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Follicular dynamics in cattle

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Abstract

Folliculogenesis is a complex and highly regulated process that governs the growth and maturation of ovarian follicles, ensuring successful ovulation and steroid hormone production. This review summarizes the stages of follicular development, including recruitment, selection, dominance, ovulation, and atresia, with emphasis on follicular wave dynamics in cattle. Follicular growth is regulated by the coordinated actions of follicle-stimulating hormone (FSH), luteinizing hormone (LH), granulosa and thecal cells, and local growth factors such as insulin-like growth factors (IGFs). The two-cell/two-gonadotropin model explains estradiol synthesis and the hormonal mechanisms underlying follicular selection and dominance. Changes in gene expression, steroid hormone concentrations, prostaglandin activity, and gonadotropin receptor regulation play crucial roles in ovulation and corpus luteum formation. Understanding these physiological and molecular mechanisms provides valuable insights for improving reproductive efficiency and developing advanced reproductive technologies in livestock.

Keywords: Folliculogenesis, Ovarian follicles, Follicular waves, Follicle-stimulating hormone (FSH), Luteinizing hormone (LH), Steroidogenesis, Ovulation, Follicular atresia

1. Introduction

Follicles are the functional units of the ovary, categorized into non-growing (primordial) and growing (primary, secondary, and tertiary) populations. Folliculogenesis represents the developmental journey from a primordial follicle to a mature, preovulatory Graafian follicle, serving two core functions

- **Gametogenesis:** The cyclic production of fertilizable ova.
- **Steroidogenesis:** The synthesis of balanced steroid hormones that regulate the genital tract, support embryo migration, and enable successful uterine implantation.

In mammals, the primordial follicle pool is established around birth. For instance, a bovine ovary contains roughly 150,000 primordial follicles at birth, dropping to about 3,000 by 15 to 20 years of age. The Fas antigen and Fas ligand system regulates this pool by mediating apoptosis.

Oocytes within primordial follicles remain in a quiescent meiotic arrest at the diplotene or dictyate stage, sustained by the oocyte maturation inhibitory (OMI) factor. While primordial follicles continuously enter the growth phase throughout reproductive life, over 99% of growing follicles ultimately undergo atresia (programmed cell death).

Stages of Follicular Growth

Follicular development is defined by three primary stages

- **Recruitment:** A cohort of follicles begins to mature under adequate pituitary gonadotropic stimulation.
- **Selection:** Specific follicles avoid atresia, continue developing, and acquire the competence to ovulate.
- **Dominance:** A single "dominant" follicle achieves supremacy over the cohort, while the remaining recruited follicles undergo atresia.

Follicular Waves in Cattle

In cattle, follicular growth occurs in waves (typically two, three, or four waves per estrus cycle). Each wave begins with a transient rise in Follicle-Stimulating Hormone (FSH) about 2.5 days prior, prompting a cohort of 1 to 6 follicles (4 to 5 mm in diameter) to emerge.

Over the next 36 to 49 hours, one follicle (growing to 8 to 9 mm) is selected for continued growth, while the others regress via atresia. The selected dominant follicle maintains its peak size for 3 to 6 days. Its ultimate fate depends on the estrus cycle phase:

- If luteal regression occurs during its growth phase, it ovulates.
- If it reaches maximum size during the luteal phase, or if it is a subordinate follicle, it undergoes atresia.

Hormonal Regulation and the Two-Cell/Two-Gonadotropin Model

Follicular growth and steroidogenesis rely on the coordinated actions of FSH and Luteinizing Hormone (LH) acting through specific receptors on granulosa and thecal cells.

The Two-Cell/Two-Gonadotropin Model for Estradiol Synthesis

- Thecal Cells: Express LH receptors (LHr) and cytochrome P450 side-chain cleavage ($P450_{scc}$) enzymes to convert cholesterol into progestins (pregnenolone or progesterone). LH binding stimulates the $P450_{c17}$ enzyme, converting progestins into androstenedione.
- Granulosa Cells: Express FSH receptors ($FSHr$) and do not produce androgens directly. Instead, androgens from theca cells diffuse into granulosa cells, where the aromatase ($P450_{arom}$) enzyme converts them into estradiol-17 β .

Recruitment, Selection, and Dominance Dynamics

1. Recruitment

- Triggered by a transient surge in circulating FSH.
- Marked by the simultaneous expression of $P450_{scc}$ and $P450_{arom}$ mRNA in the granulosa cells of recruited follicles (4 to 6 mm).

2. Selection

- Occurs 36 to 48 hours after wave initiation as FSH levels decline.
- Characterized by the expression of LHr and 3β -

hydroxysteroid dehydrogenase (3β -HSD) mRNA exclusively in healthy, dominant-bound follicles.

- Growing follicles secrete inhibin, which acts as a primary negative feedback regulator to suppress FSH secretion, depriving smaller, less-developed subordinate follicles of the FSH levels they require to survive.

3. Dominance

- The dominant follicle produces high levels of estradiol and inhibin, alongside low levels of binding proteins, reinforcing its survival while suppressing cohorts.
- It exhibits peak expression of Steroidogenic Acute Regulatory (StAR) protein mRNA in theca cells (regulating acute cholesterol transport into mitochondria) and high levels of local growth factors.

Role of Insulin-Like Growth Factors (IGFs) and IGF Binding Proteins (IGFBPs)

Intrafollicular growth factors interact closely with gonadotropins to govern follicle fate:

- IGF-I (produced in granulosa cells) and IGF-II (produced in thecal cells) act synergistically with FSH and LH to promote cellular proliferation and steroidogenesis.
- IGFBPs (particularly IGFBP-2) bind to IGFs, neutralizing their availability.
- Selected dominant follicles display high levels of IGF-I/IGF-II mRNA and nearly undetectable levels of inhibitory IGFBP-2. Conversely, subordinate follicles exhibit high IGFBP-2 expression, which sequesters IGFs, dampens their responsiveness to gonadotropins, and triggers atresia.

The Preovulatory Follicle

When a dominant follicle escapes atresia and is destined for ovulation, it transforms into a preovulatory (Graafian) structure:

- Morphology: Accumulation of follicular fluid (*liquor folliculi*) causes a blister-like protrusion on the ovarian surface, thinning the granulosa layer. The cumulus oophorus detaches, leaving the oocyte free within the fluid.
- Gene Expression Shift: Following the preovulatory LH surge, mRNA expression for $P450_{c17}$ (theca) and $P450_{arom}$ (granulosa) drops sharply. This causes a localized decline in androstenedione and estradiol-17 β , alongside a dramatic rise in progesterone concentration

Expression of mRNA for steroidogenesis enzymes & gonadotropin receptors (Mean $\pm$ SEM%) in bovine follicle after initiation of first follicular wave (Xu et al., 1995)

Day of wave	P450 _{acc}		P450 _{arom} Thecal	P450 _{arom} granulosa	LHr		FSHr granulosa
	Theca	Granulosa			Theca		
0	35 $\pm$ 8 ^{cd}	24 $\pm$ 7 ^{de}	8 $\pm$ 3 ^d	4 $\pm$ 1 ^e	15 $\pm$ 7 ^c	0 ^c	15 $\pm$ 5
2	29 $\pm$ 4 ^d	34 $\pm$ 10 ^d	20 $\pm$ 5 ^d	24 $\pm$ 5 ^d	13 $\pm$ 6 ^c	0 ^c	25 $\pm$ 4
4	53 $\pm$ 14 ^c	63 $\pm$ 13 ^c	59 $\pm$ 13 ^c	53 $\pm$ 13 ^c	59 $\pm$ 10 ^d	26 $\pm$ 10 ^d	31 $\pm$ 11
6	7 $\pm$ 3 ^c	12 $\pm$ 5 ^{de}	7 $\pm$ 2 ^d	51 $\pm$ 9 ^c	21 $\pm$ 10 ^c	24 $\pm$ 8 ^d	14 $\pm$ 4
8	5 $\pm$ 1 ^e	2 $\pm$ 1 ^e	13 $\pm$ 6 ^d	8 $\pm$ 5 ^{de}	28 $\pm$ 10 ^c	9 $\pm$ 7 ^c	12 $\pm$ 6
10	6 $\pm$ 2 ^e	0 ^e	0 ^d	0 ^e	10 $\pm$ 7 ^c	0 ^c	6 $\pm$ 3

Follicular fluid steroid hormone concentrations on different days of the first follicular wave

Day of wave	No. Of follicles	Progesterone (ng/ml)	Estradiol17 β (ng/ml)	Androstenedione (ng/ml)
0	8	18 $\pm$ 1	13 $\pm$ 3	9 $\pm$ 3
2	9	31 $\pm$ 7	39 $\pm$ 14	30 $\pm$ 8
4	3	44 $\pm$ 14	189 $\pm$ 65	39 $\pm$ 22
6	5	61 $\pm$ 24	51 $\pm$ 18	12 $\pm$ 5
8	3	51 $\pm$ 28	24 $\pm$ 15	39 $\pm$ 31
10	3	52 $\pm$ 19	9 $\pm$ 5	21 $\pm$ 10

Prostaglandins (PG) and Their Roles

- **Function:** Prostaglandins are essential for follicular rupture, operating directly at the tunica albuginea and follicular epithelium.
- **Types & Mechanisms:**
 - a. **Prostaglandin $F_{2\alpha}(PGF_{2\alpha})$:** Triggers the breakdown of epithelial cell lysosomes at the apex of the follicle.
 - b. **Prostaglandin $E_2(PGE_2)$:** Stimulates the secretion of plasminogen activator.
- **Role of Plasmin:** Plasmin facilitates tissue cell migration and the blending of theca and granulosa cells during the development of the corpus luteum.

Luteinizing Hormone (LH) and Follicular Dynamics

- **Ovulation Mechanism:** A shift toward progesterone production decreases the blood supply at the follicular apex, which triggers the release of the proteolytic enzyme collagenase. This enzyme breaks down the connective tissue in the follicular wall, weakening the stigma and ultimately causing ovulation.
- **Loss of Dominance:** Dominance is lost following a drop in estradiol secretion from the dominant follicle of the initial follicular wave.
- **New Wave Initiation:** A reduction in follicular estradiol and inhibin-A precedes the emergence of a new follicular growth wave.

Follicular Atresia

- **Triggers:** Atresia is driven by rising gonadotropin levels, inadequate hormonal support, shifts in follicular cell hormone receptors, and inhibitory substances released by the dominant follicle.
- **Dominant Follicle Atresia:** Typically initiated between days 4 and 6 of the wave. There is a sharp drop in mRNA for FSH receptors (in granulosa cells), LH receptors (in theca cells), steroidogenic enzymes ($P450scc$, $P450c17$, $P450arom$), and a corresponding severe decrease in estradiol-17 β .
- **Unselected Follicle Atresia:** Follows a similar pattern to the dominant follicle, marked by decreased gonadotropin receptor mRNA expression, along with reductions in steroidogenic enzymes and StAR regulation (Bao et al., 1997bc).
- **Enzyme Impact:** mRNA expression for $P450scc$ and $P450arom$ in granulosa cells is heavily impacted early on. In bovine follicles, early atresia features diminished $P450arom$ activity in granulosa cells, which is consistently preceded by a decline in the steroidogenic capacity of the theca cells (Mc Natty et al., 1984).

Conclusion

- **Wave-Like Growth:** Ovarian follicles develop in waves. Periodic surges in circulating FSH coincide with the appearance of new follicular waves.
- **Dominance Selection:** Selecting a dominant follicle requires a drop in FSH levels paired with the acquisition of LH responsiveness.
- **Anovulatory Cycles:** Periodic, non-ovulatory follicular waves continue to emerge until an LH surge occurs.
- **Progesterone Effects:** Progesterone inhibits both LH secretion and the growth of the dominant follicle. Follicular dominance is most pronounced during the first and final follicular waves of the estrus cycle across all

species.

Conflict of Interest

Not available

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Not available

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