Review Report

Ovarian follicular dynamics in cattle: a comprehensive review

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Abstract

Ovarian follicular dynamics in cows is characterized by well-coordinated development and maturation of ovarian follicles. In the bovine ovary, follicles advance from primordial stages (present at birth), to primary, secondary, and tertiary stages. During puberty, there is a marked increase in pulsatile secretion of gonadotropin-releasing hormone from the hypothalamus; this stimulates the anterior pituitary to release follicle stimulating hormone and luteinizing hormone, promoting follicle growth and selection with some dominant follicles ovulating. Estradiol 17-β from these developing follicles regulates the reproductive cycle, promoting estrus and cyclicity. Understanding these dynamics is vital for optimizing reproductive management and enhancing fertility. This review describes ovarian follicular dynamics and puberty in cattle.

Keywords: Ovarian follicles, ovary, recruitment, selection, dominance, ovulation

Introduction

Effective reproductive management of cattle necessitates a thorough understanding of the estrous cycle, as pregnancy rates considerably influence profitability.[1-4] For optimal breeding management, estrus synchronization, fixed time artificial insemination and superstimulation, it is crucial to understand ovarian follicular dynamics.[5] On average, every 21 days (range, 18-24 days), there is an opportunity for conception. Follicle development occurs in a wave-like pattern, usually 2 or 3 waves, governed by hormones.[1-4] *Bos indicus* cattle have later puberty compared to *Bos taurus*, but they have higher blood concentrations of insulin, insulin-like growth factor-1 (IGF-1), estradiol 17-β (E_2), and progesterone (P_4). *Bos indicus* have smaller preovulatory follicles and corpora lutea, smaller dominant follicles at deviation, more small follicles, and follicles that are more sensitive to gonadotropins.[6]

Real-time B-mode ultrasonography is crucial to monitor ovarian follicular dynamics in cattle, for both reproductive management and research. This noninvasive method can be used repeatedly for reproductive tract evaluation without disrupting reproductive function.[7-9] Consequently, ultrasonography is used for detection of pregnancy (or nonpregnancy), embryonic/fetal viability, twins, and diagnosis of pathological conditions such as pyometra, hydrometra, and metritis, facilitating herd reproductive management.[10,11]

Oogenesis and folliculogenesis

Oogenesis is the process by which oogonia develop into oocytes; the ovarian cortex contains thousands of oocytes at birth.[12,13] Oocytes can be classified based on size, number of granulosa cells, or dependence on gonadotropins. Another classification method divides them into preantral and antral follicles, with preantral follicles further categorized into primordial, primary, or secondary follicles.[14] At the antral stage, most follicles undergo atresia, with only a few progressing to the preovulatory stage,[15] with ovulation releasing the mature oocyte-cumulus complex.[16]

During folliculogenesis, a primordial follicle grows to a preovulatory size, with concurrent growth and differentiation of the oocyte.[17] In bovine ovaries, there are many follicles at various developmental stages, in growing and nongrowing pools.[18,19] Primordial follicles have an oocyte surrounded by flat pregranulosa cells, remaining in a nongrowing pool throughout the cow's reproductive life. In contrast, primary, secondary (preantral), and tertiary (antral) follicles are in the growing pool.[14] Pregranulosa cells in primordial follicles differentiate into granulosa cells, forming a primary follicle consisting of an oocyte and 20-40 granulosa cells.[15] A primary follicle transitions from the nongrowing to the growing pool,[13] triggering granulosa cell proliferation and development of a secondary follicle.[20] During this phase,

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the zona pellucida surrounding the oocyte continues to develop, and the number and layers of granulosa cells increase.[16] The antral (end-stage) follicle has an inner avascular layer of granulosa cells, theca interna and theca externa.[21] As the follicle and oocyte develop, their diameters increase.[13]

Puberty

Puberty marks the beginning of reproductive and productive processes, representing a gradual journey toward reproductive maturity.[22] *Bos taurus* heifers reach puberty at 6-24 months, an interval considered to allow natural selection to delay reproduction in weaker animals.[23] However, *Bos indicus* cattle reach puberty later than *Bos taurus* cattle,[24] substantially impacting profitability, productive lifespan, and reproductive success.[25] In *Bos indicus* beef breeds, puberty typically occurs at 22-36 months.[26]

The age at which puberty occurs is influenced by numerous factors, including nutrition, age,[26,27] genetics,[27] body size,[26] social environment, and lunar phases.[23] There is a notable relationship between body weight gain and puberty age; heifers with higher growth rates generally reach puberty earlier,[28] whereas those with low-energy diets attain puberty later.[29] As puberty approaches and sufficient body size is reached, the hypothalamic negative feedback on luteinizing hormone-releasing hormone production diminishes,[27] enabling E_2 to trigger the pubertal luteinizing hormone (LH) surge. Heifers typically reach puberty at a genetically determined size and weight; relative to their adult body weight, it is ~ 50%,[30] 55-60%,[25] or 70%,[26] depending on the breed.

Growth of the reproductive tract is supported by a complex interaction of hormones.[23] Maturation of the hypothalamic-pituitary-ovarian axis is essential for puberty and initiation of regular cycles.[25] Estradiol is the primary hormone regulating the onset of puberty, as it initiates negative feedback in the hypothalamus during the prepubertal phase, inhibiting gonadotropin releasing hormone (GnRH) release. However, when a heifer nears puberty, increased GnRH secretion and more frequent LH pulses lead to the initial ovulation.[22] Hastening puberty can be beneficial, as fertility increases after the first ovulation.[27] To predict future reproductive success in females, it is crucial to understand relationships among live weight, weight gain at various life stages, and their effects on other traits related to body composition.[26]

Estrous cycle

Bovine estrous cycle is a well-defined sequence of physiological and behavioral events regulated by interactions of the ovaries, uterus, hypothalamus, and anterior pituitary, and controlled by hormones.[31] The cycle has 2 distinct phases: follicular and luteal.[30,32] Follicular phase extends from luteolysis (demise of the corpus luteum; CL) to ovulation. During this phase, the ovulatory follicle matures and releases an oocyte for potential fertilization.[30] Most cycles have 2 or 3 follicular waves.[31,33-36] During the luteal phase, under the influence of P_4, the initial 1 or 2 waves produce a dominant follicle that does not ovulate but regresses. The ovulatory follicle ultimately emerges from the dominant follicle of the final wave.[34]

Follicular phase

Primary hormone of the follicular phase E_2 is produced by developing follicles.[37] It has a crucial role in initiating estrus and regulating the preovulatory LH surge that drives ovulation.[38] During this phase, there is a transition from P_4 to E_2 dominance. The follicular phase is characterized by 4 key events: secretion of GnRH, follicular growth, sexual receptivity, and ovulation. Release of GnRH from the hypothalamus stimulates the anterior pituitary to secrete follicle stimulating hormone (FSH) and LH, promoting follicular growth. As follicles mature, they produce increasing E_2 that induces behavioral estrus and prepares for potential fertilization.[39] Ovulation is a sequence of physiological and biochemical events with final maturation of the follicle, an increase in LH pulse frequency and amplitude, and enzymatic breakdown of the follicular wall, allowing the oocyte to be expelled and potentially fertilized.[38]

Proestrus

Proestrus, the initial stage of the estrous cycle, occurs 1-3 days before estrus, starting immediately after regression of CL from the previous cycle. As P_4 concentrations decline, the negative feedback on GnRH is removed, leading to more frequent and vigorous GnRH pulses.[38] During proestrus, FSH promotes growth of ovarian follicles, whereas increased LH stimulates their maturation, increasing E_2.[40-43] The dominant follicle from the cohort secretes E_2 that triggers estrus.[44] Estradiol has a positive feedback on the hypothalamus, increasing GnRH, leading to an increased release of LH from the anterior pituitary.[45,46] Mature follicles release E_2 into the bloodstream, causing an increase in uterine tone and redness of the vaginal mucosa.[47]

Estrus

During the estrus phase, cows exhibit signs of sexual receptivity.[38] Under the influence of FSH and LH, follicles mature and start secreting E_2 that stimulates the hypothalamic surge center. This leads to a substantial release of GnRH and LH, with the LH surge driving ovulation of the dominant follicle.[38] Ovulation typically occurs at the end of estrus, ~ 10-12 hours after its offset.[37,48,49] The duration and intensity of estrus can vary, depending on breed, parity, milk production, and environmental conditions.[50]

Bos indicus cattle have a shorter estrus compared to *Bos taurus* cattle, with an average interval of ~ 10 hours, range 1.3-20 hours.[51,52] When synchronized with prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$), the mean length of estrus does not differ between Angus (19 ± 2 hours) and Brahman (17 ± 2 hours) cows, although it is longer than in Senepol cows (12 ± 3 hours).[53] Brahman cows have lower serum LH concentrations during natural,[54] E_2-induced,[55] or GnRH-induced[56] preovulatory LH surge compared to British breeds. The interval between E_2 surge or E_2 injection and the peak LH is notably shorter in Brahman cattle compared to Brahman-Hereford and Hereford heifers.[55] Additionally, Brahman heifers have an earlier preovulatory LH surge and ovulate sooner (18.5 ± 3.1 hours) after the LH surge compared to Hereford (23.3 ± 2.1 hours) and Brahman crossbred heifers (22.2 ± 2.6 hours).[57] However, the interval between LH surge and ovulation is ~ 23.3 ± 2.2 hours[58] and 25.9 ± 0.6 hours.[59] Seasonality affect cyclicity in *Bos indicus* cattle[60]; during winter, *Bos indicus* cows had less pronounced preovulatory LH surges and had luteal cells that were less responsive to LH *in vitro*. Furthermore, Brahman cattle had higher conception rates in summer (61%) compared to fall (36%).[54]

Luteal phase

Luteal phase has 3 primary events: luteinization, i.e. transformation of follicle cells into luteal cells after ovulation; diestrus, involving CL growth and development; and luteolysis, CL regression is triggered by $PGF_{2\alpha}$ (produced by the endometrium).[38] This phase features 3 stages of luteal tissue development: corpus hemorrhagicum (CH), CL, and corpus albicans (CA). Luteal phase begins after ovulation and concludes with luteolysis; CH lasts ~ 3 days and then transforms into a CL that typically persists ~ 17 days. During the early part of the luteal phase, CH is the primary source of P_4 and is unresponsive to $PGF_{2\alpha}$ until ~ day 5 in heifers and cows. The final stage, the CA, is formed after luteolysis.[61]

Metestrus

Ovulation occurs during metestrus, which spans 3-4 days after estrus.[62] During ovulation, a preovulatory follicle ruptures and releases a mature oocyte, with formation of a red depression on the ovary called CH. Progesterone concentrations are initially low but rise as the CH develops.[40,63] After ovulation, small and large luteal cells, derived from theca and granulosa cells, respectively, produce P_4.[64,65] At this stage, the CL is not yet fully mature and lacks $PGF_{2\alpha}$ receptors, so exogenous $PGF_{2\alpha}$ does not induce luteolysis.[48,66]

Diestrus

Diestrus spans 12-15 days.[37] Early in diestrus, P_4 production and CL growth begin concurrently. By mid-diestrus, CL is fully mature and P_4 concentrations peak.[37,67] In late diestrus, the endometrium secretes $PGF_{2\alpha}$ that binds to CL luteal cells, causing breakdown of luteal tissue either locally or via vascular constriction. Additionally, $PGF_{2\alpha}$ stimulates luteal cells to release oxytocin that promotes further $PGF_{2\alpha}$ production by the uterus.[67] Estradiol from the dominant follicle of the second or third follicular wave is also necessary to initiate production of uterine $PGF_{2\alpha}$ and to increase the number of oxytocin receptors in the uterus. As diestrus concludes, luteolysis occurs, removing P_4-induced negative feedback on the hypothalamus, leading to GnRH release and subsequent stimulation of the anterior pituitary to produce FSH and LH.[53,66]

Ovarian follicular dynamics

Follicular dynamics refers to development and regression of antral follicles, culminating in formation of dominant/preovulatory follicle.[68,69] A follicular wave involves synchronous development of a group of follicles, with 1 or 2 becoming dominant and continuing to grow while inhibiting the others.[33,70,71] Follicular waves can be influenced by breed and management.[30] The 2 ovaries function together as a single unit.[5] If luteal dominance persists, ovulation may not occur, leading to additional anovulatory waves.[72] Follicular waves occur in cyclic and pregnant cattle[73] as well as in prepubertal heifers,[72] marked by the recruitment, persistence, regression, or ovulation (only in cyclic animals) of a dominant follicle.

During bovine estrous cycles, 2 or 3 waves of antral follicle growth, induced by FSH, occur at intervals of 7-10 days. Each wave begins with an increase in FSH, promoting growth of a group of 3 or 4 mm antral follicles, followed by emergence of a single dominant follicle reaching ovulatory size (12-20 mm), whereas the remainder of the initial cohort undergoes atresia.[74] Heifers generally exhibit 3 waves of follicle growth per cycle once cyclicity is established, whereas dairy cows predominantly have 2 waves per cycle.[30,75] During the interestrus interval, heifers with 2 waves have 2 FSH surges, whereas those with 3 waves have 3 FSH surges.[76] A model of follicular dynamics during prepubertal phase is illustrated (Figure 1).

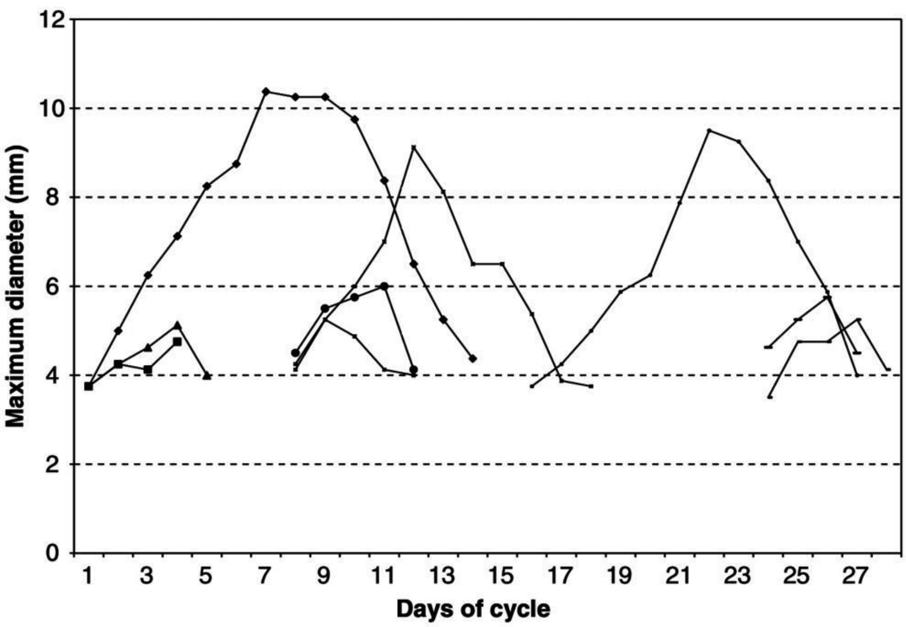

Figure 1. Model of ovarian follicular dynamics during prepubertal phase (adapted Romano et al.[29])

Transrectal ultrasonography employs high-frequency sound waves emitted by a transducer that travel through tissues to provide a quick, easy, and accurate diagnostic method. These sound waves, upon striking tissue surfaces, are reflected back to the transducer as echoes that are then displayed on the viewing screen. A linear-array contains piezoelectric crystals, arranged in a row, that emit high-frequency waves, usually 5-7.5 MHz for bovine reproductive imaging. Transducer frequency is directly related to image resolution but inversely related to penetration by sound waves.[77] A 5.0 MHz transducer provides lesser image detail but greater tissue penetration whereas a 7.5 MHz transducer offers higher resolution but less tissue penetration. Therefore, imaging growing follicles or a CL is best performed with a 7.5 MHz transducer.

Ultrasonography allows for a better understanding of bovine ovarian follicular dynamics in real-time without invasive procedures.[3] It is completely noninvasive, enabling repeated evaluations of an animal's reproductive tract without compromising its breeding capacity or causing harm.[71] Imaging bovine ovaries has revealed patterns of follicular development and provided insights into the regulation of follicular growth and development,[78] CL function, and fetal development.[78] Transrectal ultrasonography also aids in understanding the physiological and morphological changes that occur during ovarian follicle growth, regression, ovulation, and CL alterations throughout the cycle.[3] Fluid-filled structures like antral follicles appear as black circular structures (anechoic) encircled by echogenic ovarian tissue because fluid absorbs ultrasound waves rather than reflecting them. Most veterinary ultrasound scanners can resolve 2-3 mm ovarian follicles, whereas larger antral follicles can be easily monitored by serial examinations.[77]

Follicular wave pattern

Follicular waves in various breeds of cattle are summarized (Table 1). Duration of follicular dominance in the first wave is a key predictor of the number of waves during the IOI. In 2-wave cycles, dominance of the first-wave follicle extends by 3 days compared to 3-wave patterns, with delayed follicle regression. This extended dominance is accompanied by earlier luteolysis and a delay in emergence of the second-wave dominant follicle. Regulation of the wave pattern is primarily influenced by factors affecting development of the first-wave dominant follicle.[5] Although 1,[71] 4,[79] and 5 wave IOIs[1] have been documented, more than 95% of IOIs consist of either 2 or 3 follicular waves. Notably, 27% of estrous cycles in *Bos indicus* cows had 4 waves, compared to only 7% in *Bos indicus* heifers.[80] Additionally, despite no seasonal influence on the wave pattern in *Bos indicus*,[81] parity did affect the pattern.[81]

Follicular growth

Endocrine, paracrine, and autocrine signals interact in a complex network to regulate ovarian follicle growth and ovulation, influencing steroidogenesis and gametogenesis. The hypothalamic-pituitary-gonadal axis, encompassing the gonads, anterior pituitary, and hypothalamus, primarily governs follicle development. Steroid hormones and their receptors have crucial roles, participating in various signalling pathways.[91–93] For farm animals, growth, development, and maturation of ovarian follicles are vital for optimal reproductive efficiency.[30] Follicular growth has 2 distinct phases: slow and rapid growth.[20] Primordial follicles are formed during embryonic development, with their total number established during fetal development.[30]

From the pool of developing follicles, 1 or 2 dominant follicle is selected, grows, and advances during the gonadotrophin-dependent rapid growth phase that lasts ~ 5-7 days before the follicle either undergoes atresia or ovulates.[20] Growth rate of the dominant follicle was similar across the first, second, and third follicular waves.[85] Between days 1-18, growth rate of small follicles (1-3 mm) steadily increases until a single follicle is chosen as dominant, whereas all other follicles in the recruited group grow at a consistent rate.[34,94] Variations in gonadotropin pulse frequency and slowed follicular growth are often influenced by energy balance, which affects concentrations of insulin, growth hormone and IGF.[24,74,80,95]

Table 1. Pattern of ovarian follicular waves in various breeds of cows

Breed and heifer/cow	2 waves (%)	3 waves (%)	4 waves (%)
Jersey crossbred cows[82]	58.6	41.4	–
Panganur cows[83]	25.0	75.0	–
Crossbred cows[84]	66.6	33.3	–
Ongole[85]	66.0	34.0	–
Kenyan Boran cows[86]	23.5	70.5	5.8
Thai native heifers (*Bos indicus*)[35]	70.0	30.0	–
Crossbred cows[87]	25.0	75.0	–
Thai heifers[88]	38.1	47.6	–
Thai cows[88]	17.2	82.7	–
Bos indicus cows[89]	78.5	21.4	–
Native breed of Egypt[33]	71.4	28.6	–
Bos indicus cows[80]	16.0	68.0	16.0
Holstein Friesian cows[80]	17.6	82.3	–
Girolando cattle[90]	62.5	37.5	–

Recruitment

Follicle recruitment (emergence) is the process where follicles grow and become dependent on gonadotropins.[2] Recruitment involves a cohort of 5-10 antral follicles that avoid apoptosis due to elevated concentrations of FSH.[72] The increase and subsequent decrease in circulating FSH concentrations are closely related to the onset of a follicular wave and selection of the dominant follicle. A similar FSH surge initiates each wave, with mid-cycle surges often resembling the amplitude and duration of the preovulatory surge.[96]

Follicular recruitment is triggered by a temporary increase in FSH, which peaks either 1 day before or at the onset of a follicular wave.[97] In both 2 and 3 wave cycles, the rise in plasma FSH has a role in recruiting follicles and determining the dominant follicle.[72,82,96] Recruitment involves development of several follicles to ~ 4 mm that grow at a rate of 1-2 mm per day during a 'parallel' growth phase lasting 2-3 days. During a follicular wave, an average of 7 follicles will grow to > 5 mm in diameter.[83] During the growth phase, there are FSH receptors on granulosa cells and LH receptors on theca cells.[98]

Bos taurus cows typically have ~ 24 viable small antral follicles (2-5 mm) at the onset of each follicular wave. In contrast, *Bos indicus* cattle generally have more small follicles during wave emergence.[99] For instance, Nellore heifers had ~ 50 small follicles in their ovaries at the start of wave emergence.[100]

Selection

Cattle are typically monovular; out of all the recruited follicles constituting a wave, only 1 is selected to fully develop and potentially ovulate, whereas all others regress.[74] This selection process allows 1 follicle per wave to dominate functionally and morphologically. In cattle, the choice of the dominant follicle depends on FSH dependence and LH responsiveness. The transient surge in FSH enables some follicles to respond to LH.[5] As the follicle grows, deviation occurs, during which granulosa cells develop LH receptors and the follicle shifts from being primarily dependent on FSH to LH.[76] At this stage, the follicle can sustain itself without FSH, as it is responsive to LH.[5] However, despite extensive research, the fundamental biological mechanism for selecting the follicle that will ovulate remains unclear.[101] During selection, circulating FSH concentrations decrease in response to negative feedback from E_2 and inhibin produced by the growing follicle cohort. The dominant follicle has an inherent advantage, allowing it to continue developing despite decreased FSH, whereas all other follicles in the cohort cease growing and regress.[98]

Selection is described as a 'tight functional two-way coupling system' between decreasing FSH concentrations and follicular selection. FSH promotes growth of all recruited ovarian follicles, and as each follicle matures, it reduces FSH release by producing E_2 and inhibin. Once FSH concentrations decrease to baseline, only the newly selected dominant follicle continues to grow. By 5 days after follicle recruitment, subordinate follicles are atretic[72] and the dominant follicle alone maintains FSH suppression, preventing additional follicular waves from developing.[98] The end of selection is marked by a 2-3 mm size difference between the largest and the second-largest follicles in the wave. Deviation typically occurs ~ 3 days after recruitment, when the largest follicle reaches ~ 8.5 mm in diameter.[101,102] At this point, the dominant follicle continues to grow, shifting from FSH to LH dependence.[97,101,103] The difference in growth rates between the largest and the next largest follicles after wave emergence is a crucial aspect of follicle selection.[104] Before deviation, all growing follicles have potential to become the dominant follicle.[71,102]

In Holstein heifers, the future dominant follicle typically reaches a mean diameter of 8.5 mm ~ 2.5 days after wave emergence, marking the point at which follicle 'deviation' (difference in growth rates between dominant and subordinate follicles) becomes evident.[5] Both pre and postpubertal heifers have remarkably similar timing from wave emergence to divergence in growth patterns between the dominant follicle and the first subordinate follicle.[72] In *Bos indicus* cattle, follicular deviation occurs when the largest follicle reaches 5-7 mm in diameter,[103,104] whereas in *Bos taurus* breeds, deviation occurs when the largest follicle reaches 8.5-9.0 mm in diameter.[65] In some cases, deviation may involve 2 large follicles growing beyond 10 mm (codominance), with deviation between the first and third largest follicles in the wave.[98]

Dominance

Dominance is a process whereby the selected dominant follicle inhibits growth of subordinates,[72] allowing it to evade atresia and continue growing until either atresia (during the luteal phase) or ovulation (during the follicular phase) occurs.[30] Among recruited and selected follicles, 1 follicle grows more rapidly than others, whereas the remaining follicles from the same wave cease to grow.[76] The largest growing follicle becomes the dominant follicle (DF) following deviation, with the other subordinate follicles undergoing regression.[104] Although the interval between deviation and ovulation is similar in *Bos taurus* and *Bos indicus* cows, *Bos indicus* cows have a significantly smaller diameter (~ 6.0 mm) for the largest follicle at deviation.[105]

Many traits related to follicular growth and dominance are similar between *Bos indicus* and *Bos taurus* cattle. However, *Bos indicus* cows generally have smaller maximum diameters of the dominant follicle (10-12 mm) and CL (17-21 mm) compared to *Bos taurus* cows (14-20 and 20-30 mm, respectively.[80] Dominant follicles regulate follicular growth by altering systemic FSH concentrations. Increased E_2 concentrations, which align with follicular growth, are necessary to suppress subordinate follicles.[69,76] The maximum diameter of the dominant follicle in the second wave is smaller compared to dominant follicles in other waves, despite no significant difference in rates of atresia or follicle growth among various follicular waves. This difference may be attributed to the fact that the second wave occurs when the CL is producing P_4, whereas the first and third waves occur during the luteogenic and luteolytic phases, respectively.[1]

During the dominance phase, a single large follicle, typically 12-17 mm in diameter, is present while subordinate follicles regress and no new waves develop. This 'plateau' phase lasts 5-7 days.[75,106] During the first wave of ovarian follicular development, E_2 concentrations in the follicular fluid of the dominant follicle and in ovarian venous blood peak during the growth phase but decrease throughout the plateau phase.[83,107] In prepubertal calves, both dominant and largest subordinate follicles have increasing diameters with age, with the growth rate highest between 2-8 weeks and 24-40 weeks, concurrent with increases in mean LH concentrations.[5] In 2-3-month old

Nelore calves, dominant follicles and varying numbers of subordinate follicles were observed, with successive anovulatory follicular waves.[3]

Codominance

Codominance occurs when multiple follicles within a wave attain dominant status, often resulting in smaller diameters[108] due to competition for LH. Codominance happens during the ovulatory wave can lead to double ovulation. In nonlactating heifers, codominance and multiple ovulation are rare or absent,[75] but in lactating dairy cows, codominance occurs in 21-36% of follicular waves.[30] Various phases of follicular dynamics are depicted (Figure 2). High-producing dairy cows frequently experience multiple ovulations (incidence 10-39%), with all ovulatory follicles from the same follicular wave.[5] Cows with multiple dominant follicles typically have lower circulating inhibin and progesterone (P_4) during deviation compared to those with a single dominant follicle.[109] These observations correspond with higher FSH and LH at deviation, ongoing growth of the second and third largest follicles in the wave, and the presence of several dominant follicles.[5]

Ovulation and luteolysis

The age at first ovulation in cattle varies significantly; however, early puberty is beneficial, as fertility improves with cycles after the first pubertal ovulation.[27] Antral follicles are present as early as 2 weeks of age, with follicles 3 mm in diameter. Their maximum diameter increases in a pattern similar to that of ovarian dimensions, with a significant increase in maximum follicle diameter in the 80 days preceding first ovulation.[29] That ovulation in heifers often occurs without behavioral estrus, and the resulting CL (a temporary endocrine gland formed from the theca and granulosa cells of the follicle)[27] is smaller and shorter-lived (3-12 days) compared to a typical cycle.[27,30] The short cycle that typically occurs during these transitional intervals, from prepubertal to puberty[27] and from anestrus to ovarian cyclicity in postpartum cows, is associated with 1 follicular wave.[30] In pre-pubertal heifers, the initial luteal phase following the first ovulation often lasts ~ 7 days,[71] 5-7 days,[110] 7.7 days,[5] 7-12 days,[111] or 8-12 days.[112] Although the oocyte may be fertilized, embryonic mortality occurs if luteolysis occurs before maternal recognition of pregnancy.[25] Following this brief cycle, estrus and a normal, fully functioning luteal phase ensue.[27] The secretion of LH determines whether a follicle will eventually regress or ovulate. When the CL is functioning properly, high concentrations of P_4 are maintained, preventing LH pulses. The dominant follicle continues to develop until there is sufficient E_2 in the blood for ovulation. The preovulatory LH surge, triggered by decreasing P_4 concentrations following luteolysis and increasing E_2 concentrations, leads to ovulation of the dominant follicle[61]; in the absence of a functional CL, the LH surge triggers ovulation and luteinization.[73]

Luteal lifespan and P_4 secretion are regulated by processes that can either prolong (luteotropic, caused by LH) or shorten (luteolytic, caused by $PGF_{2\alpha}$) CL function.[27] Luteolysis is triggered by the endometrium's pulsatile release of $PGF_{2\alpha}$ that travels to the CL via the venous-arterial counter-current transport system, causing vasoconstriction and luteolysis.[22] When CL regression occurs before day 16 of the cycle, it is referred to as premature luteolysis,[113] characterized by a shorter lifespan, caused by a premature release of $PGF_{2\alpha}$.[111] This phenomenon is common in heifers after their first ovulation during puberty and in postpartum cows and is associated with 1 wave of follicular growth, followed by a normal-length ovulatory cycle.[71] Mechanisms underlying premature luteolysis, inadequate CL formation, and subnormal luteal function in heifers and postpartum cows are multifaceted.[27,114]

- Shortened estrous cycle duration may be caused by inadequate ovulatory follicle development,[108,111] ovulation of small follicles, or a combination of these.[115] Ovulation of small dominant follicles results in small CLs with low P_4 concentrations, low pregnancy rates, and short estrous cycles.
- CLs unresponsive to gonadotropins,[116] and decreased luteotropic stimulation.[111]
- Premature luteolytic stimulation[78,111] caused by endometrial $PGF_{2\alpha}$ production, with luteolysis commencing as soon as the CL develops $PGF_{2\alpha}$ receptors, ~ Days 6 of the cycle.[117]
- Increased sensitivity of the CL to luteolytic substances.[78]
- Ovulation without previous exposure to P_4.[22]

Atresia of follicles

In pubertal, nonpregnant, and cyclic cows, ovulation can only occur during specific phases of the cycle representing 'windows of opportunity.[98] However, the wave-like pattern of ovarian follicular growth begins within the first 4 weeks after birth and continues uninterrupted throughout life. Due to the limited window for ovulation, the majority of ovarian follicles (> 99%) are destined to regress (atresia).[98] Apoptosis, a

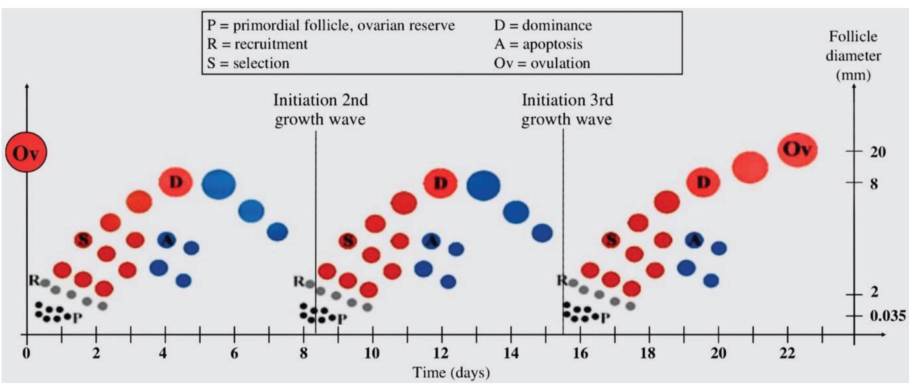

Figure 2. Recruitment, selection, and dominance phase in 3-wave growth pattern in bovine estrous cycle (adapted Evans et al.[71])

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'programmed-cell death' process, drives atresia in ovarian follicles.[118,119] Ovarian follicular atresia was discovered in the ovaries of rats,[71] chickens, and pigs,[120] suggesting apoptosis is evolutionarily conserved.[99] More than 99.9% of the primordial follicles in the ovaries at birth undergo apoptosis. In the early stages of atresia, anovulatory dominant follicles have a decrease in aromatase activity and E_2 synthesis,[121] but there are no significant changes in gonadotropin receptors on granulosa cells.[122] Models for 2 and 3 wave cycles are depicted (Figures 3a and 3b).

A decrease in the concentration of androgen precursors may,[68,77] or may not[98] be associated with a loss of estrogenic ability. Additionally, characteristics of the atretic dominant follicle include granulosa membrane erosion and a predominance of cells with pyknotic nuclei.[123] Preovulatory follicle diameter during various follicular waves in various breeds of cows are summarized (Table 2).

Research gaps and conclusion

Despite substantial progress in understanding follicular dynamics in cattle, several key research gaps remain that warrant further investigation; 1 major limitation is inadequate understanding of breed-specific variations, particularly among *Bos taurus, Bos indicus* and crossbreds. Although general

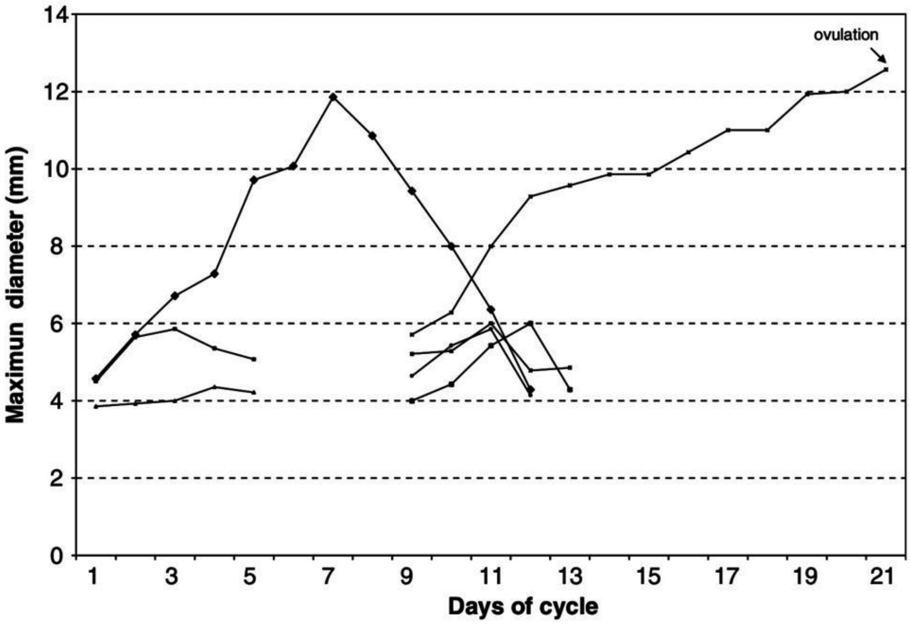

Figure 3a. Model of follicular dynamics in postpubertal interval – 2-wave cycle (adapted Romano et al.[29])

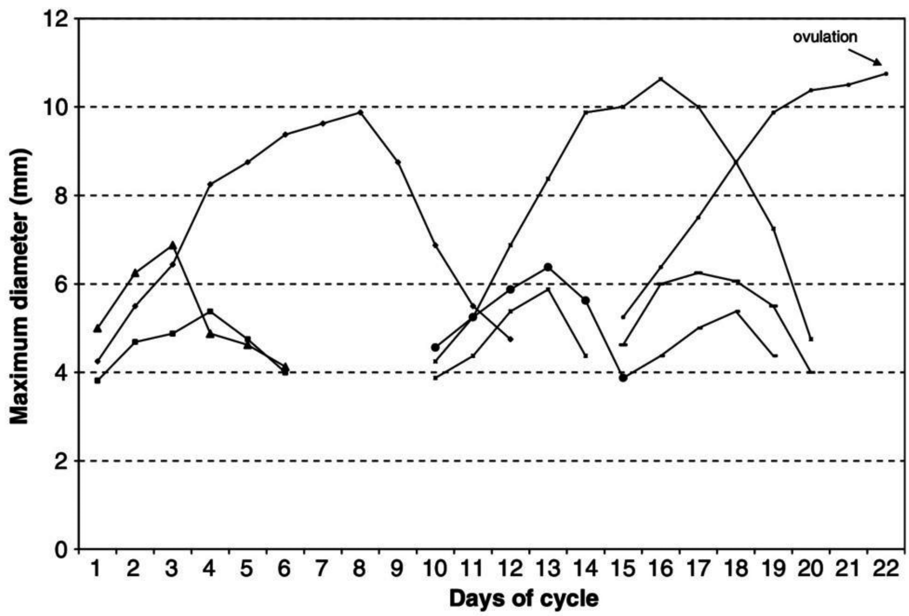

Figure 3b. Model of follicular dynamics in postpubertal interval - 3 wave cycle (adapted Romano et al.[29])

Table 2. Preovulatory follicle size during various follicular waves in various breeds of cows

Breed	Size of preovulatory follicle (mm)
Sahiwal cows[77]	Second wave: 14.71 ± 0.72
Jersey crossbred (*Bos taurus*)[82]	Second wave: 12.9 ± 0.2 Third wave: 12.1 ± 1.1
Kenyan Boran Cows (*Bos indicus*)[86]	Second wave: 14.00 ± 0.85 Third wave: 13.52 ± 0.5
Nelore calves (*Bos indicus*)[3]	Second wave: 13.03 ± 0.17
Thai native heifers (*Bos indicus*)[35]	Second wave: 8.81 ± 0.26 Third wave: 8.14 ± 0.25
Crossbred cows[87]	Third wave: 13.33 ± 0.72
Rathi Cows (*Bos indicus*)[89]	Second wave: 14.65 ± 1.24 Third wave: 12.44 ± 1.59
The native breed of Egypt[33]	Second wave: 10.9 ± 0.3 Third wave: 11.0 ± 0.9
Bos indicus cows[80]	Second wave: 10.8 ± 0.5 Third wave: 13.0 ± 0.3
Bos taurus cows[80]	Second wave: 11.1 ± 0.6 Third wave: 14.8 ± 0.6
Gir Cows (*Bos indicus*)[1]	Third wave: 12.44 ± 1.59 Fourth wave: 13.25 ± 0.96
Hereford heifers[71]	Second wave: 15.0 ± 0.5 Third wave: 12.8 ± 0.3

patterns of follicular wave emergence and deviation have been described, the molecular, genetic, and endocrine bases of these differences remain poorly characterized. Additionally, most literature has focused on temperate breeds under controlled conditions, with limited data for tropical and subtropical environments, where heat and nutrition substantially influence folliculogenesis. Role of stress-related disruptions in follicular growth, hormonal secretion, and ovulatory efficiency in indigenous breeds is largely underexplored. Furthermore, there is a paucity of validated, noninvasive biomarkers (in blood, saliva, or milk) for real-time assessment of follicular activity. Another under-researched area is the interaction between follicular development and uterine immune function, particularly during postpartum or diseased states. To address these gaps, future research should adopt integrative 'omics' approaches (e.g. genomics, transcriptomics, proteomics) to profile ovarian follicular cells and fluids, to identify markers of oocyte competence and reproductive efficiency. Studies focused on the follicular microenvironment, including angiogenesis, oxidative stress, and local hormonal milieu, should provide deeper insights into follicular health. There is also a need for field-based studies in native and crossbred cattle under diverse management systems. Technological advancements such as artificial intelligence, machine learning, and wearable biosensors offer exciting prospects for developing predictive tools for ovulation timing and follicular wave dynamics. Additionally, optimizing follicular response in assisted reproductive technologies, including superovulation and ovum pick-up, remains an important area for improving genetic gain and fertility outcomes in cattle worldwide.

Understanding ovarian follicular dynamics and its mechanisms is crucial for optimizing reproductive health and efficiency in cattle. Better knowledge of how ovarian follicles develop and mature should enhance breeding programs, including better control of follicle growth and predicting/controlling ovulation, improving fertility and herd productivity.

Conflict of interest

Authors declare no conflict of interest.

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