



Effect of exposure to bulls on the postpartum interval to resumption of ovarian cycling activity and estrus, patterns of luteinizing hormone secretion and breeding performance in first-calf suckled beef cows

by David Louis Fernandez

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

Montana State University

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Abstract:

Experiment 1. This experiment was designed to determine whether exposing first-calf suckled beef cows to mature bulls for the first 30 days, after 30 days, or continuously postpartum alters the postpartum anestrus period and first service pregnancy rates. Postpartum, first-calf, suckled, crossbred, beef cows were exposed continuously to mature, epididectomized bulls (BE; n = 18), exposed to bulls for the first 30 days postpartum (BE/NE; n = 17), after the first 30 days postpartum (NE/BE; n = 16), or isolated from bulls (NE; n = 18). Weekly blood samples were assayed for progesterone to determine resumption of ovarian cycling activity. Cows were bred for 21 days by AI and then exposed to fertile bulls for an additional 35 days. Postpartum interval to resumption of ovarian cycling activity did not differ ($P > .10$) among BE, BE/NE, and NE/BE cows but was 15.4 days shorter ($P < .05$) than for NE cows. Overall pregnancy rates did not differ ($P > .10$) among treatments. AI pregnancy rates for BE/NE and NE/BE cows were greater ($P < .05$) than for NE cows. Exposure to bulls for the first 30 days postpartum or after the first 30 days postpartum decreases the postpartum interval. Exposure to bulls may improve breeding performance in first-calf suckled beef cows.

Experiment 2. The objectives of this experiment were to determine if exposure to bulls continuously beginning on Day 30 postpartum or for two hours every third day beginning on Day 30 alters the interval to first estrus, patterns of LH secretion, and AI and total pregnancy rates. Postpartum, first-calf, crossbred, suckled, beef cows were assigned to exposure to mature epididectomized bulls (BE; n = 20), isolation from bulls (NE; n = 32), continuous exposure to bulls after Day 30 (NEBE, n = 10), or intermittent bull exposure (BEI, n = 21). Blood samples were collected from indwelling jugular catheters every 15 minutes for 6 hours every third day from Day 30 to 48 postpartum and assayed for LH. Cows were observed twice daily for estrus. On June 1, cows were combined in one pasture and bred by AI for 21 days. More ($P < .10$) BE and NEBE cows exhibited estrus before the AI breeding period than BEI cows. Day of first estrus occurred earlier ($P < .05$) for BE and NEBE cows than BEI and NE cows. AI pregnancy rates were higher ($P < .05$) for NEBE cows than for BE, BEI, and NE cows, which were not different ($P > .10$). Overall pregnancy rates were highest ($P < .05$) for BEI cows. Mean LH concentrations and pulse frequency were higher ($P < .05$) for BEI and NEBE cows than for NE cows. BEI cows had higher ($P < .10$) LH pulse frequency than NEBE or NE cows on the first day of treatment. Exposing cows to bulls increases mean LH concentrations and pulse frequency, but other factors appear to be involved in reducing postpartum anestrus.

EFFECT OF EXPOSURE TO BULLS ON THE POSTPARTUM INTERVAL TO RESUMPTION OF
OVARIAN CYCLING ACTIVITY AND ESTRUS, PATTERNS OF LUTEINIZING
HORMONE SECRETION AND BREEDING PERFORMANCE IN
FIRST-CALF SUCKLED BEEF COWS

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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, bibliographic style and consistency, and is ready for submission to the College of Graduate Studies.

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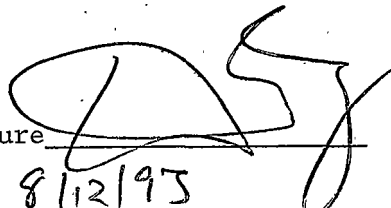
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ABSTRACT

Experiment 1. This experiment was designed to determine whether exposing first-calf suckled beef cows to mature bulls for the first 30 days, after 30 days, or continuously postpartum alters the postpartum anestrous period and first service pregnancy rates. Postpartum, first-calf, suckled, crossbred, beef cows were exposed continuously to mature, epididectomized bulls (BE; n = 18), exposed to bulls for the first 30 days postpartum (BE/NE; n = 17), after the first 30 days postpartum (NE/BE; n = 16), or isolated from bulls (NE; n = 18). Weekly blood samples were assayed for progesterone to determine resumption of ovarian cycling activity. Cows were bred for 21 days by AI and then exposed to fertile bulls for an additional 35 days. Postpartum interval to resumption of ovarian cycling activity did not differ ($P > .10$) among BE, BE/NE, and NE/BE cows but was 15.4 days shorter ($P < .05$) than for NE cows. Overall pregnancy rates did not differ ($P > .10$) among treatments. AI pregnancy rates for BE/NE and NE/BE cows were greater ($P < .05$) than for NE cows. Exposure to bulls for the first 30 days postpartum or after the first 30 days postpartum decreases the postpartum interval. Exposure to bulls may improve breeding performance in first-calf suckled beef cows.

Experiment 2. The objectives of this experiment were to determine if exposure to bulls continuously beginning on Day 30 postpartum or for two hours every third day beginning on Day 30 alters the interval to first estrus, patterns of LH secretion, and AI and total pregnancy rates. Postpartum, first-calf, crossbred, suckled, beef cows were assigned to exposure to mature epididectomized bulls (BE; n = 20), isolation from bulls (NE; n = 32), continuous exposure to bulls after Day 30 (NEBE, n = 10), or intermittent bull exposure (BEI, n = 21). Blood samples were collected from indwelling jugular catheters every 15 minutes for 6 hours every third day from Day 30 to 48 postpartum and assayed for LH. Cows were observed twice daily for estrus. On June 1, cows were combined in one pasture and bred by AI for 21 days. More ($P < .10$) BE and NEBE cows exhibited estrus before the AI breeding period than BEI cows. Day of first estrus occurred earlier ($P < .05$) for BE and NEBE cows than BEI and NE cows. AI pregnancy rates were higher ($P < .05$) for NEBE cows than for BE, BEI, and NE cows, which were not different ($P > .10$). Overall pregnancy rates were highest ($P < .05$) for BEI cows. Mean LH concentrations and pulse frequency were higher ($P < .05$) for BEI and NEBE cows than for NE cows. BEI cows had higher ($P < .10$) LH pulse frequency than NEBE or NE cows on the first day of treatment. Exposing cows to bulls increases mean LH concentrations and pulse frequency, but other factors appear to be involved in reducing postpartum anestrus.

INTRODUCTION

The primary goal of beef cattle producers is to produce a live calf from each cow every year. It is well established that long postpartum anestrus periods are a major obstacle in the attainment of this goal (Wiltbank, 1970). Cows must conceive by 85 days postpartum in order to maintain a one year calving interval. Cows with long postpartum intervals have lighter calves at weaning and are less likely to conceive during the breeding season the following year. Therefore, it is imperative to know and understand the factors controlling postpartum anestrus and the mechanisms whereby they exert their effects.

Many factors have been shown to affect postpartum interval. Dairy breeds have been shown to return to estrus by 14 to 17 days postpartum (Marion and Gier, 1968; Webb et al., 1980), whereas suckled beef cows have been shown to require from 54 to 93 or more days to return to estrus (Wiltbank, 1970). Bellows et al. (1982) reported that first-calf cows had poorer postpartum reproductive performance as measured by day of first estrus, postpartum interval, percentage in estrus by the beginning of the breeding season and pregnancy rate following a 45 day AI breeding season than older cows. Data presented by Patterson et al. (1991) indicate that postpartum interval to first estrus increased by 3.9 ± 0.2 days for each unit increase in calving difficulty score. Furthermore,

Bellows et al. (1982) reported that cows nursing female calves had higher pregnancy rates than cows nursing male calves. However, Tennant and Peddicord (1968) reported that first service conception rates did not differ between involuted and non-involuted cows. Peters and Riley (1982) reported that there is a highly significant negative correlation ($r = -.737$) between the daily photoperiod one month before calving and the length of the postpartum anestrous period. Poor nutrition (Randel, 1990) and suckling (Williams, 1990) have both been shown to increase the postpartum anestrous period.

The reproductive processes of females can be altered by the presence of males. This effect, generally referred to as biostimulation, has been established in many laboratory and domestic animal species. In domestic animal species, biostimulation can alter the postpartum interval to estrus, ovulation and pregnancy rates. Since 1984 it has been known that bulls can influence the postpartum interval to estrus in cows. However, the physiological mechanisms involved in this effect are not known. The following review of the literature will discuss the physiological changes associated with nutrition, suckling and biostimulation with particular emphasis on biostimulation.

REVIEW OF THE LITERATURE

Factors Affecting Postpartum ReproductionNutrition and Body Condition

Low levels of energy before (Dunn et al., 1969; Falk et al., 1975) or after (Dunn et al., 1969; Wiltbank, 1970) calving increased the postpartum interval to resumption of ovarian cycling activity (Perry et al., 1991b). In fact, many pluriparous cows on a low plane of nutrition failed to display estrous behavior during the next breeding season (Wiltbank, 1970). Additionally, first-calf beef cows fed low energy rations prepartum had more dystocia and weaned fewer live calves (Falk et al., 1975). On the other hand, cows fed high energy rations had shorter postpartum intervals to estrus (Bellows and Short, 1978; Henricks and Rone, 1986) and ovulation (Ducker et al., 1985), higher frequency of cows exhibiting estrus before the breeding season (Bellows and Short, 1978; Henricks and Rone, 1986), more cows ovulating by Day 150 postpartum (Perry et al., 1991b) and higher pregnancy rates (Bellows and Short, 1978; Henricks and Rone, 1986; DeRouen et al., 1993). Recently, Oss et al. (1993) reported that cows on a high fat diet had longer postpartum intervals to estrus, implying that the source or form of energy may also be important in altering postpartum reproduction. Rutter and Randel (1984) established that cows on a high plane of

nutrition had shorter postpartum intervals to estrus than cows on a maintenance diet, which in turn had shorter postpartum intervals to estrus than cows on a low plane of nutrition.

Various combinations of pre- and postpartum nutritional regimens have been shown to have differing effects. Houghton et al. (1990) reported that cows fed a low energy diet prepartum and a high energy diet postpartum had shorter postpartum intervals to estrus than any of the other treatments. Further, they showed that cows fed the Low-High regimen had a greater percentage of cows exhibiting estrus by 60 days postpartum than Low-Low cows (Houghton et al., 1990). These results indicate that postpartum nutrition has more effect on postpartum reproductive performance than prepartum nutrition. Contrary to these results, Dunn and Kaltenbach (1980) concluded that prepartum nutrition was more important than postpartum nutrition in reducing the postpartum interval. However, Doornbos et al. (1984) determined that the effect of prepartum nutrition on pre-calving, calving and postpartum data was non-significant. The lack of differences found by Doornbos et al. (1984) may have been due to a relatively high plane of nutrition (135% and 110% of NRC requirements for high and low energy treatments, respectively) fed to cows in both treatments.

One question that arises from these data is how nutritional manipulation alters ovarian response. Does nutrition alter follicular development and(or) function?

Henricks and Rone (1986) reported that estradiol-17 β concentrations were higher and there were more medium-size follicles on Day 28 and small-size follicles on Day 46 in cows on a high energy ration than in cows on a low energy ration. Perry et al. (1991b) determined that cows receiving lower energy levels prepartum had fewer large follicles; cows receiving low levels of energy postpartum had fewer small and large follicles, while cows receiving low levels of energy both pre- and postpartum could not mature follicles beyond the small stage during the postpartum anestrus period. Cows receiving high energy both pre- and postpartum had fewer medium-size follicles but more large follicles than cows fed any of the other rations. It appears that low energy rations retard follicular growth and development.

Progesterone secreted by the corpus luteum is responsible for preparing the uterus for implantation. Gombe and Hansel (1973) and Beal et al. (1978) found that plasma progesterone levels were lower for heifers fed a restricted energy diet. The low levels of progesterone in restricted-fed animals could have been due in part to the low rate of follicular development caused by poor nutrition reported by Henricks and Rone (1986) and Perry et al. (1991b). Furthermore, energy restricted heifers had smaller corpora lutea with lower progesterone contents on Day 10 of the third postpartum estrous cycle (Gombe and Hansel, 1973). Contrary to these findings, Gauthier et al. (1983) concluded that underfeeding

during the first 45 days postpartum increased progesterone levels.

Bartle et al. (1984) showed that the postpartum interval to estrus was related to estimated percent body fat, i.e. body condition and relative energy intake (ME intake ÷ energy requirement). Cows in moderate body condition at parturition returned to estrus regardless of energy intake. However, cows in moderate and thin condition at parturition had higher first service conception rates than cows that were overconditioned at parturition (Houghton et al., 1990). Postpartum intervals could be shortened by increasing energy intake above 100% of requirements (Bartle et al., 1984; Richards et al., 1986). Rutter and Randel (1984) concluded that cows that maintained their body condition regardless of diet had shorter postpartum intervals than cows that lost body condition. Similarly, cows in good body condition can lose some weight postpartum without affecting postpartum interval (Humphrey et al., 1983). Richards et al. (1986) and Osoro and Wright (1992) reported that postpartum nutritional management had no effect on interval to estrus or interval to pregnancy. They stated that body condition score at calving was the most important factor influencing return to estrus and pregnancy. Body condition at start of mating was less important than body condition at parturition, and body condition at the end of mating had no effect on reproductive performance of Hereford X Friesian and Blue-Grey cows (Osoro and Wright, 1992).

Body condition may interact with or affect other factors to influence the postpartum anestrus period. Perry et al. (1991b) reported that correlation coefficients between body condition score and number of small, medium and large follicles were .48, .19 and .66, respectively. Body condition scores were also correlated with mean LH concentrations (Perry et al., 1991b), LH pulse frequency (Wright et al., 1990) and pituitary content of LH on Day 30 postpartum (Connor et al., 1990). However, Wright et al. (1990) reported that mean LH concentrations were not affected by body condition.

Dunn et al. (1969) concluded that pregnancy rate was directly related to postpartum energy intake. Cows fed a high level of energy had higher pregnancy rates than cows fed moderate and low energy levels. Cows fed the high energy ration before calving also had higher pregnancy rates during the first 100 days postpartum than cows fed the lower energy ration prepartum. Dairy heifers fed a high level of energy prepartum and a low level postpartum had higher pregnancy rates to AI (first service) than those fed a High-High or a Low-High diet and had a shorter interval from calving to pregnancy (Ducker et al., 1985). However, Houghton et al. (1990) reported that while high postpartum energy intake resulted in higher pregnancy rates, change in prepartum weight and body condition did not affect postpartum reproductive performance. Reduced pregnancy rates in heifers fed restricted energy diets did not appear to be due to reduced

fertilization rates (Spitzer et al., 1978).

Fewer protein restricted cows exhibited estrus, had reduced first service conception rates and overall pregnancy rates and had longer interval to estrus, first service and conception than cows fed an adequate protein diet (Sasser et al., 1988). However, Farthing et al. (1993) reported that cows receiving protein supplements had lower fall pregnancy rates. Regardless of dietary protein content, weight at first estrus, weight at first service and average daily gain were negatively correlated with postpartum intervals to first estrus and first service (Sasser et al., 1988).

The effect of nutrition on serum FSH concentrations is unclear and the reports in the literature are conflicting. Gauthier et al. (1983) reported that underfeeding during the first 45 days postpartum decreased FSH concentrations. However, Perry et al. (1991b) stated that patterns of FSH secretion were not affected by diet at any time. Nolan et al. (1988) found that FSH concentrations were higher in protein deficient cows than in adequately fed cows.

Reports on the effect of nutrition on LH concentrations indicate that LH concentrations increase with proper nutrition. Gauthier et al. (1983) and Hall et al. (1991) found that cows on a low energy diet had lower mean LH concentrations and lower pulse frequency of LH in serum (Perry et al., 1991b) than cows on a high energy diet. Likewise, Echternkamp et al. (1982) and Perry et al. (1991b) reported

that cows receiving high levels of energy prepartum had increased mean concentrations of LH postpartum and tonic LH secretion was correlated with daily gain ($r = 0.75$, Echterkamp et al., 1982; $r = 0.58$, Gauthier et al., 1983), supporting the conclusion that undernutrition causes low gonadotropin concentrations. Furthermore, LH concentrations increased with time postpartum in cows on a high energy diet (Hall et al., 1991) and pulse frequency increased in cows fed adequate crude protein (Nolan et al., 1988), but not cows fed low energy or low protein diets. By 60 days postpartum, LH pulse frequency in cows fed the adequate protein diet was twice as great as deficient cows (Nolan et al., 1988). However, Gombe and Hansel (1973) reported that dairy heifers on an energy restricted diet had higher mean LH concentrations throughout the experimental period and had higher basal and peak LH concentrations during the third estrous cycle than heifers fed adequate energy.

Echterkamp et al. (1982) reported that first-calf beef cows fed a high (150% NRC prepartum and early postpartum) plane of nutrition released more LH when challenged with 10 mg estradiol benzoate than cows fed 100% NRC rations. The interval from estrogen injection to peak LH release was longer in cows fed the lower energy diet. However, dietary protein did not affect LH response to exogenous estrogen treatment (Nolan et al., 1988). At calf removal, cows on a high plane of nutrition had higher serum LH concentrations than cows on

a low plane of nutrition. Serum LH concentrations increased by 24 hours after calf removal for high energy cows but not until 48 hours after calf removal for low energy cows (Whisnant et al., 1985a).

Beal et al. (1978) determined that low energy diets increased LH release after GnRH injection in heifers and spayed cows but not in intact cows or adequate energy spayed cows. However, restricted energy spayed cows had higher pituitary LH content than intact cows. The authors concluded that energy restriction may influence LH release directly at the pituitary as well as indirectly through effects on ovarian steroid production. Another explanation may be that GnRH production or release may be reduced in cows on low energy diets. Contrary to this study, Lishman et al. (1979) determined that serum LH concentrations in underfed (60% NRC prepartum) cows rose less rapidly and to a lower peak value than in well-fed (115% NRC prepartum) cows when challenged with GnRH.

Nolan et al. (1988) determined that cows fed an adequate protein diet had higher LH peaks and total LH under the curve in response to GnRH injection than protein deficient cows. GnRH induced peak height increased linearly in adequately fed cows with time postpartum but not in cows on the deficient protein diet. However, cows on the protein deficient diet responded more rapidly to GnRH injection than cows fed the adequate protein diet. Duration of response was not affected

by diet. Anterior pituitary GnRH receptor numbers did not differ among diets. Pituitary concentrations of LH were greatest in cows on the protein deficient diet at 30 days postpartum. Pituitary LH concentrations of cows fed the protein deficient diet declined to concentrations similar to those of cows fed the adequate protein diet with increasing time of protein deficiency.

Suckling Stimulus

Suckling has been shown to affect postpartum anestrus in many experiments. Non-suckled cows and once daily suckled cows had shorter postpartum intervals to estrus than cows suckled twice daily, ad libitum or hypersuckled (Smith and Vincent, 1972; Laster et al., 1973; Carter et al., 1980; Odde et al., 1980; La Voie et al., 1981; Randel, 1981; Reeves and Gaskins, 1981; Ramirez-Godinez et al., 1982; Garcia-Winder et al., 1984; Houghton et al., 1990). Furthermore, Bellows et al. (1974) found that early weaning of calves reduced the postpartum interval to first estrus regardless of whether cows give birth to singles or twins. Cows suckling their own or foster calves had shorter intervals to first estrus than cows suckling two calves (Wettemann et al., 1978). Silveira and Williams (1991) reported that weaned cows and cows nursing calves other than their own had a higher incidence of ovulation than cows nursing their own calves by Day 26 to 29 postpartum. However, Montgomery (1982) reported that while

interval to first elevation of progesterone was shorter for cows suckled once daily than for cows suckled twice daily or ad libitum, interval to first observed estrus did not differ among treatments. Carruthers and Hafs (1980) reported that suckled cows had longer postpartum intervals to first ovulation than milked cows. However, Carter et al. (1980) reported interval to first ovulation and to conception were not different for suckled and weaned cows.

Results reported by Odde et al. (1980) and Ramirez-Godinez et al. (1982) indicate that beef cows exhibited a second estrus 8 to 10 days after the first postpartum estrus which resulted from calf removal, and that cows nursed once daily tended to have short cycles (Reeves and Gaskins, 1981). No cows showing short cycles conceived on the first estrus (Odde et al., 1980). Furthermore, Carter et al. (1980) reported that not only did all non-suckled cows demonstrate short cycles, they required more inseminations per conception. Early weaned cows (Houghton et al., 1990) and cows suckled once daily (Reeves and Gaskins, 1981) had lower first service conception rates than normally weaned cows. Similarly, in mastectomized and non-suckled cows, shorter intervals to estrus required more services per conception; thus, interval from calving to conception was not affected (Short et al., 1972). These results indicate that cows with shorter postpartum intervals have a higher incidence of short cycles and lower first service conception rates than cows with longer

postpartum intervals. However, in a study involving only suckled cows, Perry et al. (1991a) reported that all cows had short (8.5 day) estrous cycles. Furthermore, Laster et al. (1973) found that weaning increased overall conception and percentage of cows exhibiting estrus from calving to the end of the breeding season and once-daily suckling increased pregnancy rates in Brahman cross cows (Bluntzer et al., 1989).

The presence of mammary tissue itself appears to be sufficient to prolong postpartum anestrus. Short et al. (1972) demonstrated that mastectomized cows had shorter postpartum intervals to first estrus than non-suckled cows, which had shorter postpartum intervals to first estrus than suckled cows. Furthermore, Short et al. (1976) demonstrated that neural input from the udder was not responsible for the increase in the postpartum interval. Williams et al. (1987) suggested that the ability of the suckling calf to suppress tonic LH secretion derives from unique cues that are not fully simulated by frequent milking and the presence of the non-suckling calf, however, both of these factors may modulate behavioral estrus. Viker et al. (1989) and Stevenson et al. (1993) found that mastectomized cows that remained with their calves had longer postpartum intervals to estrus and ovulation than mastectomized cows whose calves were not present. Furthermore, Stevenson et al. (1993) and Viker et al. (1993) reported that stimulation of the inguinal area of mastectomized cows by their calves increased the postpartum

interval to ovulation compared to mastectomized cows which could only come into contact with their calves from the neck forward. Suckled control cows and mastectomized cows whose calves had unlimited access to the dam had similar postpartum intervals to ovulation (Stevenson et al., 1993).

Initiation and increase in LH pulsatility is the most consistently reported change preceding the postpartum return to ovarian cycling activity (Peters and Lamming, 1990). Minaguchi and Meites (1967) demonstrated that anterior pituitaries from suckled rats released more prolactin but less LH than anterior pituitaries from cycling rats. Suckling also reduced the weight of pituitaries, ovaries and uteri (Minaguchi and Meites, 1967). However, weaning had no effect on pituitary weights or pituitary LH and FSH concentrations in cows (Walters et al., 1982b). Cows in the weaned treatment were weaned on Day 21 postpartum, but GnRH induced release of LH in vitro was not affected by time after Day 21 to slaughter for weaned, suckled or estrous cows. However, LH release was similar between weaned cows and cows exhibiting estrous cycles and greater for weaned than suckled cows.

Carter et al. (1980) reported that non-suckled cows had higher systemic LH concentrations. LH concentrations rose during the first 20 days postpartum for non-suckled and once daily suckled cows, but not until Day 48 did a sustained increase occur in hypersuckled cows (Garcia-Winder et al., 1984). In fact, mean, peak frequency (Carruthers and Hafs,

1980; Whisnant et al., 1985b) and amplitude (Carruthers and Hafs, 1980; Chang et al., 1981; Whisnant et al., 1985b) of serum LH concentrations in weaned cows rose rapidly within 48 hours of calf removal whereas LH concentrations during the same time period did not change for suckled cows. The reason for depressed serum LH concentrations in suckled cows may be due to a 60% decrease in pulse frequency and a 40% decrease in amplitude reported by Carruthers et al. (1980). In support of these results, Walters et al. (1982a) found that weaned cows had more LH pulses than suckled cows. Additionally, Carruthers and Hafs (1980) stated that suckled cows had lower frequency and amplitude of episodic secretion of LH compared to milked cows. Furthermore, cows nursing their own calves had lower mean LH concentrations on Days 16 to 19 postpartum than weaned cows or cows nursing calves other than their own (Silveira and Williams, 1991). Thus, suckling may delay postpartum ovulation by depressing episodic LH secretion (Carruthers and Hafs, 1980; Dunlap et al. 1981). However, Chang et al. (1981) reported that frequency of LH pulses and basal concentrations did not differ between suckled and non-suckled cows. Likewise, although cows suckled by two calves had a significantly longer postpartum period than those suckling one, average baseline and peak concentrations of LH were not different (Gimenez et al., 1980). The number of suckling episodes did not decrease with time postpartum, but the duration of each episode did decrease (Gimenez et al.,

1980). Furthermore, plasma LH concentrations were higher in mastectomized and non-suckled cows by Day 7 than suckled cows (Short et al., 1972). However, mean maximum LH concentrations and LH pulse frequency were higher for the mastectomized, unlimited calf access cows than suckled controls (Stevenson et al., 1993). These results support the hypothesis that suppression of LH secretion is not solely responsible for prolonged postpartum anestrus or that mastectomy per se affects LH release and mastectomized cows may not be appropriate models to evaluate LH secretion during the postpartum anestrus period.

It is possible that cortisol and(or) prolactin have some effect on LH secretion in suckled cows as both have been shown to be elevated during nursing. However, cortisol concentrations remained constant except for a transient rise at 9 to 12 hours after weaning. Thus, cortisol appears to have no effect on LH secretion (Whisnant et al., 1985b; Faltys et al., 1987), and cortisol concentrations did not affect GnRH induced LH response in multiparous Holstein cows (Lefebvre et al., 1990). Alterations in prolactin, total glucocorticoids, progesterone or estradiol-17 β do not appear to mediate directly the effects of suckling on postpartum episodic LH secretion and(or) ovulation (Carruthers and Hafs, 1980). However, in first-calf beef cows, fewer LH peaks were observed during suckling periods and when prolactin was elevated than at other times (Gimenez et al., 1980). Nevertheless, Convey

et al. (1983) concluded that suckling does not acutely affect LH or FSH concentrations.

Calf removal for 72 hours (but not calf removal + GnRH at 72 hours) decreased the postpartum interval to estrus and increased pituitary responsiveness to GnRH challenge. It did not, however, alter circulating progesterone concentrations or luteal life span of corpora lutea induced by GnRH injection (Dunn et al., 1985). Smith et al. (1979) reported that use of calf-removal (48 to 60 hours) in combination with Syncro-Mate-B, a synthetic progestin, increased the number of cows detected in estrus and pregnant by 4 days and 21 days after implant removal. Similarly, Ramirez-Godinez et al. (1981) found that all cows treated with 6 mg implants of Norgestomet, a synthetic progestin, 9 days before weaning showed estrus within 10 days although 3 of 10 showed a short cycle. Cows that received implants of Norgestomet after weaning exhibited a normal luteal phase (6 of 10 within 10 days, 10 of 10 within 25 days of weaning), and 6 of 9 cows that were simply weaned showed estrus within 10 days (9 of 9 within 25 days) although 5 of 6 showed a short cycle. All the other cows either had a normal estrous cycle length or conceived at first service. Conception rates at first service were higher for cows treated with Norgestomet than cows that were not.

Acosta et al. (1983) determined that during nursing estradiol-17 β treatment suppressed serum LH concentrations below LH concentrations of non-estradiol treated cows, but

after weaning, estradiol treatment stimulated LH release above that of non-estrogen treated cows. The authors conclude that the suckling stimulus increases the sensitivity of the hypothalamus to the negative feedback of estrogen during the postpartum period resulting in reduced LH secretion.

Peters et al. (1981) reported that between Days 13 and 20 postpartum a distinct pulsatile pattern of LH secretion was detected in milked but not suckled cows. Mean concentrations and pulse frequency of LH were not affected by teat stimulation and were not related to prolactin or cortisol release. Mechanical stimulation of the teat is not singly effective in altering the pattern or quantity of tonic LH secretion in ovariectomized cows (Williams et al., 1984).

Endocrine and Neuroendocrine Factors Associated with Postpartum Cows

The endocrine system is one of the two regulatory systems used by organisms to maintain homeostasis and perform the functions associated with survival and reproduction. Reproduction is profoundly affected by the endocrine system because most reproductive functions require long term regulation and endocrine effects are long lasting when compared to neural inputs. The endocrine system cannot, however, act in isolation. The hypothalamus provides the link between the neural and endocrine systems and exerts profound control over the processes involved in reproduction. The

following sections attempt to clarify the role of this system regarding the resumption of reproductive function during the postpartum anestrus period.

Anterior Pituitary

Gonadotropins. The change most consistently reported to precede the postpartum return to ovarian cycling activity is the onset and increase in LH pulsatility (Walters et al., 1982a; Peters and Lamming, 1990). LH is a glycoprotein hormone secreted by the gonadotropic cells of the anterior pituitary. Many researchers have established that peripheral LH concentrations increase with time postpartum (Echternkamp and Hansel, 1973; Kesler et al., 1977; Fernandes et al., 1978; Goodale et al., 1978; Peters et al., 1981; Walters et al., 1982b; Cermak et al., 1983; Humphrey et al., 1983; Garcia-Winder et al., 1984; Edwards, 1985; Garcia-Winder et al., 1986; Nett et al., 1988; Wright et al., 1990). Moreover, the change in basal serum LH concentrations of weaned cows was greater than the change in LH concentrations of suckled cows (Walters et al., 1982b). In addition, LH pulse frequency (Goodale et al., 1978; Rawlings et al., 1980; Webb et al., 1980; Humphrey et al., 1983; Garcia-Winder, et al., 1984; Edwards, 1985; Garcia-Winder et al., 1986; Savio et al., 1990; Wright et al., 1990) and amplitude (Goodale et al., 1978; Rawlings et al., 1980; Webb et al., 1980; Garcia-Winder et al., 1986; Wright et al., 1990) have been shown to increase

with time postpartum. However, calf return decreased LH concentrations and pulse frequency within 8 hours in acyclic cows but no changes were seen in cyclic cows (Edwards, 1985). It would appear that once ovarian cycling activity has been initiated, LH concentrations are not affected by suckling.

Moss et al. (1985) found that anterior pituitary concentrations of LH were lower at 5 and 10 days postpartum than at 30 days. Concentrations of LH were similar between estrous and 30 day postpartum cows. Only cows slaughtered on Day 5 postpartum released less LH in vitro in response to GnRH challenge than the other cows. In contrast to these studies, Arije et al. (1974) found that serum LH concentrations from 3 weeks before calving to 72 days after calving did not differ. LH peaked approximately 5 hours after estrus and returned to baseline concentrations shortly thereafter.

Garcia-Winder et al. (1984) reported that mean concentrations and LH pulse frequency from Days 6 to 27 and Days 6 to 55 were lower for ovariectomized cows suckled once daily or hypersuckled than ovariectomized cows that were not suckled. In a more recent experiment, Garcia-Winder et al. (1986) found no difference in mean LH concentrations, pulse frequency or amplitude between intact and ovariectomized cows before and after suckling. However, ovariectomized estrogen-treated cows had lower mean LH concentrations after suckling on Days 44 and 58 postpartum. Forrest et al. (1979) reported that injection with .5 mg of estrone or calf removal resulted

in elevated serum LH concentrations, but the initial elevation in LH concentrations occurred earlier and lasted longer in cows that had their calves removed than in cows treated with estrone. Maximum serum LH levels did not differ between treatments. There were more peaks on Day 2 for cows that had their calves removed than either controls or estrone treated cows. The results of these experiments indicate that while estrogen interacts with suckling to reduce LH concentrations, the suckling-estrogen interaction is not solely responsible for decreased LH during the postpartum anestrus period. Meyers et al. (1989) concluded that suckling, at least partially, suppresses the release of LH through endogenous opioid mechanisms.

Despite the effect suckling has on serum LH concentrations, suckling appears to have no effect on pituitary LH content (Wagner et al., 1969; Walters et al., 1982b). Wagner et al. (1969) reported that there appeared to be a slight, but non-significant, rise in pituitary LH content from Days 7 to 30 postpartum, but Nett et al. (1988) found that LH increased rapidly from Days 15 to 30. In vitro response of pituitary explants from suckled cows secreted 50% less LH in response to LHRH or K^+ than those from non-suckled cows (Carruthers et al., 1980; Walters et al., 1982b). Decreased pulse frequency and amplitude of LH release as well as reduced ability to respond to LHRH may be the cause of suckling induced anestrus (Carruthers et al., 1980).

