The Events of Normal and Abnormal Postpartum Reproductive Endocrinology and Uterine Involution in Dairy Cows: A Review

K. E. LESLIE

Department of Clinical Studies, Ontario Veterinary College, University of Guelph, Guelph, Ontario N1G 2W1

SUMMARY

The results of numerous hormonal profile studies in the dairy cow are reviewed with respect to specific hormone changes in the early postpartum period, and factors contributing to the onset of cyclic reproductive activity. Variations from the normal pattern of postpartum hormonal activity or uterine involution are reviewed also. The normal involutionary changes of the bovine uterus are discussed.

RÉSUMÉ

Une revue de l'endocrinologie reproductive puerpérale normale et anormale, ainsi que de l'involution utérine, chez la vache laitière

Cet article présente une revue des résultats de plusieurs études hormonales effectuées chez la vache laitière et relatives aux changements hormonaux qui se produisent dès le début de la période puerpérale, ainsi qu'aux facteurs qui contribuent au retour de l'activité reproductrice cyclique. Il passe également en revue les variations du profil normal de l'activité hormonale puerpérale et de l'involution utérine. Il présente aussi des commentaires relatifs à l'involution utérine bovine normale.

NORMAL POSTPARTUM REPRODUCTIVE ENDOCRINOLOGY AND UTERINE INVOLUTION

Normal Postpartum Reproductive Endocrinology

A balanced, coordinated endocrine system is important for normal reproductive function. This involves homeostasis among gonadotrophin releasing hormones (GnRH) from the hypothalamus; follicle stimulating hormone (FSH), luteinizing hormone (LH) and prolactin (PRL) from the adenohypophysis; prostaglandin F2-alpha ($PGF_{2\alpha}$) from the uterus and the gonadal steroids (36).

During pregnancy one of the ovaries contains a well developed corpus luteum (CL) and both ovaries have small follicles that are barely detectable on the ovarian surfaces. Occasionally larger follicular structures ($\geq$ 10 mm) are found. Approximately six weeks prior to parturition, the biosynthetic functions of the fetoplacental unit result in gradually increasing plasma levels of estrogens (11). The peripheral blood level of a metabolite of $PGF_{2\alpha}$ undergoes a dramatic incease shortly before parturition and early in the postpartum period (57). This was viewed as an indication that $PGF_{2\alpha}$ is involved in the prepartum luteolysis of the CL of pregnancy which is in agreement with other reports (15,27).

This increase in $PGF_{2\alpha}$ concentration appears to be extremely important for normal uterine involution. The $PGF_{2\alpha}$ levels parallel the rate of uterine involution with a peak at day 4 postpartum and thereafter remain elevated for up to 20 days (27,31).

Progesterone levels decline rapidly during the last 48 hours before parturition and remain at very low levels ($<$ 0.5 ng/mL) throughout the early postpartum period (25,26). This decline is related to regression of the CL of pregnancy.

After parturition, the plasma estrogen levels decrease sharply to values below those found during the normal estrous cycle (18). Increases in estrogen levels have not been reported in the early postpartum period, even though follicular activity is initiated early. It has been suggested that the same feedback mechanism which controls the pituitary during the normal estrous cycle is responsible for initiating the first postpartum estrus (23). This feedback mechanism involves follicular growth and estrogen secretion.

Follicle stimulating hormone is maintained at relatively constant levels throughout the life of the postpubertal dairy cow (50). Plasma FSH concentrations fluctuate between 30 and 70 ng/mL and are somewhat independent of other hormonal changes. Follicle stimulating hormone release, in response to exogenous GnRH injections, is reduced during the period from nine days before to six days after parturition (49). It has been demonstrated also that FSH levels are slightly increased and are maintained at constant levels through parturition and into the postpartum period (13). Thus, it would appear that delay of onset of cyclic function is unlikely to be due to low FSH levels.

Several investigators have studied LH concentrations during various reproductive stages. Luteinizing hormone follows a release pattern that is characterized by a rapid increase followed by a more gradual return to normal levels (3,44). These spasmodic episodes of rapid increase in LH level are described as pulsatile LH release (20). A tonic release maintains basal LH levels. Superimposed on this release pattern is a rapid and marked increase in basal LH levels just prior to ovulation. This has been called the preovulatory LH surge. The same basic LH concentrations and release patterns found during the normal estrous cycle have been observed in cows during the early postpartum period (6,20,49,61).

Follicular activity has been detected as early as five to ten days postpartum (48). The follicles continue to grow until at least one becomes ready to respond to a preovulatory LH surge. Extensive investigation has been necessary to accurately determine the factors which initiate the first postpartum ovulation. It has been suggested that the ovary regulates LH secretion in cattle (44). However, from studies in primates, it has been proposed that LH secretion, and ovulation are under neural control (30).

In sexually mature female cattle, both estradiol 17-beta (51) and GnRH (49) can induce the release of LH from the anterior pituitary gland. The interaction of these two hormones to cause a LH surge depends primarily on the estradiol 17-beta concentration. Ovariectomized heifers display only a pulsatile LH release pattern (3).

Gradually increasing estrogen concentrations to markedly elevated levels may have an inhibitory effect on the production and/or release of a LH surge by the pituitary. This effect has been demonstrated in late pregnancy and in animals with cystic ovarian disease and is different from the effect of a synchronous rapid elevation in estrogen during late proestrus of the normal cycle. Firstly, in late pregnancy from 40 to 60 days prepartum until six days after calving, estrogen levels are high and there is a decrease in LH peak values. Several workers have examined the pituitary response to exogenous GnRH during the prepartum and postpartum periods and have described LH release in response to GnRH injection to be substantially reduced from five weeks before until eight to ten days after parturition (19,26,49). Full responsiveness returned by day 10 postpartum. A full LH response has been artificially produced at day 2 postpartum by using a combination of estrogens, progesterone, and then, GnRH (2). Secondly, elevated estrogen levels have been found in cows with ovarian cysts (24). Such animals have elevated basal levels of LH, but no LH surge (38). This negative feedback activity is in contrast to the one day estrogen peak that occurs during a normal estrous cycle which is followed by the preovulatory LH surge (23).

On the other hand, high levels of progesterone appear to suppress the hypothalamus and not the pituitary. Progesterone levels are constantly elevated during gestation (42), except for a small decrease from day 60 to day 90 after conception (47). Yet, the pituitary can fully respond to exogenous GnRH throughout pregnancy (49).

In summary, the endocrine changes responsible for the resumption of postpartum cyclic activity are complex. A particular set of hormonal circumstances are necessary for the first postpartum cycle to be initiated. After a short-term elevation, plasma progesterone levels must be low and estradiol 17-beta must be at an appropriate threshold level (51). The rise and decline of progesterone, followed by the rise in estradiol 17-beta that occur prior to the first postpartum cycle, are similar to the changes during proestrus of a normal estrous cycle. It is speculated that GnRH initiates the preovulatory LH surge in late estrus. The presence of a large mature follicle is necessary for all of these changes to occur and the ovulation which follows.

The need for specific hormonal conditions to precede and induce ovulation is supported by the research on the use of GnRH in the early postpartum period (21,26). In one of these studies the ovaries were examined by laparoscopy, and then the cows were treated with GnRH. Induced ovulation occurred only if a large follicle ($>$ 10 mm) was present on the ovary (21).

The first ovulation usually occurs between ten and 25 days postpartum (33,40). Approximately 50% of cows exhibit short cycles during the early postpartum period (39,50). It has been suggested that immature corpora lutea may be the cause of these short cycles (39). The first postpartum endogenous preovulatory LH surges have been shown to be too low to produce complete luteinization (14). It is also possible that reduced blood flow to the ovary may interfere with normal CL formation as has been demonstrated in sheep (41).

The CL of pregnancy is still palpable on the ovary until ten to 14 days postpartum, even though functional activity ceases before parturition (40). The regressed CL of pregnancy does not appear to influence the timing of the first postpartum ovulation. Short-term increases in plasma progesterone have been reported prior to the initiation of the first cycle, which are speculated to be from luteinized follicles (61). These workers suggest that a delay in the time of first ovulation may be due to suppression of GnRH activity by these small increases in progesterone (61). This might, in turn, inhibit pulsatile LH release.

Hormonal profiles of the first estrous cycle have been described in great detail (14). Few endocrinological differences exist compared to subsequent estrous cycles (62). The estradiol levels preceding first estrus were lower than in subsequent cycles. Likewise, LH levels during the first estrus and progesterone concentrations following first ovulation were comparatively lower (50,53).

The ovary ipsilateral to the nongravid horn has been shown to resume activity more rapidly (33). When ovulations occurred between day 10 and day 15 postpartum, 90% of these ovulations were on the ovary contralateral to the gravid horn. Whether this is due to a local inhibitory effect of the CL of pregnancy or a uterine inhibitory effect of reduced bloodflow remains a matter for speculation.

Several studies indicate that few animals ($<$ 30%) show behavioral signs of estrus accompanying first ovulation (5,28,29). The incidence of silent estrus decreases to less than 30% at the second and third ovulatory cycles (5).

In beef cows, the return to cyclic ovarian function is markedly delayed, the cause of which is poorly understood. The presence of a sucking calf postpones the commencement of cyclic activity (43). Suckling inhibits the pulsatile release of LH and assures continued high PRL levels. In dairy cows, PRL increases at parturition (11), but declines to lower levels within two or three days of calving (58). Elevated PRL levels have been recorded in a selected group of higher producing dairy cows (57). The suppression of PRL does not alter the rate of return to cyclic function (49). Thus, its role in controlling the onset of cyclic activity is suggested to be minimal.

Normal Postpartum Uterine Involution

Several authors have described normal and abnormal involution of the uterus (4,22,39,40,45,46,55).

Shortly after parturition, the uterus is a large organ measuring roughly one meter in length and weighing 8 to 10 kg (46). The most profound involution occurs between the time of calving and day 3 postpartum (38). The rapid decrease in size is due to vasoconstriction and peristaltic contractions, which occur at three to four minute intervals and gradually diminish by day 4 postpartum.

Events during involution of the uterus include necrosis of the caruncular stalk, breakdown of the superficial layer of the caruncle and formation of the lochial discharge (22,46). This process is generally complete by day 12 postpartum. Normal involution can be an aseptic process, but this is the exception rather than the rule (54). Spontaneous puerperal infection, with massive bacterial growth in the lochia, is common (45). It has also been reported that 93% of bovine uteri are infected up to day 15, 78% up to day 30, 50% up to day 45 and 9% up to day 60 postpartum (16). *Corynebacterium pyogenes* and *Escherichia coli* are the most commonly cultured bacteria.

An extensive study of postpartum involution of the uterus and cervix has been carried out (40). The size of the bovine uterus decreases slowly between days 4 and 9 postpartum. At this time, the diameter of the previously gravid horn ranges from 12 to 14 cm in normal cows and by day 10 the uterus could be completely defined by rectal palpation. Normal cows exhibit a marked increase in uterine tone and decrease in uterine size from days 10 to 14 postpartum which coincide with the onset of first estrus. The uterine horn averages 7 to 8 cm in diameter by day 14. Subsequent involution was rapid and by day 25 a diameter of 2 to 4 cm was usually attained with the uterine horns being almost equal in size (40).

Regression in uterine weight, in a similar pattern and proportion to the reduction in size, has been reported (34). Histological evidence of repair of the endometrium is reported to proceed at a slightly slower rate than gross uterine involution (32).

Involution of the cervix is slower than that of the uterus (40). Normal cows, on average attain complete cervical involution by day 30 postpartum.

ABNORMALITIES OF REPRODUCTIVE ENDOCRINOLOGY AND UTERINE INVOLUTION IN THE EARLY POSTPARTUM PERIOD

Abnormal hormonal (7,10,18) and uterine involutionary changes (40,55) during the early postpartum period have been reported.

Primary predisposition of cows to retained placenta (RP) has been associated with numerous infectious, nutritional, genetic and physiological etiologies. However, it has been suggested that these predisposing factors could lead to a common prepartum temporal change of certain hormones (7). Synchronized hormonal changes have been described in relation to lactogenesis (11), parturition (17), and placental release (10). Interference with these changes by ovariectomy during pregnancy has resulted in a high frequency of RP (8,37). Similarly induction of premature parturition by glucocorticoid therapy has been associated with a high incidence of RP (9,37,60).

Hormonal profile studies have demonstrated that prepartum plasma progesterone values were elevated in RP cows compared to non-RP cows that calved either spontaneously (1,10) or following glucocorticoid induction (9). Prepartum plasma estrogens were lower in RP cows than in non-RP cows either after both spontaneous and induced parturition (7,8).

The balance between plasma levels of progesterone and estradiol 17-beta on day 6 prepartum was significantly associated with the subsequent occurrence of RP (7). When plasma progesterone was at an intermediate level (4 to 8 ng/mL) and estradiol 17-beta was high (exceeding 99 pg/mL) there was a tenfold lower incidence of RP than when progesterone was high or when progesterone and estradiol 17-beta were both low. Plasma profiles of PRL and estrone were almost identical in RP and non-RP groups. This experiment was conducted as a case control study with peer matching on several parameters (7).

It has been demonstrated that cows with prolonged uterine involution times also had relatively extended periods of elevated plasma $PGF_{2\alpha}$ levels in comparison to cows with normal uterine involution times (15,31).

The fetoplacental unit produces large amounts of estrogen in late pregnancy, which sensitizes the myometrium to both oxytocin and prostaglandin. A decrease in the estradiol 17-beta/17-alpha ratio has recently been reported to result in a reduced rate of release of prostaglandins from the uterus and a slower rate of uterine involution (18). In other words, a lower concentration of biologically active estrogens may result in a slower rate of involution possibly due to reduced $PGF_{2\alpha}$ release. In this regard, an increase in $PGF_{2\alpha}$ release into the utero-ovarian vein occurred in response to the administration of estradiol 17-beta in the goat (12).

Uterine involution is more rapid in suckled beef cows than in milking dairy cows (48). Involution was complete in 15 to 25 days in suckled cows and in 25 to 30 days in milking cows. The sucking stimulus was believed to cause frequent release of oxytocin from the posterior pituitary, which enhanced the reduction in size of the uterus through its myometrial contractile effect. Milking also causes oxytocin release, but the frequency would be less than that with suckling. It has been shown that milking Holstein cows four times a day until day 25 postpartum improved uterine involution, without affecting the pulsatile LH release and the onset of first estrus (6).

Normal uterine involution and resumption of cyclic ovarian activity progressed more slowly in cows with periparturient diseases, such as dystocia, milk fever, ketosis, RP and metritis, than in cows which had experienced normal parturition (40). The uterus did not reach nongravid size until approximately day 30 in cows with such diseases. The uterus was significantly larger at ten and 20 days postpartum after an abnormal parturition. Similar results have been reported by other investigators (4).

Shortly after 30 day postpartum, the differences in involutionary status between cows which had calved normally and those with periparturient abnormalities, were no longer detectable (40). Age and parity are important considerations when evaluating the size of uterine horns on a postpartum examination (4,39). Other authors have also shown that RP significantly delayed uterine involution (34).

Prolonged luteal function has been demonstrated in cows with pyometra (52). It was hypothesized that this might result from failure of $PGF_{2\alpha}$ synthesis due to endometrial damage. It is therefore tempting to assume that uterine infection in the immediate postpartum period may reduce $PGF_{2\alpha}$ release and consequently delay involution.

In studies, in which sequential plasma progesterone concentrations were plotted, ovarian function and estrous activity during early lactation have been monitored (28). It was found that 57 of 69 cows established early regular cycles and their ovarian activity was considered normal. However, the duration of the estrous cycles in some of the normal cows was considered aberrant, being less than 17 days or more than 25 days in length. The incidence of aberrant cycles was 25% after first ovulation, 12% after second ovulation and 8% after third ovulation (27).

The 12 abnormal cows in this study presented a wide variety of postpartum abnormalities (27). Follicular cysts, with plasma progesterone levels of less than 1 ng/mL, were observed following none, one or two normal ovulations. Smooth nonfunctioning ovaries resulted after failure of CL formation subsequent to first ovulation in one case studied. Even in the absence of clinical uterine pathology, a persistent CL was occasionally found after first or second ovulation. All cows commenced the postpartum period with basal plasma progesterone levels, indicating the CL of pregnancy did not remain functional after parturition (27).

Others have reported similar findings using the milk progesterone assay (5,35,59). Incidence rates of 5 to 10% were found for both ovarian cysts and postpartum anestrus.

It has been found that a normal CL formed during only 62.5% of postpartum cycles (40). A CL was considered indicative of a normal estrous cycle. Follicular ovarian cysts developed during 12.3% of the observed cycles and occurred more frequently in the first 30 days postpartum than in the 31-60 day period. Spontaneous recovery, however, was common (40).

Differences between cows with periparturient diseases and cows that calved normally were also reported (40). Ovarian cysts were more common in the former group. They also required more services per conception and had longer calving to conception intervals than the normal cows. The authors emphasized that normal cows had two ovulations during the first 30 to 35 days after parturition, whereas cows with periparturient diseases had only one ovulation during this period (40). These findings were in agreement with the results of other workers (33) and are important in view of the finding that the number of cycles prior to day 30 postpartum was an important indicator of reproductive performance (56).

It is evident from this review of reproductive endocrinology and uterine involution of the postpartum dairy cow that normal ranges have been extensively described. Reports of hormonal values and uterine events are less frequently reported with respect to abnormalities of the postpartum period, such as might exist in cases of retained placenta or metritis. The underlying endocrinological mechanisms necessary for initiation of cyclic ovarian activity after parturition are still not well understood and the reasons for the delay or advancement of resumption of reproductive activity are poorly described. Many questions remain to be answered concerning the postpartum period of the dairy cow. For example, resumption of cyclic ovarian activity in RP cases has not been well documented. Concurrent hormonal profile studies and reproductive tract examinations could provide useful information on this important period in the reproductive life of both dairy and beef cattle.

REFERENCES

1. AGTHE, O. and H.P. KOLM. Oestrogen and progesterone levels in the blood plasma of cows with normal parturition or with a retained placenta. J. Reprod. Fert. 43: 163-166. 1975.
2. AZZAZI, F., G.F. KRAUSE and H.A. GARVERICK. Alteration of GnRH induced LH release early post partum in dairy cattle with estrogen and progesterone. Ann. Meet. A.S.A.S. Ithaca, N.Y. 72: 367. 1980.
3. BECK, T.W. and E.M. CONVEY. Serum LH in heifers after ovariectomy. J. Anim. Sci. 43: 274. 1976.
4. BUCH, N.C., W.J. TYLER and L.E. CASIDA. Postpartum estrus and involution of the uterus in an experimental herd of Holstein-Friesian cows. J. Dairy Sci. 38: 73-79. 1955.
5. BULMAN, D.C. and G.E. LAMMING. Milk progesterone levels in relation to conception, repeat breeding and factors influencing acyclicity in dairy cows. J. Reprod. Fert. 54: 447-458. 1978.
6. CARRUTHERS, T.D. and H.D. HAFS. Suckling and four times daily-milking: Influences on ovulation, estrus and serum luteinizing hormone, glucocorticoids and prolactin in postpartum Holsteins. J. Anim. Sci. 50: 919-925. 1980.
7. CHEW, B.P., R.E. ERB, Z.N. CLAUDIE, V.F. COLEBRANDER, P.V. MALVEN and M.R. D'AMICO. Variables associated with peripartum traits in dairy cows. Hormonal profiles associated with retained fetal membranes. Theriogenology 12: 245-253. 1979.
8. CHEW, B.P., R.E. ERB, J.F. FESSLER, C.J. CALLAHAN and P.V. MALEN. Effects of ovariectomy during pregnancy and of prematurely induced parturition on progesterone, estrogens and calving traits. J. Dairy Sci. 62: 557-566. 1979.
9. CHEW, B.P., R.E. ERB, R.D. RANDEL and F.M. ROQUETTE JR. Effect of corticoid-induced parturition on lactation and on prepartum profiles of serum progesterone and the estrogens among cows retaining and not retaining fetal membranes. Theriogenology 10: 13-25. 1978.
10. CHEW, B.P., R.E. KELLER, R.E. ERB and P.V. MALVEN. Periparturient concentrations of prolactin, progesterone and the estrogens in blood plasma of cows retaining and not retaining fetal membranes. J. Anim. Sci. 44: 1055-1060. 1977.
11. CONVEY, E.M. Serum hormone concentrations in ruminants during mammary growth, lactogenesis and lactation: A review. J. Dairy Sci. 57: 905-917. 1974.
12. CURRIE, W.D. and G.D. THORBURN. The fetal role in timing the initiation of parturition in the goat. The fetus and birth. Ciba Foundation Symp. Elsevier, Amsterdam. 47: 49-53. 1977.
13. DOBSON, H. Radioimmunoassay of FSH in the plasma of post-partum dairy cows. J. Reprod. Fert. 52: 45-49. 1978.
14. ECHTERNKAMP, S.E. and W. HANSEL. Concurrent changes in bovine plasma hormone levels prior to and during the first postpartum estrus cycle. J. Anim. Sci. 37: 1362-1370. 1973.
15. EDQVIST, L.E., H. KINDAHL and G. STABENFELDT. Release of prostaglandin $F_2\chi$ during the bovine peripartal period. Prostaglandins 16: 111-119. 1978.
16. ELLIOT, K., K.J. MCMAHON, H.T. GRIER and GB MARION. Uterus of the cow after parturition: Bacterial content. Am. J. vet. Res. 29: 77-81. 1968.
17. ERB, R.E. Hormonal control of mammogenesis and onset of lactation in cows: A review. J. Dairy Sci. 60: 155-169. 1977.
18. ERB, R.E., F. D'AMICO, B.P. CHEW, P.V. MALVEN and C.N. ZAMET. Variables associated with peripartum traits in dairy cows. VII Hormonal profiles associated with dystocia. J. Anim. Sci. 52: 346-358. 1981.
19. FERNANDES, L.C., W.W. THATCHER, C.J. WIL-

COX and E.F. CALL. LH release in response to GnRH during the postpartum period of dairy cows. J. Anim. Sci. 46: 443-448. 1978.

20. FOSTER, J.P., G.E. LAMMING and A.R. PETERS. Short-term relationships between plasma LH, FSH and progesterone changes in postpartum dairy cows and the effect of GnRH injection. J. Reprod. Fert. 59: 321-327. 1980.
21. GARVERICK, H.A., R.G. ELMORE, D.H. VALLAINCOURT and A.J. SHARP. Ovarian response to gonadotrophin-releasing hormone in postpartum dairy cows. Am. J. vet. Res. 41: 1582-1585. 1980.
22. GIER, H.T. and G.B. MARION. Uterus of the cow after parturition. Involutionary changes. Am. J. vet. Res. 29: 83-96. 1968.
23. GLENCROSS, R.G., I.B. MUNRO, B.G. SENIOR and G.S. POPE. Concentrations of estradiol 17-beta, estrone and progesterone in jugular venous plasma of cows during the oestrous cycle and in early pregnancy. Acta Endocr. 73: 374-384. 1973.
24. GLENCROSS, R.G. and I.B. MUNRO. Estradiol and progesterone levels in plasma of cows with ovarian cysts. Vet. Rec. 95: 169. 1974.
25. HOFFMAN, B., D. SCHAMS, R. BOPP, M.L. ENDER, T. GIMINEZ and H. KARG. Changes of PG, total estrogens and progesterone at parturition in the cow. Acta Endocr. 73: 385-395. 1973.
26. KESLER, D.J., H.A. GARVERICK, R.S. YOUNGQUIST, R.G. ELMORE and C.J. BIERSCHWAL. Effect of days post partum and endogenous reproductive hormones on GnRH induced LH release in dairy cows. J. Anim. Sci. 46: 797-806. 1977.
27. KINDAHL, H., J.O. LINDELL and L.E. EDQVIST. Luteolysis in domestic animals: Control of $PGF_{2\alpha}$ release. Proc. 9th Intern. Congr. on Anim. Reprod. and A.I. Madrid. Vol. II: 17-26. 1980.
28. KING, G.J., J.F. HURNIK and H.A. ROBERTSON. Ovarian function and estrus in dairy cows during early lactation. J. Anim. Sci. 42: 688-692. 1976.
29. KING, G.J., J.F. HURNIK and H.A. ROBERTSON. Abnormalities of reproductive function in intensively studied Holstein cows. Proc. 8th Int. Cong. on Anim. Reprod. Krakow. Vol. VI: 593-602. 1976.
30. KNOBIL, E. The neuroendocrine control of the menstrual cycle. Recent Prog Horm Res 36: 53-39. 1980.
31. LINDELL, J.O., H. KINDAHL, L. JANSSON and L.E. EDQVIST. Post-partum release of prostaglandin $F_2\chi$ and uterine involution in the cow. Theriogenology 17: 237-245. 1982.
32. MARION, G.B. and H.T. GIER. Histological and cytological changes in the bovine uterine epithelium. J. Anim. Sci. 18: 1552-1553. 1959.
33. MARION, G.G. and H.T. GIER. Factors affecting bovine ovarian activity after parturition. J. Anim. Sci. 27: 1621-1626. 1968.
34. MARION, G.B., J.S. NORWOOD and H.T. GIER. Uterus of the cow after parturition. Factors affecting regression. Am. J. vet. Res. 29: 71-75. 1968.
35. MATHER, E.C., P.M. CAMPER, F. VAHADAT, H.L. WHITMORE and B.G. GUSTAFSON. Assessment of ovarian activity in the post-partum dairy cow by use of a milk progesterone assay. Theriogenology 10: 119-129. 1978.
36. McDONALD, L.E. Veterinary Endocrinology and Reproduction. 3rd Ed. pp. 21-23. Philadelphia: Lea & Febiger. 1980.
37. McDONALD, L.E., S.H. McNUTT and R.E. NICHOLS. Retained placenta. Experimental production and prevention. Am. J. vet. Res. 15: 22-24. 1954.
38. MORI, J., J. MASAKI, T. WAKABARAYASHI, T. ENDO and T. HASODA. Serum LH levels in cattle under various reproductive states. Theriogenology 1: 131-136. 1974.
39. MORROW, D.A. Postpartum ovarian activity and involution of the uterus and cervix of dairy cattle. Vet. Scope 16: 2-13. 1969.
40. MORROW, D.A., S.J. ROBERTS, K. McENTEE and H.G. GRAY. Postpartum ovarian activity and uterine involution in dairy cattle. J. Am. vet. med. Ass. 149: 1596-1609. 1966.
41. NISWENDER, G.D., T.J. REIMERS, M.A. DIEKMAN and T.D. NEFF. Blood flow: A mediator of ovarian function. Biol. Reprod. 14: 64-81. 1976.
42. POPE, G.S., S.K. GUPTA and T.B. MUNRO. Progesterone levels in the systemic plasma of pregnant, cycling and ovariectomized cows. J. Reprod. Fert. 20: 369-381. 1968.
43. RADFORD, M.J., C.D. NANCARROW and P.E. MATTNER. Ovarian function in suckling and nonsuckling beef cows post partum. J. Reprod. Fert. 54: 49-56. 1978.
44. RAHE, C.H., R.E. OWENS, J.L. FLEEGER, H.J. NEWTON and P.G. HARMS. Pattern of Plasma luteinizing hormone in the cyclic cow: Dependence upon the period of the cycle. Endocrinology 107: 498-505. 1980.
45. RASBECH, N.O. The normal involution of the uterus of the cow. Nord. VetMed. 2: 655-704. 1950.
46. ROBERTS, S.J. Veterinary Obstetrics and Genital Diseases. Second Edition. pp. 317-336. Ann Arbor, Michigan: Edward Bros. Inc. 1971.
47. ROBERTSON, H.A. Sequential changes in plasma progesterone in the cow during the estrous cycle, pregnancy, at parturition and postpartum. Can. J. Anim. Sci. 52: 645-658. 1972.
48. SAIDUDDIN, S., J.W. RIESEN, W.J. TYLER and E. CASIDA. Relation of post-partum interval to pituitary gonadotrophins, ovarian follicular development, and fertility in dairy cows. Studies on the post-partum cow. Res. Bulletin 270. pp. 15-22. University of Wisconsin. 1968.
49. SCHALLENBERGER, E., D. SCHAMS and K. ZOTTMEIER. Response of lutropin (LH) and follitropin (FSH) to administration of gonadoliberin (GnRH) in pregnant and post-partum cattle including experiments with prolactin suppression. Theriogenology 10: 35-53. 1978.
50. SCHAMS, D., E. SCHALLENBERGER, C.H. MENZER, J. STANGL, K. ZOTTMEIER, B. HOFFMAN and H. KARG. Profiles on LH, FSH and progesterone in post-partum dairy cows and their relationship to the commencement of cyclic function. Theriogenology 10: 453-468. 1978.
51. SHORT, R.E., R.D. RANDEL, R.B. STAIGMILLER and R.A. BELLOWS. Factors affecting estrogen induced LH release in the cow. Biol. Reprod. 21: 683-689. 1979.
52. STABENFELDT, G.H., D.P. NEELY, J.P. HUGHES and H. KINDAHL. Modification of uterine PGF_{2a} in domestic animals through pathology or pharmacologic processes. Proc. 9th Int. Cong. on Anim. Rep. and A.I. Madrid. Vol. II: 27-34. 1980.
53. STEVENSON, J.S. and J.H. BRITT. Relationships among luteinizing hormone, estradiol, progesterone, glucocorticoids, milk yield, body weight and postpartum ovarian activity in Holstein cows. J. Anim. Sci. 48: 570-577. 1979.
54. STUDER, E. and D.A. MORROW. Relationships of post-partum genital tract examination per rectum to endometrial biopsy and uterine culture results. J. Am. vet. med. Ass. 172: 489-494. 1978.
55. TENNANT, B. and R.G. REDDICORD. The influence of delayed uterine involution and endometritis on bovine fertility. Cornell Vet. 58: 185-192. 1968.
56. THATCHER, W.W. and C.J. WILCOX. Postpartum estrus as an indicator of reproductive status in the dairy cow. J. Dairy Sci. 56: 608-610. 1973.
57. THATCHER, W.W., S.G. LEWIS, R.M. ELEY, F.W. BAZER, M.J. FIELDS, W.F. WILLIAMS and C.J. WILCOX. Contribution of the bovine conceptus to the endocrinological phenomenon existing at implantation, during gestation and around parturition. Proc. 9th Int. Cong. on Anim. Rep. and A.I. Madrid. Vol. II: 9-22. 1980.
58. TUCKER, H.A. Endocrinology of lactation. Seminars in Perinatology 3: 199-208. 1979.
59. VAN DE WIEL, D.F.M., C.H.J. KALIS and S.N.H. SHAH. Combined uses of milk progesterone profiles, clinical examination and oestrous observation for the study of fertility in the post-partum period of dairy cows. Br. vet. J. 135: 568-577. 1979.
60. WAGNER, W.C., R.L. WILLHAM and L.E. EVANS. Controlled parturition in cattle. J. Anim. Sci. 38: 485-489. 1974.
61. WEBB, R., G.E. LAMMING, N.B. HAYNES and G.R. FOXCROFT. Plasma progesterone and gondotrophin concentrations and ovarian activity in post-partum dairy cows. J. Reprod. Fert. 59: 133-143. 1980.
62. WETTEMAN, R.P., H.D. HAFS, L.A. EDGERTON and L.V. SWANSON. Estradiol and progesterone in blood serum during the bovine estrous cycle. J. Anim. Sci. 34: 1020-1024. 1972.