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Endocrine regulation of postpartum ovarian activity in cattle: a review (1)

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Summary. The problem of postpartum anoestrus is a real one because it results in prolongation of the time between calvings. The interval between the calving and resumption of cyclic ovarian activity depends on several factors, i.e., amount of feeding before and after parturition, level of milk yield, age of the animal, calving difficulty, presence of a bull in the herd, season and its photoperiodism and particularly the suckling or lactating status of the cow. The anoestrus period is longer in suckled cows (30 to 110 days) than in milked cattle (20 to 70 days).

The physiology of the hypothalamic-pituitary-ovarian axis is still far from clear. Nevertheless, some events are very well demonstrated. The pulsatile release of LH and GnRH and the pituitary sensitivity to GnRH increase gradually after calving. They are inhibited by suckling, which acts more on LH and GnRH release than on their synthesis. Suckling or the presence of a calf can exercise its action via oestrogens. Suckling inhibits oestrogen synthesis by follicular cells and diminishes their feed-back positive effect on the hypothalamic-pituitary axis. The suckling effect depends on oestrogen concentrations and on time after calving. The progressive LH release induces the synthesis of progesterone. After calving, the first luteal phase is shorter and the progesterone plasma concentrations are lower than what is observed during a normal cycle. Amongst some hypotheses proposed, premature luteolysis induced by uterine prostaglandins offers a new and very interesting field of research related to the utero-ovarian relationship after calving. The effects of FSH, prolactin and glucocorticoids hormones are much less understood.

1. Clinical aspects of postpartum anoestrus.

Clinically, the postpartum period is characterized by a period of behavioural anoestrus, the duration of which differs in different breeds.

If the detection of oestrus is optimal, anoestrus lasts for 20 to 70 days in dairy cows (Graves et al., 1968; Callahan et al., 1971; Schams et al., 1978; Pirchner et al., 1983; Richardson et al., 1983; Etherington et al., 1984). This period is highly variable in suckled cows and lasts from 30 to 110 days (Wiltbank and Cook 1958; Oxenreider 1968; Graves et al., 1968; Casida et al., 1968;

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2. Factors affecting postpartum anoestrus.

In our European agricultural areas, an average 12-month calving interval is generally considered as the ultimate goal of economic efficiency in cattle reproduction. In both suckled and milked cows, postpartum anoestrus is a paramount obstacle affecting this goal.

The length of the anoestrus period is variable and depends on several factors. Most authors admit that before or after calving, extended periods of over- or underfeeding of cows (10 to 20% of the required needs) can affect ovarian function and consequently the duration of postpartum anoestrus (Wiltbank et al., 1962, 1964; Dunn et al., 1969; Lammond, 1970; Corah et al., 1975; Whitman et al., 1975; Duffour, 1975; Holness et al., 1978; Carstairs et al., 1980; Dunn and Kaltenbach, 1980; Gauthier and Thimonnier, 1982; Peters and Riley, 1982; King and Mc Leod, 1983/1984; Rutter and Randel, 1984). Some authors have found that overfeeding improves ovarian (Wiltbank et al., 1962, 1964; Hansen et al., 1982) or pituitary (Beal et al., 1978; Jordan and Swanson, 1979; Lishman et al., 1979; Moss et al., 1982) function. Others have found no relation between feeding and the ovarian (Lishman et al., 1979; Carstairs et al., 1980) or pituitary (Hill et al., 1970; Dunn et al., 1974; Spitzer et al., 1978; Haresign, 1981; Rutter and Randel, 1984) activity.

Little is known about the mechanism under which diet exerts its effect. It is conceivable that feeding influences the ovarian response to gonadotropins (Gombe and Hansel, 1973). There was a positive correlation between the degree of fatness of an animal and the plasma concentration of 17β-oestradiol, 7 weeks after calving (Lishman et al., 1979).

Feeding affects the release of luteinizing hormone (LH) and subsequent luteal function (Dunn et al., 1974; Spitzer et al., 1975; Apgar et al., 1975; Beal et al.,
1978). It has been observed that the release of LH induced by gonadotropin releasing hormone (GnRH) injection was greater in underfed heifers (Beal et al., 1978; Gauthier and Mauleon, 1983), underfed ewes (Haresign, 1981) and underfed rats (Campbell et al., 1977) than in normally fed controls. Other reports have failed to record any difference (Cummins et al., 1975; Beal et al., 1978) or have noted a lower release of LH (Lishman et al., 1979; Jordan and Swanson, 1979; Echterkamp et al., 1982).

In the same way, underfed animals after calving have lower plasma (Terqui et al., 1982; Echterkamp et al., 1982; Gauthier et al., 1983) or pituitary LH concentrations (Beal et al., 1978). On the contrary, overfeeding does not induce variations in LH plasma concentrations or in pituitary response to GnRH (Rutter and Randel, 1984).

These contradictory results may be due to differences between studies in the nature of feed treatments, i.e., the quantitative or qualitative aspects of the ration given to or absorbed by the animal. In general, the amount of food actually absorbed by the animal in connection with the state of its own reserves has not been considered. Now it appears that animals which remain in good condition after calving have, irrespective of the rations received, higher LH plasma concentrations and a greater pituitary response to GnRH and consequently a shorter calving — first oestrus interval (Gauthier et al., 1983; Rutter and Randel, 1984).

Some workers have reported a positive relationship between milk yield and time to first oestrus or ovulation (Marion and Gier, 1968). The duration of anoestrus also depends on the age of the animal. Heifers have a longer calving-first oestrus interval than pluriparous cows (Germ Plasm Evaluation Program, 1975; King and Mc Leod, 1983/1984; Tervit et al., 1977). It also depends on calving difficulty. Dystocia and retained placenta, both of which extend the duration of uterine involution, reduce the rate of pregnancies 100 days after calving (Laster et al., 1973) and result in a longer acyclic period after calving (Erb et al., 1958). The presence of a bull in a herd reduces the time before resumption of cyclic activity (male effect) (Zalesky et al., 1984).

Season or photoperiod (Tucker, 1982) also changes the duration of anoestrus after calving (Thibault et al., 1966; Montgomery et al., 1980). The longer the duration of illumination at the time of calving, the shorter the duration of anoestrus (Bulman and Lamming, 1978; Peters and Riley, 1982; Hansen and Hauser, 1983). Animals calving between May and November have a calving-first ovulation interval significantly shorter than those calving between December and April (Lamming et al., 1981; Peters and Riley, 1982; King and Mc Leod, 1983/1984). This effect is even more important in primiparous than in pluriparous animals. It is also increased by an inadequate diet (Hansen and Hauser, 1983; Montgomery et al., 1985). How this effect works is still rather vague. Higher plasma LH (Mc Natty et al., 1984) and prolactin concentrations (Munro et al., 1980; Mc Natty et al., 1984) in summer than in winter could be the explanation, though it is not corroborated by some authors (Hansen and Hauser, 1984). Moreover feeding factors can also have a direct or indirect effect upon the process.
The suckling or lactating status of the animals must be considered as the determining factor. It is unanimously admitted that suckling induces a lengthening of the calving-first oestrus interval (Clapp, 1937; Graves et al., 1968; Morrow et al., 1969; Short et al., 1972; Randel and Walker, 1976; Edgerton, 1980). This interval is shortened by early weaning (Smith and Vincent, 1972; Laster et al., 1973; Bellows et al., 1974; Carter et al., 1980) or by a temporary suspension (48 to 72 hr) of suckling (Smith et al., 1979; Dunn et al., 1985).

This influence depends on the intensity of the mammary stimulation. According to some authors (Wettemann et al., 1978) but not to others (Peters and Riley, 1982), a cow suckling two calves will have a longer anoestrus (96 days vs 67 days) than a cow suckling only one calf. It also depends on the duration and the frequency of this stimulation (Kaiser, 1975). As a matter of fact, the duration of anoestrus is longer when access to the mammary glands is ad libitum than if it is restricted to one or a few daily periods (Carruthers and Hafs, 1980; Montgomery, 1982; Randel and Walker, 1976).

3. Hormonal mechanisms of postpartum anoestrus.

Several steroid or peptide hormones are directly or indirectly involved in the physiology of the hypophysis and the hypothalamus, the main centers regulating reproduction.

3.1. Luteinizing hormone (LH).

Pregnancy has an inhibitory effect on the sensitivity of the pituitary to hypothalamic GnRH (Schallengerber et al., 1978).

The sensitivity of the hypophysis to GnRH and LH plasma concentrations gradually increases after calving. The same holds true for GnRH pulsatile release which increases from 0-0.25 pulse an hour to 0.25-1.25 pulse an hour (Echterkamp and Hansel, 1973; Kesler et al., 1977; Webb et al., 1980; Carruthers et al., 1980; Peters et al., 1981; Gauthier et al., 1982; Humphrey et al., 1983). These changes are principally emphasized during the days preceding the first increase in progesterone and the first ovulation in dry as well as in lactating or suckling animals. In addition, LH concentrations in suckled cows are lower than those in milked or non suckled postpartum cows (Short et al., 1972; Humphrey et al., 1976; Webb et al., 1977; Kesler et al., 1977; Schallengerber et al., 1978; Fernandes et al., 1978; Stevenson et Britt, 1979; Carruthers and Hafs, 1980; Carruthers et al., 1980; Rawlings et al., 1980; Webb et al., 1980; Foster et al., 1980; Peters et al., 1981; Ramirez-Godinez et al., 1982; Azzazi et al., 1983).

The time of appearance of this pulsatile release and of pituitary sensitivity varies according to breed. In dairy cows, the pulsatile release of LH and the sensitivity of the pituitary to hypothalamic GnRH appears 10 days after calving and is greater between 12 and 15 days after calving (Echterkamp and Hansel, 1973; Kesler et al., 1977, 1979; Peters et al., 1981). On the other hand, in suckled cows, suckling induces a difference in the time of appearance and
intensity of this response, extending up to 20-30 days after calving (Radford et al., 1978; Carruthers et al., 1980; Irvin et al., 1981; Peters et al., 1981).

But neither the mechanism by which suckling interferes with the hypothalamic-hypophyseal axis, nor the nature of specific stimuli required to produce this effect are well-defined. Recent work has suggested that mechanical manipulation of teats does not in itself constitute an exteroceptive stimulus capable of altering LH release patterns in the cow (Williams et al., 1984). It is possible that other factors such as physical presence of a calf or social interaction are necessary in order for teat stimulation to be effective.

Suckling may have an effect at three levels.

It reduces the frequency (Carruthers and Hafs, 1980; Walters et al., 1982a; Edwards, 1985) and amplitude of LH release (Radford et al., 1978; Carruthers and Hafs, 1980; Troxel et al., 1980; Webb et al., 1980; Peters et al., 1981), pituitary sensitivity to GnRH (Carruthers et al., 1978; Smith et al., 1981) and pulsatile release of GnRH by the hypothalamus (Carruthers et al., 1980; Walters et al., 1982c; Schallenberger and Peterson, 1982).

The inhibitory effect of suckling on resumption of cyclic activity after calving acts more on the LH and GnRH release and action mechanism than on their synthesis. Many demonstrations support this proposition.

Pituitary concentrations of LH (Saiduddin et al., 1968; Graves et al., 1968) and hypothalamic concentrations of GnRH (Carruthers et al., 1978) are similar in both milked and suckled cows. Suckling is capable of inhibiting the positive effect of endogenous or exogenous oestradiol on the release of pituitary LH (Nancarrow et al., 1977; Short et al., 1979; Stevenson et al., 1983).

Temporary weaning (48 hr) induces an increase of the plasma LH concentrations (Smith et al., 1977; Walters et al., 1982b) which decrease to pre-calf removal concentrations within 4 hrs of calf return (Walters et al., 1982d). It also induces an increase of the follicular concentrations of LH receptors (Walters et al., 1982a). Calf removal stimulates an increase in LH concentration by increasing LH pulse frequency but the induced activity appears to be in relation to LH plasma concentrations and pulse frequency before calf removal (Edwards, 1985).

Suckling not only delays but also reduces the amount of LH released in response to GnRH injection. Temporary removal enhances over time the amount of LH release induced by GnRH injection (Dunn et al., 1985).

The number of animals, whether being milked or suckled, which respond positively to injection of GnRH or oestradiol increases during the postpartum period. On the other hand, suckled cows are less likely to respond by LH release after injection of oestradiol or GnRH than milked cows during the first 15 days after calving. This difference diminishes during subsequent weeks (Schams et al., 1973; Britt et al., 1974; Kesler et al., 1977; Webb et al., 1977; Schallenberger et al., 1978; Carruthers et al., 1980; Smith et al., 1981; Walters et al., 1982c).

At last, as well as a diminution in the interval between injection of oestradiol or GnRH and the LH peak, there is also an increase in the amplitude of this peak during the first 4 weeks after calving (Stevenson et al., 1983; Azzazi et al., 1983). The magnitude of the GnRH-induced release of LH was directly proportionnai la...
follicular diameter (Smith et al., 1983; Lishman et al., 1979) and oestrogen concentrations in postpartum cattle (Fernandes et al., 1978).

3.2. Follicle stimulating hormone (FSH).

Concentrations of FSH vary in an unpredictable manner (Schams et al., 1978; Manns et al., 1983) but tend to increase during the first few days after calving (Webb et al., 1980; Peters et al., 1981).

Suckling does not affect FSH plasma concentrations (Carruthers et al., 1980; Convey et al., 1983) or the number of ovarian receptors to FSH (Walters et al., 1982a). It seems that during the early days of the postpartum period, the role of this hormone is of a facilitating or permissive nature (Webb et al., 1980; Walters et al., 1982c; Peters and Lamming, 1984) because it induces the formation of LH receptors on granulosa cells under influence of oestrogen (Richards et al., 1976).

3.3. Oestrogens.

Concentrations of oestrogens (17β-oestradiol and oestrone) in blood plasma progressively increase toward the end of pregnancy and are at their highest 24-48 hours before calving (Smith et al., 1973; Arije et al., 1974; Stellflug et al., 1978). Peripheral levels of oestradiol-17β fall after calving and then fluctuate considerably before first ovulation (Pope, 1982).

Oestrogens such as 17β-oestradiol and to a lesser extent oestrone (Azzazi and Garverick, 1984) are involved in the effects of suckling on the hypothalamic-hypophyseal axis. In the hypothalamus, suckling increases the threshold of sensitivity to the negative retro-action of oestradiol on the tonic center (Acosta et al., 1983). Suckling inhibits oestrogen synthesis by the follicular cells (Bellin et al., 1984) for a few days but not for three weeks after calving (Walters et al., 1982a). This fact is important because in rats it was demonstrated (Richards et al., 1976) that follicular sensitivity to gonadotropins depends partly on their oestrogen and androgen concentrations.

In the pituitary, suckling diminishes the LH response to exogenous oestradiol (Short et al., 1979). Oestrogens have a positive effect on the amplitude of the LH peak and on LH release induced by injection of GnRH. These effects may occur by an increase in the rate or amplitude of GnRH secretion or an increase in pituitary sensitivity to GnRH stimulation (Zolman et al., 1974; Yen et al., 1974; Kesler et al., 1977; Beck et al., 1978; Hsueh et al., 1979; Zaied et al., 1980; Kesner et al., 1981; Azzazi et al., 1983; Peters, 1984).

This effect depends on the dose of oestrogens. High doses (10 mg) of oestradiol benzoate inhibit the pituitary response to GnRH (Barraclough, 1973; Manns and Richardson, 1976) and low doses increase this response (Hobson and Hansel, 1972). It also depends on the right time of injection in relation to calving (Stevenson et al., 1983) and on the period of injection. In ovariectomised ewes treated (for a period equivalent to that of gestation) with a daily dose of oestradiol equivalent to that which occurs during gestation, there is a progressive reduction in the amount of LH released following GnRH injection and also a fall in pituitary LH, both these parameters being directly correlated. Simultaneously there was an
increase in the number of GnRH receptors in the pituitary (Crowder et al., 1982). After calving, injection of oestrogens for 7 days with a dose sufficient to produce plasma concentrations similar to those present before calving, at first increased and then diminished the amount of LH released after GnRH injection, a positive effect which also occurred after the injections had ceased. The decrease of the amount of LH released may have resulted from a negative effect of oestrogens on LH synthesis. The second increase could have been due to progressive development of GnRH receptors (Azzazi et al., 1983). Perhaps oestrogens stimulate the synthesis of LH but inhibit its release (Tang, 1977).

3.4. Progesterone.

Concentrations of progesterone in the plasma of cows are high throughout gestation. They diminish slowly during the final 3-4 weeks and rapidly 2-3 days before calving (Short, 1958; Randel and Erb, 1971; Smith et al., 1973). Milked or suckled cows, 50 to 80 % of the time, have a first luteal phase which is shorter and progesterone plasma concentrations which are lower than observed during a normal cycle (Donaldson et al., 1970; Edgerton and Hafs, 1973; Humphrey et al., 1976; Schams et al., 1978; Stevenson and Britt, 1979; Kesler et al., 1980; Webb et al., 1980; Odde et al., 1980; Lavoie et al., 1981; Peters and Riley, 1982; Troxel et al., 1983; Pirchner et al., 1983; Manns et al., 1983). That hormonal abnormality can result in embryonic mortality (Ramirez-Godinez et al., 1982b; Troxel et al., 1983).

More precise studies of hormones have shown that two types of luteal activity occur after calving (Troxel et al., 1983). The first is a luteal phase lasting 6-12 days and referred to as the short luteal phase (or SLP), while the second is a luteal phase of normal duration, lasting more than 14 days, but accompanied by progesterone concentrations lower than normal (inadequate luteal phase or ILP). The reason for this is not fully understood. Such a dual possibility has also been observed after GnRH injection (Webb et al., 1977; Lishman et al., 1979; Kesler et al., 1980; Fonseca et al., 1980; Sheffel et al., 1980; Troxel et al., 1983) or after early weaning (Odde et al., 1980) or limited suckling with (Dunn et al., 1985) or without (Flood et al., 1979) GnRH injection.

Many hypotheses have been put forward to explain this. Morphological and endocrine studies (Manns et al., 1983) indicate that these first short-lived corpora lutea are not destroyed by the usual luteolytic process, but by a loss of ability to synthesize progesterone.

The lower FSH plasma concentration before oestrus preceding a short cycle may imply a possible influence of this hormone on the lifespan of the corpus luteum (Ramirez-Godinez et al., 1982a).

Progesterone might be formed by a follicle which has failed to ovulate (Tribble et al., 1973; Corah et al., 1974; Webb et al., 1980). The absence of differences in LH plasma concentrations observed before or after an oestrus associated with a short cycle does not lead one to a conclusion of an insufficient LH synthesis (Ramirez-Godinez et al., 1982a).

The reduced lifespan might be related to GnRH-induced LH surge having a short duration (Troxel et al., 1980). However the luteal receptors for LH or the
number of granulosa cells (Channing et al., 1981) may not be sufficient to give an optimum response to this luteotropic stimulus (Schams et al., 1979). As a matter of fact, while the corpus luteum from cows with regular cycles gives a positive response in vitro to LH addition in culture medium, this response cannot be observed with a corpus luteum whose formation has been induced by injection of GnRH. This difference may be because the luteal tissues are unable to recognize LH (Kesler et al., 1981). Histological studies have indicated that the response of postpartum corpora lutea to LH in vitro is similar in all the first three cycles, but that is related to the integrity of luteal tissue at the time of removal (Duby et al., 1985).

These last two observations support the concept of a premature luteolysis. The presence of a luteolytic agent such as prostaglandin F2α (PGF2α) synthesized after calving by the caruncular uterine tissues (Guilbaut et al., 1981, 1984b) may be responsible for this premature luteolysis and short luteal phase (Troxel and Kesler, 1984b). In fact, concentrations of one of the metabolites of PGF2α, 13, 14 dihydro-15-ceto-PGF (PGFM), increase during and after calving. They reach peak values on days 2 or 3 postpartum and return progressively to a basal concentration by 2 or 3 weeks after calving both in milked (Edqvist et al., 1978; Thatcher et al., 1980; Lindell et al., 1982; Kaker et al., 1984; Madej et al., 1984) and suckled (Troxel et al., 1984) cows. Its concentration decreases after the increase of progesterone in the blood (Lewis et al., 1984). It is generally agreed that PGF2α is not luteolytic during the first 4 or 5 days of the cycle. Nevertheless, its repeated injection during this period reduces progesterone concentration during the rest of cycle (Beal et al., 1980).

Oxytocin injected (Troxel et al., 1984) or released in response to milking or suckling or the presence of uterine infection (Roberts et al., 1975; Lindell et al., 1982; Watson, 1984) may be responsible for an increased concentration of PGFM and consequently earlier luteolysis and earlier resumption of a normal luteal phase (Madej et al., 1984). It has also been shown that intrauterine infusion of indomethacin, an inhibitor of prostaglandins synthesis, not only diminishes basal or induced concentrations of oxytocin and of the PGF metabolite (Troxel et al., 1984) but also prolongs the life of corpora lutea induced by GnRH (Troxel and Kesler, 1984a).

These various observations have led research workers to study the physiological significance of abnormal luteal phases and with experiments to determine the effects of treatments with progestagens or progesterone before an injection of GnRH. Injection of progesterone (25 or 100 mg) 12 days after calving and 48 hrs before GnRH injection (Williams et al., 1982) or implantation of norgestomet for 8 days, starting 17 days after calving, followed by an injection of 250 mcg GnRH 24 hrs after removal of the implant (Troxel and Kesler, 1984c) have beneficial effects on the amount of progesterone secreted by the corpora lutea thus induced (Ramirez-Godinez et al., 1981; Sheffel et al., 1982; Pratt et al., 1982). Such pretreatment is without effect if applied 40 days after calving (Troxel et al., 1980).

The mechanism of this effect is still unknown.

A direct effect on the ovary cannot be ruled out, although experiments on
rats have failed to confirm the role of progesterone in follicular development (Saidu- 
duddin and Zassenhaus, 1978).

A local utero-ovarian mechanism has also been proposed. In the first days 
after calving, the ovary bearing the gestation corpus luteum produces smaller 
folicles than the contralateral ovary (Lewis et al., 1984). The oestrogen 
concentration of these follicles is also smaller (Bellin et al., 1984). This has also 
been observed during the oestrous cycle (Matton et al., 1981; Brantmeier et al., 
1984). Thirty days after calving, a corpus luteum or a follicle is less often palpated 
on the ipsilateral ovary than on the contralateral ovary (Lewis et al., 1984), which 
confirms earlier reports about the location of the first ovulation (Marion and Gier, 
1968). It is possible that through the prostaglandins it synthesizes, the involuting 
pregnant horn influences the ipsilateral ovary more than the contralateral ovary 
(Guilbaut et al., 1983). It has been suggested that progesterone could influence 
the concentrations of luteolytic and luteotropic factors (Pratt et al., 1982). It has 
been shown that progesterone pretreatment induces low and constant concentra-
tions of PGFM, though not to a significant degree (TroxeI and Kesler, 1984c).

An effect of progesterone on the hypothalamo-hypophyseal axis cannot be 
rulled out. It is well known that during the oestral cycle progesterone decreases 
the pulsatile secretion of LH (Ireland and Roche, 1982), because it has a negative 
feedback effect on its synthesis in the pituitary (Echterkamp and Hansel, 1973; 
Convey et al., 1977). This effect acts on higher nervous centers since progeste-
ronc modifies neither the LH content nor the number of GnRH receptors in the 
pituitary (Moss et al., 1981). This sensitivity of the pituitary to negative feedback 
exercised by progesterone increases during the postpartum period (Peters et al., 
1983). During the postpartum period, the amplitude and the duration of the LH 
peak induced by GnRH injection is higher in animals pretreated with progesterone 
(TroxeI et al., 1980; Troxel and Kesler, 1984c). Such an effect has not been 
confirmed by others (Williams et al., 1982; Azzazi et al., 1983). This observation 
should be taken in the context of the higher frequency of ovulation which occurs 
after progesterone treatment (Troxel and Kesler, 1984c). However, this did not 
 occur after norgestomet treatment 40 days after calving (Troxel et al., 1980).

The opposing effects of progesterone on LH release are not necessarily con-
tradictory. They may depend on the timing of the experiment in the period after 
calving. Thus the effect may be inhibitory during the first 3 weeks (Williams et al., 
1982; Azzazi et al., 1983) and stimulatory later (Troxel et al., 1980; Troxel and 
Kesler, 1994c). The further away from calving it is given, the more likely it is for 
progesterone to have a favourable effect on LH release and the amount of pro-
gesterone synthesized by the resulting corpus luteum (Peters et al., 1983). This 
inhibitory effect is brought about by a decrease in the amount of GnRH released, 
by a decrease of the self-regulating (or self-priming) effect of GnRH (Kesner et 
al., 1982; Padmanabhan, 1982) or by oestradiol acting on the pituitary receptors 
of GnRH (Azzazi et al., 1983).

3.5. Prolactin.

During lactation, prolactin is released in response to a mammary stimulation 
(Tucker, 1971). In rats (Amenomori et al., 1970) and in women (Rolland et al.,
1975), the high blood prolactin concentrations are closely correlated with the gonadotropin synthesis inhibition. On the other hand, the high induced blood prolactin concentrations in rats (Fraser et al., 1982) or gestation or lactation (Reeves et al., 1982) is accompanied by a reduction of the number of pituitary GnRH receptors.

In the bovine, the anti-gonadotropic effect of prolactin cannot be accepted. The prolactin plasma concentrations are the same in milked or suckled cows (Goodman et al., 1979; Smith et al., 1981), and in dairy cattle they are associated with increased milk yields (Akers et al., 1980). Prolactin release is not systematically connected with suckling (Gimenez et al., 1980; Convey et al., 1983). Moreover, anoestrus length was observed by some (Chang et al., 1981) but not others (Webb et al., 1980) to be closely correlated with plasma prolactin concentrations. Finally, the injection of prolactin (Forrest et al., 1980) or of bromocryptin (Williams and Ray, 1980), an inhibitor of prolactin release, influences neither the variations of LH or FSH concentrations nor the resumption of cyclic activity after calving delay at least in bovines. However, we cannot rule out an ovarian local effect of this hormone on the synthesis of progesterone (Mc Natty et al., 1976, 1977) and on follicular development (Tsai-Morris et al., 1983). The prolactin follicular concentration and the number of LH receptors are in fact significantly higher in weaned cows than in suckled cows (Walters et al., 1982a).

3.6. Other hormonal factors.

Experiments carried out with ovariectomized animals confirm that the ovary and its steroidal or peptide factors (Channing, 1978; Fraser, 1982; Sharpe, 1982) cannot play a determining part in the LH release mechanism after calving. The presence of higher concentrations of glucocorticoids in the blood of suckled than non suckled cows before (Wagner and Oxenreider, 1972; Schallengerber et al., 1982) or after (Dunlap et al., 1981; Ellicott et al., 1981) a weaning period indicated that might play a role in LH release, the more so as they are likely to inhibit LH secretion in bovines (Wagner and Li, 1982). Recent work (Convey et al., 1983) has failed to confirm glucocorticoid release during suckling in non ovariectomized animals and again set the problem of the exact part played by those steroids in postpartum anoestrus in cows.

Conclusions.

Clinical and physiological studies lead to the conclusion that suckling has a major inhibitory effect on the resumption of regular sexual activity following parturition in the bovine species. Most specialists in bovine reproduction have tried to demonstrate and understand hormonal manifestations of the hypothalamo-hypophyso-ovarian axis during the postpartum weeks. They have stated the action mechanism of enhancing and determining factors and shown the importance of a pulsatile discharge of LH under GnRH control. So new approaches emerge. An increasing influence on follicular growth is attributed to the involuting uterus. Moreover, the isolation and purification of ovarian cytokinins will allow a better understanding of the determinism of anoestrus. It would
also be interesting to elucidate more precisely the effect of stresses such as partu-
rition and suckling on neuromediators and endorphins at the level of the central
nervous system level. Epidemiological research in bovine reproduction is now
expanding. Because of its application in animal husbandry, it must define more
accurately the respective roles of the different factors involved in anoestrus and
clarify the economic implications of the therapeutic means already proposed to
improve the fertility and fecundity of cattle.

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Résumé. Régulation endocrinienne de l’ovaire au cours du postpartum dans l’espèce
bovine.

Dans l’espèce bovine, l’intervalle entre vêlages dépend notamment de la durée de
l’anoestrus du postpartum. Plusieurs facteurs sont susceptibles d’influencer la physiologie
de l’ovaire après la parité : l’alimentation avant et après le vêlage, le niveau de
production laitière, l’âge de l’animal, la nature du vêlage, la présence d’un taureau dans le
troupeau, la saison et son photopériodisme mais surtout le caractère lactant ou allaitant de
la vache. L’anoestrus est plus long chez la vache allaitante (30 à 110 jours) que chez la
vache traitee (20 à 70 jours).

Bien qu’encore incomplètes, les connaissances relatives à la physiologie de l’axe
hypothalamo-hypophyso-ovarien au cours du postpartum ne cessent de progresser.
Plusieurs faits apparaissent maintenant bien établis. La libération pulsatile de la LH et du
GnRH ainsi que la sensibilité hypophysaire à la GnRH augmentent progressivement après le
vêlage. Elles sont inhibées par l’allaitement qui agit plus sur la libération que sur la synthèse
de la LH et du GnRH. La diminution de la synthèse d’oestrogènes par les follicules et la
réduction de leur rétro-action positive sur l’axe hypothalamo-hypophysaire constituent la
manifestation physiologique de cet effet inhibiteur. Après la parité, la première phase
lutéale est de plus courte durée et la synthèse de progestérone inférieure à celle observée
au cours d’un cycle normal. Il est possible qu’une lutéolyse prématurément induite par les
prostaglandines d’origine utérine soit à l’origine de cette particularité. Les effets de la
FSH, de la prolactine et des corticoïdes, apparaissent nettement moins bien définis. De
nouvelles voies d’approche se font jour. Nous citerons celles qui ont pour but de préciser le
rôle de l’utérus en involution sur la croissance folliculaire ainsi que celles relatives aux
cybernines ovariennes. L’étude du mécanisme d’action des facteurs de stress pourrait aussi
revêtir des implications pratiques. Enfin, les recherches épidémiologiques en reproduction
bovine permettront de cerner davantage l’effet respectif des différents facteurs impliqués
dans l’anoestrus.

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