



The puerperium in dairy cows: ovarian activity, uterine involution and follicular dynamics

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Abstract

The study of ovarian follicular dynamics (OFD) and other changes in the bovine reproductive tract has progressed significantly over the past two decades, primarily due to the use of non-invasive investigative approaches such as ultrasound. Advances in ultrasonographic examinations have provided a better understanding of ovarian activity, uterine involution, oviducts, and other segments of the reproductive tract in the bovine postpartum period. Procedures including tracking of the reproductive tract have likewise aided in the development of new methodologies and techniques to improve reproductive performance in cattle. This aim of this review was to summarize knowledge regarding the reproductive tract in dairy cows during the postpartum period.

Keywords: ovarian activity; anestrus; follicular dynamics; dairy cows; puerperium

Introduction

Animal efficiency is considered one of the most important aspects related to profitability in the livestock industry, as it directly affects herd productivity, and depends primarily on nutrition, health, genetics, and management factors. The bovine female may be affected by metabolic or physiological disorders that cause infertility. Similarly, there is a need to adopt and implement preventive and therapeutic practices that are dependent on routine and systematic gynecological control.

The postpartum period, also called the puerperium, is a physiological and global process of modifications occurring in the female reproductive tract after parturition that leads to recovery from the changes that took place during pregnancy. Consequently, six weeks after parturition, the bovine reproductive tract achieves the volume, size, position, and reproductive capacity required for the next pregnancy (Grunert and Birgel, 1998).

According to Opsomer et al. (2000), a normal ovarian cycle in the puerperium is one of the most important reproductive events related to high production in modern dairy cattle herds, which is aimed at achieving maximum potential after parturition. However, the slow return of reproductive function during the puerperium period in dairy cows is a major limitation that affects the success of subsequent reproductive management programs, such as artificial insemination (AI), and marks the beginning of the voluntary waiting period (VWP). The occurrence of early and frequent estrus after parturition is associated with increased reproductive performance due to a consequent restoration of the uterine environment (Thatcher and Wilcox, 1973; Thatcher et al., 2006).

Factors related to nutrition, including kind, quantity, and intake capacity (Domínguez, 1995; Zain et al., 1995; Laven et al., 2004; Roche, 2006; Artunduaga et al., 2008; Castaneda-Gutiérrez et al. 2009), as well as

body condition score (BCS), energy, and metabolism (Zurek et al., 1995; Kendrick et al., 1999; Butler, 2000), can positively or negatively influence follicular development and ovulation in the early puerperium. General or local uterine disorders also cause delays in ovarian activity (Sheldon, 2002a; Mateus et al., 2003; Peter, 2004; Sheldon, 2004; Sheldon and Dobson, 2004; Foldi et al., 2006; Azawi, 2008), and can consequently hinder subsequent reproductive events. The aim of this review was to present viewpoints related to follicular dynamics in dairy cows, and to highlight the influence of follicular dynamics on the reproductive performance of dairy cattle during the puerperium period.

Follicular dynamics in the puerperium in dairy cattle

According to Sá Filho et al. (2014), knowledge of follicular dynamics allows for the efficient control of reproduction and other related procedures such the manipulation of the oestrous cycle and the induction of postpartum estrus, and promotes the more effective use of reproductive biotechnologies. The ovaries function as units, and primarily influence follicular development through the endocrine pathways that involve ovarian and uterine endocrine secretions, as well as gonadotropins and their receptors. The dominant and subordinate follicles act throughout the stages of recruitment, growth, and stasis, as well as during regression, as determined by distinct morphological and biochemical characteristics (Adams et al., 2008).

Several prior reports have stated that knowledge of follicular dynamics and the physiology of the corpus luteum (CL) increased reproductive performance applying hormones and others related drugs (McMillan and Thatcher 1991; Figueiredo et al., 1996; Aerts and Bols 2010; Cummins et al. 2012; Salis et al. 2012; Uslenghi et al., 2014), for AI, induction and synchronization of oestrus, ovarian superovulation, and embryo transfer among others.

In cows, almost all of the ovarian follicles undergo atresia, and around 60 days are required to activate the primordial follicle to reach ovulatory size (Vasconcelos, 2000). During this time, a standard follicular wave follows (Ireland et al., 2000; Lucy, 2000; Ginther et al., 1996) that stimulates several stages of follicular growth and atresia, based on

subsequent oocyte maturation or degeneration (Viana et al., 2010; Cerri et al. 2011). Throughout puberty, a large number of primordial follicles are recruited from the follicular reserve population that develop into ovulatory follicles, and are released as oocytes with the potential for fertilization (Kornmatitsuk et al., 2009). Consequently, the number of primordial follicles present in ovaries is positively correlated with the number of pre-ovulatory follicles that will reach maturity (Fortune et al., 2013).

The number of follicular waves varies among animals of the same breed, and even in an individual animal, and can occur once, twice, or three or four times (Figueiredo et al., 1996; Gambini et al., 1998; Bo et al., 2000; Cummins et al., 2012). Such variations can occur due to factors including nutrition, management, milk yield, lactation period, and early postpartum period (Ginther et al., 1996). The first follicular wave emerges during ovulation on day 0 (d0). The emergence of the second wave occurs on days 9 and 10 (in cases of two wave cycles), or on days 8 or 9 (in three wave cycles). By the third wave, the follicular wave emerges on day 15 or 16. The dominant follicles, under the influence of progesterone (P4; diestrus), undergo atresia. The dominant follicle (DF) present at luteolysis becomes the ovulatory follicle, and the emergence of the next wave is delayed. By the second wave cycle, the CL begins to regress on day 16, and by the third wave cycle, the CL regresses by day 19, which results in 19–20 or 22–23 day estrous cycles, respectively (Adams et al., 2008). In addition, an increase in the proportion of three wave cycles has been associated with poor nutrition and heat stress (Bo et al., 2003).

The theory of follicular waves was first described by Rajakoski (1960), who demonstrated the existence of two waves of bovine antral follicular development, and the resulting production of pre-ovulatory follicles in each wave. Further, the existence of follicular waves was confirmed in slaughterhouse animals many years before the development of the ultrasound machine. Other studies were subsequently reported, but the data was discrepant following the use of ultrasound, when changes in the ovaries could be tracked with greater accuracy.

The primordial follicle reserve is formed during fetal development, or immediately after birth. The resulting oocytes remain latent in prophase I of meiosis

(Tabatabaei et al., 2011). This pause in oocyte development persists for a variable length of time from follicle to follicle (Hafez 1995). The mechanisms responsible for triggering follicular growth (activation of the primordial follicles) as well as the mechanism that determines variation in the period of time to the beginning of growth remain unknown (Casasola et al., 2014). The reserve of primordial follicles could be used to resolve specific issues related to infertility, to create new contraceptive methods, or to delay menopause in women. However, this will be possible only after the factors responsible for the extension of follicular growth from the primordial stage to ovulation are elucidated (Adams et al., 2012; Stubbs et al., 2013).

According Driancourt (2001), follicular recruitment (the beginning of folliculogenesis dependent on gonadotropins contained in the pre-ovulatory follicle) occurs during a "window of recruitment," which lasts for two days in cattle, and only gonadotropin dependent follicles are recruited. In cattle, five to 10 follicles (on average) are recruited by wave, and all are potentially capable of being discharged during ovulation as an oocyte (Gibbons et al., 1997).

The follicles are continuously recruited, with the variation in intensity dependent on the stage of follicular development and the estrous cycle. The increase in the mitotic rate of the follicular epithelium cells, as well as the development of the antrum, is more accelerated at the end of the estrous cycle. The "chosen follicle" is selected to progress to ovulation according to maturity state and the onset of pre-ovulatory gonadotropin (Adams, 1999).

In cattle, the emergence of the follicular wave is characterized by two or three days of growth, and the presence of 8 to 41 small follicles (three to four mm diameter,) that are detected by ultrasound (Adams and Pierson, 1995; Utt et al., 2003; Figueiredo, 1995). These waves provide to find a small, medium, and large follicle population in each ovary during all days of the estrous cycle (Santos and Vasconcelos, 2007). A significant number of reports have characterized these wave patterns in the estrous cycle in European cattle breeds (*Bos taurus*). Borges et al. (2001), Viana et al. (2010), and Chasombat et al. (2013) reported similar types of wave patterns for Holstein-Zebu crossbred heifers and zebu cows (*Bos taurus indicus*). Further, the data was confirmed by studies conducted

by Zeitoun et al. (1996) and D'enjoy et al. (2012) that evaluated follicular dynamics in Brahman cows (*Bos taurus indicus*). The rate of follicular growth was similar for all follicles in the wave for approximately two days, until one was selected to continue development to a DF, while the others became atretic and regressed (subordinate follicles). This reports suggested that the DF suppressed the growth of the subordinate follicles in the same wave, as well as emergence in the subsequent follicular wave by blocking recruitment (Ko et al. 1991; Adams and Pearson, 1995). Further, the magnitude of dominance was usually defined by the size difference between the DF and the subordinate follicles (Driancourt, 2001).

During the stages of follicular growth and atresia, a reorganization of the blood capillaries occurs to provide the tissues with the required blood supply. The process is called angiogenesis, and is dependent on the production of specific angiogenic factors (Barboni et al., 2000). Although the mechanisms involved in follicular development are not completely characterized, it is known that the gonadotropins have a relevant function. The regulation of ovarian vasculature may be involved in these mechanisms, and may improve the blood supply to the follicle and consequently, the contact of the gonadotropins and other factors with the follicular cells. Research conducted in rodents, primates, and buffalos has indicated that both *in vitro* and *in vivo*, vascular endothelial growth factor-(VEGF) was the main angiogenic factor in the ovarian vasculature, and that production was influenced by gonadotropins (Fatima et al., 2013).

In cattle, the appearance of LH receptors in granulosa cells is a pre-requisite for the establishment of dominance and ovulation after the LH peak (Ireland and Roche, 1983, Simões et al., 2012). Another contributing factor was the reduction in IGF binding proteins like including IGFBP2 and IGFBP4 (De la Sotta et al., 1996;. Mihm et al., 1997;. Satchel et al., 2013). Follicular dominance can be enhanced by IGF-1 and the VEGF. According to Chase et al. (1998), a growth hormone (GH) deficiency in cattle will limit the production of IGF-1, and may impair follicular dominance. This indicated that the induction of LH receptors might be partially mediated by IGF-1. Reports have shown that LH stimulates the production of VEGF, a potent stimulator of angiogenesis, and that IGF1 may enhance the action of LH during

angiogenesis (Zeleznik et al., 1981; Pretheeban et al., 2010; Satchel et al., 2013).

The emergence of a follicular wave is preceded by an increase in plasma follicle stimulating hormone (FSH) concentrations. The main effects of FSH are to induce aromatase activity in granulosa cells so that they gain the ability to produce estradiol, to stimulate the production of inhibin and follistatin (Singh and Adams, 1998; Takedoni et al., 2005), and to suppress the release of FSH by inhibiting the emergence of new waves (Singh et al., 1999; Takedoni et al., 2005). At the end of a dominance period (ovulation or static phase in an anovulatory DF), circulating FSH levels begin to rise within two days, and the peak is expected approximately 12–24 hours after the emergence wave (Bergfelt et al., 1994).

The pulse frequency and amplitude of LH are influenced by circulating concentrations of P4 and estradiol. High levels of P4 produced by a functional CL in diestrus or pregnancy suppresses the pulsatile frequency of LH. The DFs grow, and become dominant for a long period when the LH pulse frequency is high. An increase in estradiol concentrations following a decrease in P4 due the luteolysis increased the frequency of LH pulses, concurrent with the appearance of a large pre-ovulatory follicle (Adams et al., 2008; Aerts and Bols, 2010). LH has little influence on the control of follicular recruitment, since recruitment occurs when the frequency of LH pulses was reduced (Murphy et al., 1991; Evans et al., 1994; Aerts and Bols, 2010).

The consensus was that LH is involved in late DF growth, while the remaining follicles are subject to the atresia process. Sirois and Fortune (1990) and Fortune (1993) demonstrated that the regression of the CL in cows treated with a slow release P4 device was associated with an increase in LH pulsatility and length of the dominance phase. Duffy et al., (2000) found that injections of exogenous LH resulted in an increase in the DF diameter. LH plays a key role in the development of follicles larger than 8 mm. The main effect of LH was the stimulation of androgen production by theca cells. Inhibin, which is produced in large quantities by granulosa cells, may also stimulate androgen production via paracrine signaling (Mazerbourg et al., 1999). This increases the bioavailability of IGF-1 and IGF-2 at the level of granulosa and theca cells, respectively. In the

granulosa cells, the IGFs increase sensitivity to LH (Driancourt, 2001), and consequently maximize sensitivity to ovulation.

As previously reported, circulating concentrations of P4 and estradiol exert influence on the pulse frequency and amplitude of LH. When the total plasma concentrations of P4 reached 1.7 ng/ml, six LH pulses at an amplitude of 0.2 ng/ml per eight hours were observed. Conversely, 1.8 pulses every eight hours at an amplitude of 0.34 ng/ml were observed when the concentration of P4 was 5 ng/ml (Jaiswal, 2007). Further, an increase in the concentration of estradiol at reduced P4 concentrations after luteolysis increased the frequency of LH pulses, and resulted in the appearance of a pre-ovulatory follicle (Aerts and Bols, 2010).

After the ovulation, the luteinization of the corpus hemorrhagicum ensues, which causes the DF to rupture and the formation of a CL, which produces P4 (Skarzynski et al., 2013). The morphology of the CL and plasma progesterone concentrations are good indicators of its synthesis. Intense angiogenesis, proliferation of granulosa and theca cells from the follicular wall after ovulation, and differentiation (luteinization) during the first five to six days after ovulation results in a progressive increase in plasma P4 concentrations from < 1 ng/ml three days after ovulation to approximately 3 ng/ml six days following ovulation. The peak in plasma progesterone levels occurs between 10 and 14 days post-ovulation (> 4 ng/ml). However, a decline occurs after the 16th day due to induced release of prostaglandin F2a in the endometrium (Singh et al., 2003), which promotes luteolysis.

Ovarian activity along the puerperium

During the puerperium period, the uterus involutes, and the hypothalamic-pituitary-ovarian axis releases cyclical secretions of gonadotropic and gonadal hormones, which results in the first postpartum ovulation and regular estrous cycle. In the physiological puerperium, these events are completed six weeks after delivery (Peter et al., 2009). Further, ninety percent of cows will have the first postpartum ovulation in this period (Peter and Bosu, 1988). However, the three-week or greater interval between parturition and ovulation can be extended in dairy cows (Opsomer et al., 1998). The reproductive organs

return to normal physiological and anatomical pre-pregnancy status, and the major events involved in the functioning of the postpartum hypothalamic-pituitary-ovarian axis are delayed due to the redistribution of energy for milk production (Aguilar et al., 2004).

Clinical and subclinical infections in the puerperium affect ovarian activity (Azawi, 2008). Uterine diseases suppress the release of GnRH and LH and their localized effects, which in turn decreased folliculogenesis (Mateus et al., 2002). The ensuing mechanisms triggered by the negative effects of uterine infection may involve an inflammatory response (Sheldon and Dobson, 2004; Williams et al., 2007), changes in the uterine bacterial flora (Elkjær et al., 2013), or changes in the uterus that might decrease blood flow in the uterus (Heppelmann et al., 2013; Mateus et al., 2002). Cows that experience an abnormal puerperium will be affected by a delay in uterine involution and the surge in ovarian activity may be impaired (Kozicki, 1982). High circulating concentrations of prostaglandin F_{2a} (PGF_{2a}) and serum albumin in the first three weeks after parturition (a common outcome of subclinical infections) act as a uterine signal, and prevent the early onset of ovarian activity (Peter e Bosu, 1988; Peter et al., 1990; Sheldon et al., 2002b; Krause et al., 2014; Gabler et al., 2009).

The suppression of ovarian activity in the early postpartum period may improve uterine involution in cows with or without uterine disease (Heppelman et al., 2013). According Silvestre et al. (2009), treatment with deslorelin (5 mg) during the postpartum period suppressed ovarian follicular development by stimulating uterine and cervical involution, increased the tonus of the uterine wall, decreased the frequency of purulent cervical discharge, and reduced inflammation in the reproductive tract. These reports highlight some topics related to the advantage of full ovarian activity in the early puerperium that require further discussion.

In the puerperium period, nutritional requirements increase rapidly due to milk production. Consequently, cows may be affected by a negative energy balance (NEB) and/or disproportionate energy metabolism (e.g. fatty liver, ketosis, acute and sub-acute ruminal acidosis), diseases related to mineral imbalance (e.g. milk fever, clinical and subclinical hypocalcemia), or immune function disorders (e.g. retained placenta,

mastitis, and metritis). Dehydration is also associated with NEB events and the reduction of raw intake (Esposito et al., 2014). Dairy cows are highly susceptible to oxidative stress associated with metabolic adaptation processes in early lactation that increase the production of reactive-oxygen species such as melondialdeíd, and cause a reduction in serum glucose (Turk et al., 2008). Cows affected by NEB can head nutrients from the reproduction limiting the number of ovarian growth and maximum size delaying the first ovulation, hindering estrus expression and decreasing plasma P4 concentrations from the DF. Further, Ovulation is delayed by inhibition of the LH pulse frequency and suppression of blood glucose, insulin, and IGF-1, which reducing reduces the production of estrogen by the DF (Leroy et al., 2008). Conversely, increased food intake can suppress reproduction due to steroid metabolism. The increased food intake enhances hepatic perfusion, which increases the metabolism of estradiol and progesterone (Sangsritavong et al., 2002), and contributes to anovulation (Walsh et al., 2007), the release of an enlarged DF (Sartori et al., 2004.), multiple ovulation (Lopez et al., 2005.), or poor luteal function (Villa-Godoy et al., 1988.) and delayed luteal regression (Opsomer et al., 2000; Petersson et al., 2006). These events are most likely caused by the development of a DF to a no estrogen-sensible, resulting on in inadequate endometrial PGF₂ production of endometrial PGF₂ (Sangsritavong et al., 2002; Sartori et al., 2004).

Hepatic function also influences the reproductive performance of cows in the puerperium period. According to Bertoni et al., (2008), cows with low or intermediate hepatic activity exhibited a greater number of days open (139 versus 93, respectively), a greater number of services per pregnancy (2.68 versus 1.65, respectively), and lower milk production (38.3 versus 40.8 kg/day, respectively) compared to cows with a high rate of hepatic activity. Animals with a low rate of hepatic activity (bilirubin and blood urea) also had a higher number of inflammatory conditions in the first month of lactation and more severe NEB, and exhibited lower milk production and fertility than cows with high hepatic activity. High dietary protein levels (16–17%) can likewise be detrimental to reproductive performance due to high concentrations of urea (Tamminga, 2006). According to Oliveira Filho et al. (2010), proper nutritional supplementation and good body condition score (BCS) during

parturition help to maintain ovarian follicular function, favoring the follicular emergence. According to Silvestre et al. (2011), the supply of oils, rich in fatty acids, provide improved immunity, balanced NEB, and better postpartum reproductive rates.

Ultrasound characterization of ovarian and uterine activity in postpartum

The first ovarian ultrasound scans in cattle were performed by Ginther and Pierson (1984). Consequently, they observed the presence of two waves of follicular growth during the bovine estrous cycle. The ultrasound images were composed of two-dimensional arrays that differed in their gray scale values (Pierson and Adams, 1995; Kremkau, 1998). Each pixel was described by one of 256 shades of gray (0 = black and 255 = white), and represented a discrete tissue reflector (Pierson and Adams, 1995). The ultrasound image of a tissue was referred to as echotexture, and was confirmed by the histological structure of the tissue (Singh et al., 1997). Computer algorithms designed specifically for the analysis of ultrasound images have since been developed to overcome inconsistencies in visual evaluations, and to provide a quantitative approach to the analysis of the gray-scale pixel values (Vassena et al., 2003).

These algorithms have been used extensively in studies that characterized the echotexture dynamics of ovarian structures for different stages of the follicular wave (Tom et al., 1998). Specific changes in the phases of DF, SF, and CL were characterized by images on the computer.

In vivo studies employing ultrasonography to evaluate follicular development and ovulation relative to the position of the CL or DF were not consistent with the local effect (Adams, 1999). Consistent changes in the ultrasound images have been associated with the physical and endocrine status of ovarian follicles (Singh et al., 1998).

Vassena et al. (2003) found that the average gray scale values of the antral DF were smaller than values from the subordinate follicles. The type of follicle (dominant or subordinate) on day 7 (d7) had mean gray scale values lower than the values on d2, d3 or d5. As well, the interaction between the days of the wave and the type of follicle was not significant. The heterogeneity analysis revealed no influence from the

day of the wave or from the follicle type. The authors also found a similar pattern in the gray scale values for the wall, peripheral antrum, and perifollicular stroma in the DF and SF. The values tended to follow a pattern in days five to seven, which was maintained in all follicular segments. The same authors found no local effects of the DF or CL on the echotexture of the subordinate follicles examined. Additionally, there was no local effect of the DF on the CL echotexture, except those involving the levels of gray scale in the antrum. Singh and Adams (2000) observed reduced thickness of the granulosa layer between the end of growth and the early static phase (d3) leading to the regression phase (d6). Vassena et al. (2003) described average gray scale values and decreasing gray scale levels from the onset of the static phase to the dominant follicle phase, as well as the regression to subordinate follicles. However, according to Singh et al. (1998), the average gray scale values of both follicles in the perifollicular stroma during the late static phase and the regression phase were higher than during the previous phase. Vassena et al. (2003) explained this apparent discrepancy by the difference in the perifollicular vascular flow and quality of the images.

The sonographic characterization of ovarian follicles and verification of oocyte competence was also performed by Vassena (2001). The results indicated that oocytes collected from SF on d5 of the follicular wave were more competent than oocytes collected from d2, d3, or d7 of the wave. The differences between the values of the DF and SF in all segments analyzed were lower on d5. Following the analysis of oocyte competence associated with follicular status, it was possible to analyze the ultrasound images to identify follicles that produced competent oocytes (Salamone et al., 1999).

Studies conducted using uterine ultrasonography in the puerperium period contributed valuable information to current knowledge of uterine events in this period. Using Doppler, Herzog and Bollwein (2007) reported a sharp decline in uterine blood flow during the postpartum period, especially in the first week after parturition. The average frequency and amplitude of myometrial contractions were described by Bajcsy et al. (2005), who reported a decrease in contractions during the early puerperium period in cows. After a significant peak in uterine contractions during the first post-treatment wave, the values of oxytocin and

carbetocin groups remained high during the second hour, returned to baseline levels during the third hour, and reached physiological levels after 12 hours. According to Gaiewski et al. (1999), the intravenous injection of oxytocin and carbetocin always caused strong uterine contractions, and changes in uterine activity were commonly associated with plasma P4 and estrogen levels.

Final Consideration

The resumption of ovarian activity in the postpartum period constitutes a fundamental factor of good reproductive performance in dairy cattle. Ovarian activity induces optimal uterine involution and the postpartum restoration of endocrine function, which results in the desired reduction in the reproductive waiting period. As well, the knowledge and tracking of physiological ovarian follicular dynamics provides the veterinarian with the necessary information to take preventative action and to treat disorders that could cause significant losses. Finally, ultrasonography has proven to be a promising tool with relevant applicability to

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