respectively). In agreement with this study, Bartle et al. (1984) found that increasing postcalving energy intake shortened the postpartum interval of 2- to 6-year-old cows. Bellows and Short (1978) found that the effect of precalving feed level on subsequent postpartum reproduction is dependent on postcalving feed level. They reported that high postcalving feed level tended to be advantageous when the precalving feed level was high but was detrimental to postpartum intervals when the precalving feed level was low. Low levels of feed postcalving prolong the postpartum interval and high levels of feed postcalving cannot overcome the detrimental effects of low precalving feed levels.

The information on precalving and postcalving feeding levels on postpartum interval to estrus raises questions as to the effect of body condition or composition on postpartum reproductive function. Walters (1981) stated that body condition was the ratio of the amount of fat to the amount of non-fatty matter in the body of the living animal. Rutter and Randel (1984) classified females according to whether or not they were able to maintain body condition after calving, regardless of dietary nutrient level, and reported a dramatic decrease in the postpartum interval of females that maintained body condition compared with females that lost body condition after calving, (31 and 60 d, respectively). Also, they reported that 88 % of the females that were able to maintain body condition after parturition were observed in estrus within 42 d postpartum compared with only 36 % of females that were unable to maintain body condition after calving. Richards et al. (1986) reported that cows calving with a body condition score less than or equal to 4 or more than or equal to 5, had mean postpartum intervals to estrus of 61 and 49 d, respectively. Humphrey et al. (1983) reported that reduced prepartum energy intake did not seem to prolong the postpartum interval of cows in their study, however, backfat thickness for the six suckled beef cows in their study was 8 ± 3 mm at the beginning of the study, 5 ± 3 mm at parturition and 4 ± 2 mm just before first postpartum estrus. They suggested that cows that are in relatively good body condition precalving can loose some weight without having a dramatic effect on the length of the postpartum interval. In agreement with these studies, several researchers have found that postpartum intervals of cows in good body condition were shorter than cows in poor body condition. Body condition at calving, prepartum feed level and to a lesser degree postcalving nutritional level may act with body composition to effect resumption of ovarian activity in the postpartum cow.

Restriction of dietary energy intake and subsequent loss of body condition are inhibitory to postpartum reproductive function in cattle. Several studies have attempted to determine the site of action of this inhibition and its effect on endocrine patterns of postpartum cows. Gombe and Hansel (1973) reported a progressive increase in both basal levels and peaks of LH from the first to third estrous cycles in heifers fed a low level of dietary energy compared to those fed a high level of dietary energy. Also, they found that during the first cycle, plasma progesterone was slightly higher in the low energy group, but became progressively lower in the subsequent cycles. Similarly, Beal et al. (1978) reported that peripheral concentrations of progesterone tended to be reduced when dietary energy was restricted in heifers and cows. However, Spitzer et al. (1978) reported no differences in systemic concentrations of progesterone or LH in yearling beef heifers fed either a ration meeting NRC recommendations for all nutrients or a ration with only one third of the recommended energy. Several studies have reported that low levels of dietary energy either decreased (Echternkamp et al., 1982; Gauthier et al., 1983; Whisnant et al., 1985a) or did not effect the concentration, pulse frequency or pulse amplitude of LH in postpartum cows (Rutter and Randel, 1984; Easdon et al., 1985; Wright et al., 1987). However, Rutter and Randel (1984) reported marked differences in LH characteristics between females that lost and those that maintained body condition after calving, regardless of the level of nutrient intake. Brangus females that were able to maintain body condition after calving released more endogenous LH and more LH in response to an exogenous gonadotropin releasing hormone (GnRH) challenge, than females that lost body condition after calving. Lishman et al. (1979) reported a delayed and reduced response of LH to GnRH in postpartum cows receiving inadequate dietary energy during late gestation and early lactation. However, Beal et al. (1978) found that low dietary energy increased the LH response after a GnRH injection in intact heifers and spayed cows but not in intact cows. In a more recent study, Whisnant et al. (1985b) reported that the LH response to GnRH was greater in postpartum cows fed a low energy diet compared to postpartum cows fed a high energy diet. Rutter and Randel (1984) stated that comparisons of systemic LH levels and pituitary responsiveness between postpartum and normally cycling cows may be misleading due to the possibility that different mechanisms may be involved in regulating onset of cycling activity in the postpartum cow compared with maintenance of cycling in the normal cycling animal.

Echternkamp et al. (1982) demonstrated that release of LH was greater in response to an injection of estradiol benzoate (which could act both at the pituitary and the hypothalamus) in cows fed a high energy diet as opposed to cows fed a low energy diet. Restricting dietary energy intake in the postpartum cow acts at the level of the pituitary by increasing the responsiveness to GnRH and possibly decreasing the sensitivity of the hypothalamus to increased levels of estrogen or increasing the inhibitory effects of low levels of estrogen.

Endocrine and Neuroendocrine Factors Associated with Postpartum Cows

The endocrine and neuroendocrine systems are major physiological regulatory systems involved with resumption of estrous cycles in postpartum suckled beef cows, however, their exact role is not fully understood. The early postpartum period is usually characterized by ovarian inactivity and the absence of estrus in suckled beef cows. The following sections review three major regulatory components of the reproductive system (pituitary, hypothalamus and ovaries) and their relationships in the suckled beef cow.

Anterior Pituitary

Gonadotropins. The anterior pituitary gland synthesizes and secretes glycoprotein hormones that stimulate ovarian activity in females. These are luteinizing hormone (LH), follicle stimulating hormone (FSH) and prolactin (PRL). Pituitary content of LH of suckled cows is low at parturition and increases during the first 30 d of the postpartum period (Graves et al., 1968; Wagner et al., 1969; Cermak et al., 1983). A more recent study indicated that content of LH in the anterior pituitary gland was lowest on Day 1 postpartum and remained low through Day 15 postpartum, however by Day 30 postpartum there was a more than six fold increase in pituitary content of LH compared with that observed on Day 1 (Nett et al. 1988). Carruthers et al. (1980) and

Faltys (1985) reported that concentrations of LH in the anterior pituitary increased after calving independent of suckling. LH synthesis by the anterior pituitary increases during the early postpartum period and does not appear to be limited by the suckling stimulus.

Saiduddin et al. (1968) reported that pituitary FSH content in postpartum cows decreased during the first 20 d postpartum and was lower on Day 20 than on Days 10 or 30. However, Cermak et al. (1983) and Nett et al. (1988) reported that pituitary content of FSH in postpartum cows showed no change during the postpartum period. Carruthers et al. (1980) reported that suckling did not alter the pituitary concentration of FSH. Therefore, pituitary content of FSH does not appear to be a limiting factor in the resumption of reproductive activity in the postpartum cow.

Riesen et al. (1968) reported that pituitary content of PRL in suckled and nonsuckled dairy cows did not change as time postpartum increased from 1 to 30 d, although suckled cows had a tendency to have a lower PRL contents than nonsuckled cows. In contrast, Carruthers et al. (1980) reported that suckling did not alter pituitary content of PRL in dairy cows. PRL synthesis by the anterior pituitary does not increase during the early postpartum period and is not dramatically effected by suckling.

Several researchers have reported that serum concentrations of LH are low at parturition and during the early postpartum period then gradually increase by 30 d after calving in suckled beef cows (Arije et al., 1974; Kesler et al., 1977; Carruthers et al., 1980; Rawlings et al., 1980; Humphrey et al., 1983). Echternkamp and Hansel (1973) reported that LH concentrations in plasma were low (1.0 $ng \cdot ml^{-1}$) at parturition and remained low (.5 to 3.0 $ng \cdot ml^{-1}$) except on the day of estrus at which time large increases were observed. However, the absence of changes in LH in their study was a consequence of infrequent sampling since LH appears to be secreted into the blood in a pulsatile manner (Rawlings et al., 1980; Humphrey et al., 1983). Frequency and amplitude of pulsatile LH release increases prior to the first postpartum ovulatory surge of LH in suckled and nonsuckled beef and dairy cows (Short et al., 1972; Forrest et al., 1979; Goodale et al., 1978; Carruthers and Hafs, 1980; Carruthers et al., 1980; Rawlings et al., 1980; Garcia-Winder et al., 1984).

Many investigations have been performed to examine the nature of postpartum LH release and its physiological significance on resumption of ovulatory cycles. Edwards (1985) examined the influence of short-term calf removal on serum LH concentrations and found that mean LH concentration and LH pulse frequency increased by 48 to 56 h following calf removal and that returning the calf decreased both LH concentrations and LH pulse frequency within 8 h. Furthermore, several researchers have reported that suckling decreased serum LH concentrations and pulse frequencies in postpartum beef and dairy cows (Carruthers and Hafs, 1980; Dunlap et al., 1981; Peters et al., 1981; Walters et al., 1982a; 1982b; Garcia-Winder et al., 1984; Faltys, 1985; Whisnant et al., 1985b; Garcia- Winder et al., 1986). Carruthers and Hafs (1980) and Carruthers et al. (1980) reported that suckling decreased the amplitude of episodic peaks of LH in the postpartum cow.

Taken together data support the hypothesis that suckling inhibits the release of LH in the postpartum cow primarily by a reduction in the frequency and amplitude of pulsatile LH release which results in delaying return to estrus.

Available information on serum concentrations of FSH during postpartum anestrous in cattle is limited. Gauthier et al. (1982) reported that serum concentrations of FSH were higher on Day 50 postpartum than on Day 5 postpartum in anovulatory beef cows. In agreement with this study, Webb et al. (1980) demonstrated that circulating FSH levels remained low during the first two weeks postpartum then increased in two of four dairy cows. However, Dobson (1978) reported that serum FSH concentrations between 21 to 48 d postpartum in dairy cows were not different from concentrations between 0 to 20 d postpartum.

Information on the effect of suckling on serum concentrations of FSH is limited. Rothchild (1960) reported that suckling suppresses FSH secretion in rats and this suppression is directly proportional to litter size. Walters et al. (1982b) reported that serum FSH concentrations of weaned cows were greater than that of suckled cows. However, Carruthers et al. (1980) found that suckling did not affect serum concentrations of FSH in dairy cows during the first 14 d postpartum. The contradictory nature of the data on FSH makes it difficult to determine the role that FSH plays in resumption of cyclic activity in postpartum cows.

Humphrey et al. (1983) reported that serum concentrations of prolactin tended to decrease as time postpartum increased in four of six suckled beef cows. However, the two animals with the shortest postpartum intervals were found to have the highest serum concentrations of prolactin just prior to first estrus. On the other hand Carruthers et al. (1980) reported that ad libitum suckling did not alter basal or milking-induced serum concentrations of prolactin and that suckling by two calves did not increase prolactin secretion in comparison to controls. Similar results have been reported for first-calf beef heifers suckling either one or two calves (Gimenez et al., 1980).

The physiological significance of data for prolactin during the postpartum period in cattle is not well understood, however Cummins et al. (1977) tested whether or not lowering prolactin levels by injecting CB-154 (ergocryptine, a dopamine agonist), effected interval to estrus or conception in first-calf suckled beef heifers. They found that suppression of prolactin with CB-154 did not effect postpartum interval to estrus or conception in these cows. Furthermore, Clemente et al. (1978) reported similar results in mature cows, and Montgomery (1982) reported that injection of bromocryptine was not effective in reducing the interval from calving to first estrus in crossbred beef cows. However, Short et al. (1978) demonstrated that injection of a prolactin secretion inhibitor (CB-154) was effective in reducing the interval from calving to estrus in beef cows. Except for the results of Short et al. (1978), most evidence tends to support the hypothesis that prolactin does not appear to be a limiting factor in the resumption of estrous cycles in the postpartum cow.

Ovarian Steroids and Follicular Growth

Estrogen. At parturition, estradiol-17β levels are elevated and then decline rapidly during the early postpartum period and remain low until just prior to first estrus (Arije et al., 1974; Stevenson and Britt., 1979; Rawlings et al., 1980; Humphrey et al., 1983). Several investigators have reported that serum concentrations of estrogen do not differ between suckled and nonsuckled dairy (Carruthers and Hafs, 1980; Carruthers et al., 1980) or beef cows (Chang et al., 1981) throughout the postpartum period.

Pituitary responsiveness to exogenous estrogen, assessed by inducing a preovulatory-like release of LH, increases as time postpartum increases. Forrest et al. (1981) reported that a single injection of estradiol benzoate (EB) failed to induce a release of LH in 100 percent (6 of 6) of the cows at 2 to 3 d postpartum. However, 4 of 6 and 2 of 5 cows responded to an injection of EB on Days 9 to 10 and 16 to 17 postpartum, respectively. These findings are in agreement with Cermak et al. (1983) who reported that anterior pituitary receptors for estrogen were lowest immediately following parturition and increased to their highest concentration by Day 15 postpartum.

Several researchers have reported that the positive feedback effect of estrogen on LH secretion is delayed by suckling until 2 to 4 wk postpartum in beef (Radford et al., 1978; Short et al., 1979) and dairy cows (Stevenson et al., 1983). Furthermore, Peters (1984) reported that responsiveness of the hypothalamo-pituitary axis to the positive feedback effects of estrogen is functional by Day 10 postpartum and this responsiveness increases as time postpartum increases through Day 17 in suckled postpartum beef cows.

Acosta et al. (1983) reported no significant changes in LH concentrations or number of LH pulses in response to estrogen treatment during the first three weeks postpartum in ovariectomized suckled beef cows. When cows were weaned at 21 d postpartum they found no difference in the frequency of LH pulses between weaned and suckled ovariectomized cows, however, in estrogen-implanted cows, suckling suppressed the frequency of LH release compared to the weaned cows. The authors proposed the hypothesis that suckling contributes to lactational anestrus in the postpartum cow by increasing the sensitivity of the hypothalamus to the negative feedback of low, relatively constant circulating estrogen concentrations which result in a reduction in pulsatile release of GnRH which in turn decreases pulsatile release of LH from the anterior pituitary gland.

Progesterone. Circulating concentrations of progesterone decline after parturition remained at these low basal concentrations until just prior to estrus in suckled beef (Arije et al., 1974; Rawlings et al., 1980; Humphrey et al., 1983) and dairy cows (Stevenson and Britt, 1979). Several investigators have reported a rise in progesterone concentrations 2 to 5 d prior to the first postpartum estrus (Arije et al., 1974; Corah et al., 1974; Stevenson and Britt, 1979; Rawlings et al., 1980; Lavoie et al., 1981; Humphrey et al., 1983). The source of the preestrus progesterone increase in postpartum cows has not been clearly established. Corah et al. (1974) suggested that since there are no apparent functional corpora lutea present, that either luteinized follicles or adrenal glands are responsible for the pre-estrual progesterone rise. Berardinelli et al. (1979) observed a similar progesterone rise prior to first estrus in prepuberal beef heifers and concluded that the source of progesterone was from nonpalpable luteal tissue embedded in the ovary. Castenson et al. (1976) reported that the rise in serum progesterone which precedes first estrus in postpartum cows is frequently due to ovulation and subsequent corpus luteum formation, without expression of estrus.

The relationship of the increase in progesterone before postpartum estrus and the onset of regular cycling activity in postpartum cows is not well understood. However, Lavoie et al. (1981) reported that plasma progesterone levels were greater for nonsuckled than for cows suckled twice daily or suckled ad libitum throughout the postpartum period. In addition, the magnitude of the preestrus progesterone peak was greater in cows suckled ad libitum than in those suckled twice daily or nonsuckled. Furthermore, only two of six cows from the nonsuckled group had normal first estrous cycles preceded by a preestrus rise in progesterone compared to nine of twelve in the two suckled groups. The authors suggested that progesterone is involved in the reestablishment of estrous cycles in the postpartum cow. Faltys (1985) hypothesized that the increase in LH (discussed in previous section) and progesterone that is seen prior to normal estrus cycles in postpartum cows may act to prime an endocrine system that has been acyclic during gestation and the postpartum anestrous period.