Pattern of Antral Follicular Development in Goats - A Review

by Abdul Malik

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Abstract

Aspects of ovarian follicular development in goats differ from those of cattle and sheep. This review aims to highlight these characteristics. As in cows and ewes, follicular development occurs in a wave-like pattern. As many as 6 and 7 follicular waves had been reported in does; higher than in mare, cow and ewe. Furthermore, more than one preovulatory dominant follicle could be found on the ovary (co-dominance). The number of follicular waves, the number of follicles, plasma insulin-like growth factor 1 (IGF-1) and corpora lutea diameter, were not significantly different in prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$), progesterone oestrus synchronised and in naturally cycling does. The morphology and progesterone secreting properties of $PGF_{2\alpha}$ oestrus synchronised and naturally cycling goats were different. The reason for higher number of follicular waves and the mechanism of follicular co-dominance in does is yet to be elucidated fully.

Key words: Goat, ultrasonography, ovary, follicular waves, $PGF_{2\alpha}$, IGF-1

Introduction

Much of what is currently known on follicular dynamics in domestic animals was made possible by the application of ultrasonography to study ovarian follicular development (Evans, 2003; Ginther, 2014). Previous methods used to study ovarian follicular development consisted of abattoir specimens (Ariyaratna and Gunawardana, 1997), serial slaughter (Bukar, *et al*., 2006) and laparoscopy (Simoes *et al*., 2005). Different population of follicles could be found on the ovary at any given time and this determines the size, shape and functionality of the ovary (Ginther and Kot, 1994; Simoes *et al*., 2006).

Compared with monovular species such as cows, female goats are prolific breeders with frequent multiple births. For this and other reasons, goats have very important socio-economic significance particularly in developing countries (Lebbie, 2004; Devendra and Solaiman, 2010). Key to understanding and exploiting this beneficial characteristic of goat reproduction is a clear understanding of the dynamics of follicular development in this important species. However, compared with goats, more research has been conducted on ovarian follicular development in cattle and sheep.

1. Use of ultrasound in study of ovarian follicular development

Ultrasonography is based on the echo principle whereby sound waves are produced from materials with piezo-electric properties and propagated through tissues with different acoustic impedance to give echotextural images that could be interpreted (Ginther, 2014). Ultrasound techniques were used to study ovarian follicular development in cows for several years before the first ultrasonographic study of goat ovarian follicular development was described in 1994 (Ginther and Kot, 1994). As in cattle and sheep, the introduction of ultrasound techniques in goats has resulted in significantly better understanding of development, morphology and function of the ovarian follicles (Ginther and Kot, 1994; Gonzalez-Bulnes *et al*., 2004; Rosales-Torres *et al*., 2012). Subsequently, more studies elucidated some factors influencing the characteristics of antral follicular development in goats.

2. Prenatal, postnatal development, anatomy and physiology of the ovaries

2.1 The ovaries

The ovaries are the primary reproductive organs of the female because they produce the female gamete (ovum) and the sex hormones (oestrogen and progesterone) (Bearden *et al*., 2004). The ovary consists of the inner 'medulla' composed of blood vessels and connective tissue, and the outer 'cortex' composed of developing follicles and steroidogenic cells (Pineda and Dooley, 2003; Bearden *et al*., 2004).

2.2 Prenatal development

Embryonic development (Ariyaratna and Gunawardana, 1997; Picton, 2001), as well as the postnatal histologic development of the ovaries and folliculogenesis (Smitz and Cortvrindt, 2002; Bearden *et al*., 2004; Bukar *et al*., 2006), in goats has been described. Of recent, ultrasonography has become the method of choice for studying the growth and development of the ovaries as illustrated by the large number of published information that relied on ultrasonographic techniques for their investigations (Adams *et al*., 2008; Rosales-Torres *et al*., 2012). The use of serial ultrasonography has enabled us to monitor growth and regression of individual ovarian follicles, repeatedly in the same animal (Bukar *et al*., 2012a; Bukar *et al*., 2012b). Thus, ultrasonography has helped to elucidate the process of follicle development in domestic animals including goats (Ginther *et al*., 2000; Fortune *et al*., 2001; Adams *et al*., 2008).

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Follicular development begins during embryogenesis and continues through the neonatal and postnatal periods (Flint, 2004; Bukar *et al*., 2006). During foetal life, follicular development is characterised with predominance of primordial follicles (Ariyaratna and Gunawardana, 1997; Picton, 2001). About 3 weeks after fertilization, primordial germ cells appear in the endoderm of the embryonic yolk sac from where they migrate to the gonadal ridge and undergo mitotic divisions (Smitz and Cortvrindt, 2002). The large pool of primordial follicles formed during foetal stage of development is non-renewable during the lifetime of the animal (Picton, 2001; Evans, 2003). The ovary of a newborn calf may contain up to 150,000 primordial follicles at birth (Erickson, 1966). Primordial follicles consist of an oocyte surrounded by a single layer of flattened follicular (granulosa) cells. The granulosa cells are necessary for the growth and maintenance of the oocyte (Picton *et al*., 1990).

2.3 Postnatal development

In the postnatal period, some of these primordial follicles grow to become primary, secondary and tertiary (antral) follicles. Primary follicles are formed from primordial follicles when primary oocytes are enveloped by a single layer of cuboidal granulosa cells. The zona pellucida separating the oocyte from the granulosa also begins to form (Picton *et al*., 1990). Secondary follicles are formed from the primary follicles with the development of two or more additional layers of granulosa cells (Fortune, 2003). Transition of the secondary follicles to antral (tertiary or vesicular) follicles occurs with the development of follicular fluid in the follicles which is clearly discernible macroscopically (Fortune, 2003; Pineda and Dooley, 2003).

Upon attainment of puberty, one or more follicles from the pool of antral follicles in the ovary, become dominant and ovulate while the remaining follicles regress at various stages of development under the influence of gonadotrophins (Picton *et al*., 1990; Campbell *et al*., 1998). Antral follicles in cattle were shown to grow in two distinct phases: the 'slow' and 'fast' growth phases (Mihm and Bleach, 2003).. The slow growth phase occurs from antrum formation in the secondary follicle to about 3 mm diameter; whereas, the second 'fast' phase is the gonadotrophin-dependent phase from 3 mm to ovulation (Mihm and Bleach, 2003).

According to Ariyaratna and Gunawardana (1997), adult goat ovaries obtained from the abattoir contained an average of 35,092 and 1,067 primordial follicles and antral follicles, respectively. The primordial follicles, surrounded by a single layer of epithelial cells were located at the periphery of the cortex near the *Tunica albuginea*. The more centrally placed secondary follicle consisted of two or more layers of cuboidal epithelial cells surrounding the oocyte, while the oocyte of the antral follicles was

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surrounded by about six layers of epithelial cells with distinct thecal layers and zona pellucida. According to Bukar *et al.* (2006) small antral follicles were present on the ovaries of goats at birth. The secondary and antral follicles were more centrally placed towards the medulla.

3. Follicular development and wave pattern

Current information on ovarian follicular development in cattle, sheep and goats shows that follicles grow in a distinct wave-like pattern (Adams *et al*., 2008). A follicle wave is described as the synchronous growth of a cohort of follicles, with one (or species-specific number) follicle which continues growing while the other follicles regress at variable intervals (Evans, 2003). In goats, a cohort of antral follicles that are 2-3 mm in diameter, emerge every few days (Ginther and Kot, 1994).

Previous studies have shown that 2- to 6-follicular waves were observed in estrus synchronized and naturally cycling does (Rubianes and Menchaca, 2003). The 3-wave pattern was the most frequently observed pattern (Ginther and Kot, 1994; Simoes *et al.,* 2006; Vazquez *at al.,* 2010). Bukar *et al* (2012a) similarly reported that 58% of Boer goats raised in humid tropical environment had 3 waves of follicular development, while 31.6% displayed a 4-wave pattern. However, Filho *et al* (2007) found no significant difference in the pattern of antral follicular development in six multiparous Anglo-Nubian goats kept in an acclimatized chamber simulating the hot and humid tropical environment.

On the one hand, Simoes et al (2006) stated that parity, type of oestrous cycle (induced or natural), interovulatory interval, number of CL and time of onset of first follicular did not significantly affect the number of follicular waves per oestrous cycle in goats. Furthermore, a previous study in ewes indicated that there were no apparent endocrine or follicular differences that could explain the varying numbers of follicular waves between cyclic ewes with three- or four-follicular waves (Seekallu, *et al.* 2010).

On the other hand, Baby and Bartlewski (2011) found that higher progesterone concentrations early in the luteal phase shortened the time to the first post-ovulatory FSH peak in ewes, indicating that progesterone might be a key endocrine regulator of the number of follicular waves in sheep. These endocrine mechanisms and possible role in the control of follicular wave pattern in does is yet to be clarified

Studies in cattle showed a relationship between follicular development and serum FSH concentrations, with a transient increase in circulating FSH as a prerequisite for the emergence of a wave of follicle development (Adams *et al*., 1992b; Ginther *et al*., 1996; Driancourt *et al*., 2001; Burns *et al.,* 2005). This alignment of endocrine FSH concentration with the pattern of follicular development in cows led to the suggestion of cause-effect relationship between rise in FSH concentration and development of a cohort of

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follicles (Adams *et al*., 1992b). Subsequent researchers confirmed that follicular wave emergence was preceded by a transient peak in serum FSH concentrations in sheep (Bartlewski *et al*., 2000; Evans *et al*., 2000), cattle (Adams *et al*., 2008) and goats (Schwarz and Wierzchos, 2000).

4. Follicular deviation and ovulation

Follicular deviation refers to the different growth rates of antral follicles in the ovary (Ginther *et al*., 2003). The largest follicle becomes the dominant follicle and these dominant follicles become increasingly more responsive to FSH and grow faster than the subordinate follicles (Beg *et al*., 2002). The interesting question of which and how, among the monovular farm species, one of the antral follicles in a particular wave gets to become the dominant follicle and not the others was reviewed by Ginther *et al.* (2003). An important characteristic of the dominant follicle is its increased capacity for oestradiol production through better blood supply and ability to respond to the rise in FSH release (Fortune *et al*., 2001). Increased intrafollicular concentration of oestradiol and IGF, but not inhibin/activin system, accounts for the increased responsiveness of the future dominant follicle (Beg *et al*., 2002). The increased production of oestradiol by the dominant follicle induces oestrus behavior. It also acts as a positive feedback to increase GnRH secretion which induces the preovulatory LH surge, ovulation and luteinization of follicular cells (Fatet *et al*., 2011).

5. Nutrition and follicular development

The influence of nutrition on reproduction is already established as extensively reviewed by Dupont *et al.* (2014). However, with particular respect to follicular development, Meza-Herrera *et al.* (2013) found that nutritional supplementation with betacarotene increased the total number of ultrasonographically detectable antral follicles and corpora lutea LH secretion in adult goats during the breeding season. In addition, the ovulation rate was enhanced through LHRH-independent pathways or direct effects of betacarotene on ovarian function.

An increase in ovulation rate in goats was related to a reduced incidence of follicular atresia and an extended period of ovulatory follicle recruitment (Cueto *et al*., 2006). However, since co-dominance is a recognised feature of follicular development in goats, it yet unclear, the role(s) and relationships between oestradiol, IGF-1, and the inhibin/activin system in co-dominance and multiple ovulations, respectively.

6. Steroidogenesis

Steroidogenesis is defined as the enzyme-induced biosynthesis of steroids from cholesterol in the ovaries. Cholesterol is converted to pregnenolone in the mitochondria, regulated by the cytochrome P450scc

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enzyme, CYP11A1 (Pikuleva, 2006). Regulation of steroidogenesis and secretion of the reproductive hormones in the ovary is influenced by the gonadotrophins, FSH and LH (Christenson and Devoto, 2003).

Follicular growth and steroidogenesis are dependent on the coordinated actions of FSH and LH with their receptors on the granulosal and thecal cells of ovarian follicles (Bao and Garverick, 1998). The widely accepted model for steroidogenesis is the two-cell-two-gonadotropin model which states that granulosa and theca interna cells as well as both gonadotrophins are needed for proper ovarian steroidogenesis (Allrich, 1994). This model compartmentalizes the process of steroidogenesis in the ovary, the first compartment consists of theca cells, which are stimulated by LH to produce androgens. The second compartment consists of granulosa cells, which are stimulated by FSH to convert androgens to oestrogen (Drummond, 2006). Progesterone and oestrogen are the dominant hormones during the luteal and follicular phases of the oestrous cycle respectively.

6.1 Corpus luteum

Corpus luteum (CL) is a transient endocrine gland which develops from follicular cells that have ovulated (Diaz *et al*., 2002). It is a complex tissue consisting of small and large luteal steroidogenic cells, and non-steroidogenic cells, such as fibroblasts, endothelial and immune cells (Sangha *et al*., 2002). According to Pineda and Dooley (2003), Progesterone is the principal hormone secreted by the CL although oestrogen, oxytocin, relaxin, inhibin and vasopressin are also secreted in minute quantities (Sangha *et al*., 2002; Webb *et al*., 2002). Declining concentration of progesterone, in synergistic action with rising oestrogen levels in blood, results in behavioural oestrus in most domestic animal species (Pineda and Dooley, 2003).

Some factors affecting progesterone concentration, such as restricted feeding (Al-Azraqi, 2007) and social ranking (Alvarez *et al*., 2010), had been described. Social ranking refers to the hierarchical relationship between members of a herd and in a group of animals, dominant females tend to have higher progesterone concentration and conception rate than the non-dominant or lower-ranking females although the time to ovulation were similar (Alvarez *et al*., 2010). Similarly, restricted feeding, inhibited oestrus behaviour and decreased the plasma progesterone concentration in Ardi goat breed (Al-Azraqi, 2007). Furthermore, a previous study in farmed red deer hinds showed that postovulatory luteal progesterone secretion was higher in dominant females and in hinds fed with improved nutrition than in the non dominant females (Goodwin *et al*., 1998). At the end of the luteal phase and with the absence of pregnancy, oxytocin released from the neurohypophysis interacts with its receptor in the endometrium to release $PGF_{2\alpha}$ for luteolysis (Bazer *et al*., 1991).

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7. Follicular development during the natural oestrous cycle

Fatet (2011) defined the oestrous cycle to consist of all morphological and physiological changes in the ovaries and genital tract leading to oestrus expression (phase of receptivity towards males) and ovulation followed by the preparation of the genital tract for copulation, fertilization and embryo implantation. The oestrous cycle is controlled by the interactions of the organs in the hypothalamic-pituitary axis (HPA) with the cyclic ovarian structures and uterus (Adams *et al*., 2008). It is known that the oestrous cycle is divided into follicular and luteal phases. In the follicular phase, follicular stimulating hormone (FSH), released by the anterior pituitary gland stimulates synchronous growth of a cohort of follicles (Bartlewski *et al*., 2000). In sheep and goats, the recruitment of this cohort of gonadotrophin-dependent antral follicles that are 2-3 mm in diameter is followed by selection of only 2-3 follicles to enter the dominance phase that reach the preovulatory size (6-9 mm) under the influence of leutinizing hormone (LH), whereas, the subordinate follicles undergo atresia (Ginther and Kot, 1994; Evans, 2003). Oestradiol, secreted by the large follicles, induces oestrus behavior and acts as a positive feedback on the gonadotrophin axis to increase gonadotrophin releasing hormone (GnRH) secretion, resulting in the preovulatory LH surge that induces ovulation 20-26 hours later (Evans, 2003; Fatet *et al*., 2011). However, the rise of progesterone concentration from the developing corpus luteum after ovulation suppresses pulsatile LH secretion and ovulation of the dominant follicle present on the ovary (Suganuma *et al*., 2007).

7.1 Effects of $PGF_{2\alpha}$ and progesterone on follicular development

The effects of oestrus synchronisation with $PGF_{2\alpha}$ and progesterone on pre-ovulatory and ovulatory follicular development in goats have been described earlier by several researchers (Fernandez-Moro *et al*., 2008; Vazquez *et al*., 2010). Similarly, the effects of oestrus synchronisation with $PGF_{2\alpha}$ as well as progesterone methods on follicle development during post-ovulatory period in goats was described (Bukar *et al*., 2012a; Bukar *et al*., 2012b; Bukar *et al*., 2012c).

Vazquez *et al.* (2010) reported that compared with natural oestrous cycle, oestrus synchronised with $PGF_{2\alpha}$ in goats with regular length of oestrous cycles had higher occurrence of short-length oestrous cycles (≤ 13 days) and larger CL diameter than those of untreated goats. However, progesterone is secreted in lower amount due to decreased functionality of the CL. In addition, the number of small and large follicles were significantly higher in the $PGF_{2\alpha}$ synchronised compared with natural oestrous cycle, probably due to the lower secretion of progesterone and the consequent reduced suppression of follicular growth during the mid-luteal phase

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Oestrus synchronisation in sheep using progestogen sponge inserts altered the number of follicular waves and modified the size of the largest follicles depending on whether the progestogen treatment was at early, middle or late luteal phase (Leyva *et al*., 1998). In heifers, exogenous progesterone decreased the number of hypothalamic oestradiol receptors, resulting in increased follicular steroidogenesis as a result of increase in gonadotrophins (FSH and LH) secretions after treatment with the exogenous progesterone ceased (Evans *et al*., 1994; Leyva *et al*., 1998). Similarly, in cows, high dose of progesterone suppressed the dominant follicle during its growing phase in a dose dependent manner (Adams *et al*., 1992a). Maintenance of progestogens at high concentration and low LH concentrations also increased follicular turnover (Leyva *et al*., 1998). A similar mechanism exists in goats, low concentrations of progesterone particularly towards the end of progestogen treatment during oestrus synchronisation in goats led to inadequate suppression of LH resulting in abnormal follicular development such as large persistent follicles (Savio *et al*., 1993; Menchaca and Rubianes, 2004). These large persistent follicles inhibit the growth of smaller subordinate follicles (Yu *et al*., 2005).

8. Follicular development in goats

Compared to cattle and sheep, less information is available on the pattern of follicular development in goats (Evans, 2003). However, many more studies were undertaken by several researchers within the last decade and this has elucidated further, the characteristics of antral follicular dynamics in goats. Thus, the highlights of current information on the pattern of antral follicular development during the natural and synchronised oestrous cycles in goats are listed below:

8.1 Natural oestrous cycle

1. Follicular development occurs in a wave pattern, similar to other domestic animals (Ginther and Kot, 1994; Rubianes and Menchaca, 2003).
2. The number of follicular waves in goats is different from those reported in cattle and sheep (Evans, 2003; Rubianes and Menchaca, 2003).
3. There are between 2 and 6 waves of follicle development during the goat's oestrous cycle with three or four waves as most prevalent (Menchaca and Rubianes, 2002; Filho *et al*., 2007).
4. Emergence of follicular waves occurs every 5 to 7 days (Simoes *et al*., 2006).
5. The number of follicular waves occurring during the interovulatory interval is influenced by the duration of the first follicular wave (Ginther and Kot, 1994; Simoes *et al*., 2006).
6. The emergence of each follicular wave is preceded by increased FSH secretion (Schwarz and Wierzchos, 2000).

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7. Follicular dominance occur particularly during wave 1 and the last or ovulatory wave (Ginther and Kot, 1994; Simoes *et al*., 2006).
8. More than one dominant follicle may be present on the ovaries (co-dominance) (Ginther and Kot, 1994; Gonzalez-Bulnes *et al*., 2004).
9. The echo-textural characteristics were different between the preovulatory follicles and other large non-ovulatory follicles (Gonzalez-Bulnes *et al*., 2004).
10. Following luteolysis, the ovulatory follicle might be the dominant follicle of an existing wave in either its growing or static phase (Gonzalez-Bulnes *et al*., 2005).
11. The preovulatory follicles did not suppress the emergence of new follicles but inhibit the growth of small antral follicles (Cueto *et al*., 2006).
12. There are usually five to ten follicles that are greater than 3 mm in diameter present on goat ovaries throughout the oestrous cycle and ovulation occurs when they are 6 to 9 mm in diameter (Gonzalez-Bulnes *et al*., 1999; Lehloenya *et al*., 2008).

8.2 Synchronised oestrous cycle

1. As with other domestic ruminant species, oestrus synchronisation in goats could be achieved using either progesterone or $PGF_{2\alpha}$ with and without gonadotrophins (Whitley and Jackson, 2004).
2. The dynamics of growth and functionality of preovulatory follicles was influenced by the type of oestrus synchronisation treatment either with intravaginal progesterone or with administration of two doses of $PGF_{2\alpha}$. The number of follicles was higher and the diameter of the follicles was larger in the progesterone compared with the $PGF_{2\alpha}$ synchronised goat (Fernandez-Moro *et al*., 2008).
3. Oestrus synchronisation with $PGF_{2\alpha}$ resulted in a larger corpus luteum compared with naturally cycling goats but the larger corpus luteum secreted less progesterone than the naturally cycling goats (Vazquez *et al*., 2010).
4. The day of onset of the first and second waves for oestrous cycles with three, four or five follicular waves were not significantly different in $PGF_{2\alpha}$ synchronised Serrana goats during the breeding season. However, a delay occurs in the day of onset of the third and fourth waves occurred in goats with higher number of follicular waves. The day of onset of the ovulatory wave was influenced by luteolysis and decreased plasma progesterone concentration (Menchaca and Rubianes, 2002; Simoes *et al*., 2006).

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In conclusion, the mechanisms underlying the peculiarities observed in goats such as the higher number of follicular waves and co-dominance need to be elucidated so that advances made in methods of control of reproduction in cattle and sheep can also be utilised in goats.

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