



Review

The theory of follicle selection in cattle

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ABSTRACT

Selection of the dominant follicle (DF) during a follicular wave is manifested by diameter deviation or continued growth rate of the largest follicle (F1) and decreased growth rate of the next largest follicle (F2) when F1 reaches about 8.5 mm in cattle. The process of deviation in the future DF begins about 12 h before diameter deviation and involves an F1 increase in granulosa LH receptors and estradiol and maintenance of intrafollicular free insulin-like growth factor 1 (IGF1). Thereby, only F1 is developmentally prepared to use the declining FSH in the wave-stimulating FSH surge and to respond to a transient increase in LH to become the DF. A follicle that emerges first may maintain an F1 ranking and become the DF by being first to reach a critical developmental stage. However, an early size advantage is not a requisite component of the deviation process as indicated by (1) F1 and F2 may switch diameter rankings during a common growth phase that precedes diameter deviation owing to intraovarian factors that affect growth of individual follicles; (2) any follicle that reaches 5 mm regardless of diameter ranking may become a DF unless it is selected against during deviation; (3) a subordinate follicle may become dominant if the DF is ablated; (4) when F1 is ablated at 8.5 mm, the next largest follicle that is greater than 7.0 mm or the first follicle to subsequently reach 7.0 mm becomes the DF; (5) after ablation of F1 at 8.5 mm, IGF1 and estradiol increase in the intrafollicular fluid of F2 beginning at 6 h, and F2 grows to 8.5 mm in 12 h to become the DF. These considerations indicate that selection of a DF or partitioning into a DF and subordinate follicles is not initiated before the end of the common growth phase. That is, the deviation process represents the entire follicle selection mechanism.

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1. Introduction

The mystery of follicle selection or ovulation from a single follicle in monovular species (eg, cattle, horses, and humans) has been with us ever since it was known that ovulation occurs from 1 follicle, although the ovaries contain many follicles. Follicle selection has been studied most extensively in cattle owing to economic importance, availability of slaughterhouse or excised ovaries, follicle accessibility by transrectal palpation, and more recently and most

importantly by follicle monitoring with transrectal ultrasound and follicle manipulation by transvaginal ultrasound. Ultrasound technology was a giant leap forward in that previous research in bovine follicle dynamics was limited primarily to examining the ovaries by transrectal palpation, studying slaughterhouse and excised specimens [1], and marking individual follicles with India ink [2].

It has been over 3 decades since 1984 when transrectal ultrasound was introduced as a noninvasive method for sequentially monitoring the morphologic dynamics of bovine ovarian follicles [3]. The accuracy of ultrasonic imaging for measuring and counting follicles in various diameter categories was determined by independently comparing in vivo ultrasound records with results from

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excising and slicing the ovaries 4 h later [4]. In addition to counting and measuring follicles, innovative transvaginal ultrasound technologies were developed for ablating individual follicles at specified diameters, treating by intra-follicular injection [5–7], and sampling follicular fluid [8,9] with minimal interference with follicle diameter or growth [8]. In vivo ultrasound-guided transvaginal techniques that have been used for studying the selection mechanism in cattle are illustrated (Fig. 1). The ultrasound technologies elicited high hopes for imminent resolution of the follicle selection mystery. This review will describe how “imminence” has been underway for more than 30 yr and in many laboratories involving hundreds of research reports.

Other reviews of the selection mechanism are available [10–16]. However, this review will propose the theory that the process of follicle selection is the same as the mechanism for deviation in growth rates between the 2 largest follicles during a follicular wave. The beginning of deviation is manifested by continued growth rate of the future

dominant follicle (DF) and a decrease in growth rate of the future largest subordinate follicle when the largest follicle is about 8.5 mm [10,11]. The review will concentrate on research that used the observed or expected beginning of diameter deviation as a reference point and research progress that was dependent primarily on ultrasonic imaging (Table 1).

Frequently used abbreviations are: Day 0 (capital D), day of ovulation; F1 and F2, largest and second largest follicles at specified times; DF, established dominant follicle; SF, established largest subordinate follicle; IOI, interovulatory interval. Esoteric terms that describe the dynamics of antral follicles and are essential to this review are the following: (1) Waves. The development of 2 or 3 clusters of many growing antral follicles (eg, 20) during an IOI. (2) Selection. A process wherein 1 follicle of a wave becomes the DF and the remaining follicles become regressing subordinate follicles. (3) Emergence. The diameter used for first detection of follicles in a given study and requires diameter definition in each report. (4) Tracking or mapping. Maintaining the identity of individual follicles over successive ultrasound examinations. (5) Common growth phase. A period of 2 or 3 d after emergence at 4 mm when all follicles of the wave are increasing in diameter. (6) Divergence. The concept that follicle selection is represented by a gradual increase in the difference in diameter between F1 and F2 beginning as early as emergence at 4 mm. (7) Diameter deviation. Relatively abrupt beginning of change in growth rates between the 2 largest follicles, characterized by continued growth rate of the future DF and the beginning of a decrease in growth rate of the future SF at the end of the common growth phase. (8) Observed deviation. Determination of the time of deviation by retrospective inspection of follicle diameter graphs in individuals. (9) Expected deviation. A reference point for the beginning of deviation for experimental purposes based on the examination when F1 is closest to 8.5 mm. (10) Deviation process. Preparatory mechanisms that begin in the future DF before the manifestation of diameter deviation. The term dominant follicle will be used only after dominance is established by the deviation process. That is, a follicle does not represent dominance over other follicles before the deviation process. If the identity of a follicle that later becomes the DF is known before deviation or during the common growth phase by retrospective inspection of recorded diameters, it will be termed the future DF. This is an important clarification for this review in that some investigators are using the term “dominant” for the largest follicle during the common growth phase [14] or, for example, for the largest follicle 2 d after emergence at 3 mm [15].

2. Development of follicles in waves

The concept that groups of antral follicles develop in 2 waves during the bovine estrous cycle was proposed in 1960 based on morphologic and histologic study of ovaries obtained on various days of the estrous cycle [1]. Conflicting reports for 28 yr after the 2-wave proposal were clarified in 1988 owing to development of the transrectal ultrasound technique for maintaining the identity or tracking of each individual follicle of a wave from

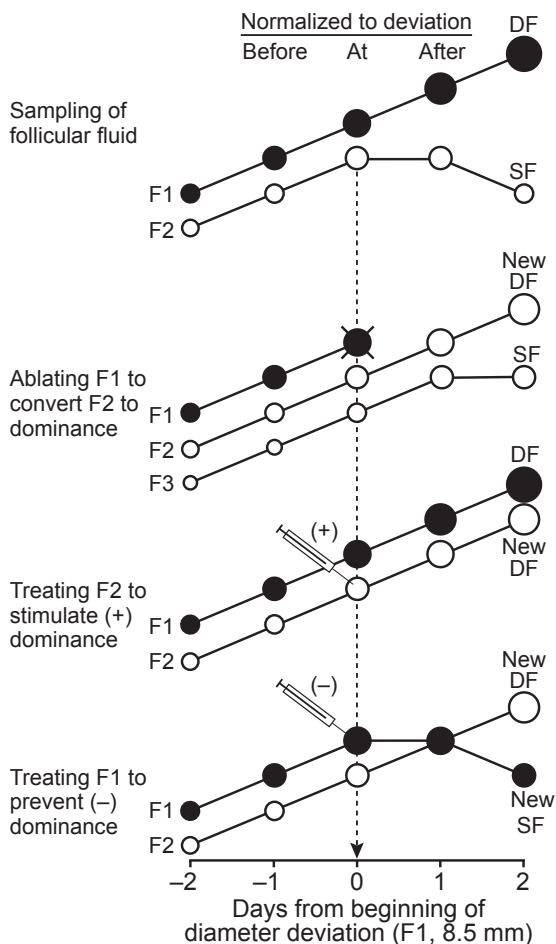


Fig. 1. Illustrations of intrafollicular in vivo transvaginal techniques with ultrasound guiding for sampling follicular fluid, ablating, treating for stimulation, and treating for inhibition of specific follicles normalized to before (day -1), at (day 0), and after (day 1) the expected beginning of diameter deviation (F1, 8.5 mm). DF, dominant follicle; SF, subordinate follicle. Adapted from [10].

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