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Theriogenology

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Persistence and recovery of regressing 3-mm ovarian follicles in heifers

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ARTICLE INFO

Article history:

Received 10 March 2015

Received in revised form 16 June 2015

Accepted 14 July 2015

Keywords:

Minor follicular wave

Follicle persistence

FSH

Rescue of regressing follicle

Transient diameter increase

ABSTRACT

The persistence and outcome of 3-mm follicles before the emergence of follicular wave 1 were studied every 6 hours in 15 heifers beginning on Day 14 (Day 0 = ovulation). A mean of 9.1 ± 1.3 persistent 3-mm follicles (P3Fs) per heifer was detected with persistence for 3.5 ± 0.1 days. The P3Fs either regressed continuously and remained in the 3-mm range (3.0–3.9 mm) or regressed but with a transient increase in diameter during regression. Some (43%) P3Fs were rescued to become growing follicles in wave 1. The number of follicles that became part of wave 1 was less ($P < 0.0001$) for follicles that originated from a P3F (4.2 ± 1.0 P3Fs) than for follicles that did not originate from a P3F (11.9 ± 1.6 follicles). The day of rescue of wave 1 follicles from a P3F (Day -1.1 ± 0.6) was earlier ($P < 0.001$) than for emergence of follicles at 3 mm that did not originate from a P3F (Day -0.5 ± 0.5). A cluster of 5.1 ± 0.6 P3Fs was identified in 10 of 15 heifers by the synchronized peaks of transient diameter increases at the 6-hour interval corresponding to Day -4.0 ± 0.3 . Concentrations of FSH oscillated at 12-hour intervals with a peak ($P < 0.05$) 6 hours before and 6 hours after the beginning of a transient diameter increase during a P3F. Concentration of FSH was greater ($P < 0.02$) in heifers with a high number (11–18) of P3Fs per heifer (0.27 ± 0.02 ng/mL) than with a low number (2–9) per heifer (0.17 ± 0.008 ng/mL). Results supported the novel hypothesis that 3-mm follicles may persist for two or more days and may be rescued to become growing follicles of wave 1.

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1. Introduction

The complexity of the bovine estrous cycle at the morphology, endocrinology, and molecular levels [1] and specifically for the molecular, cellular, and hormonal events during the dynamics of ovarian antral follicles have been reviewed [2–4]. Each of the two or three major follicular waves that occur during the interovulatory interval (IOI) or estrous cycle in cattle [5,6] is stimulated by a surge in FSH that encompasses several days [7,8]. The ascending portion of the FSH surge that stimulates wave 1 (perioovulatory wave) occurs before ovulation and reaches a peak on about the day of ovulation when the follicles of wave 1 are 4 or

5 mm. That is, most of the growing smaller follicles (≤ 3 mm) are first detected before ovulation. An initial study using number of follicles in various diameter categories indicated that the number of 2- and 3-mm follicles increased before ovulation [9] during what was later shown to be the ascending portion of the FSH surge that initiated wave 1 [7,8]. In a study in which each follicle was tracked (identity maintained) every 8 hours, 3-mm growing follicles of wave 1 were detected more than 24 hours before ovulation [10]. On the basis of daily examinations during wave 1: (1) the maximal number of 1- to 3-mm follicles occurred the day before the future dominant follicle was 4 or 5 mm (equivalent to the day of ovulation) [11] and (2) the number of 2- and 3-mm follicles reached maximum 2 days before ovulation and on the day of ovulation, respectively [12,13]. The small follicles (2 and 3 mm) during the 4 or 5 days before ovulation may be from the initial

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portion of wave 1 but also may be regressing follicles from a previous major follicular wave or growing or regressing follicles from a minor wave. A minor follicular wave occurs in about 50% of heifers, and the maximal diameter of the largest follicle of the minor wave occurs about 4 days before ovulation [14,15].

Spontaneous and experimental rescue and resurgence of a regressing large follicle (e.g., 8.0 mm) has been reported in heifers [16], and spontaneous rescue of a regressing CL has been reported in mares [17]. Spontaneous rescue of the largest subordinate follicle of wave 1 after it had regressed from about 8.0 mm to less than 6.5 mm occurred in 11% of heifers [16]. Experimental conversion of the regressing subordinate follicle of wave 1 into the dominant follicle of wave 2 occurred in 33% of heifers after ablation of other follicles when the dominant follicle of wave 1 was 11.0 mm. However, it is unknown whether smaller follicles can persist for a few days and then be rescued to become part of a follicular wave. The FSH surge that induces wave 2 contains fluctuations or subsurges at 24-hour intervals in plasma samples collected at 6-hour intervals [11]. The peak of a subsurge is followed by an increase in diameter of 1- to 3-mm follicles approximately 6 hours later.

In the present study, the origins and diameter changes of 3-mm follicles during the preovulatory period and the frequency and nature of persistence of 3-mm follicles were considered. The temporal association between follicle persist and circulating FSH was assessed at 6-hour intervals. *Hypothesis 1* was that 3-mm follicles may be persistent for 2 or more days and may be rescued to become growing follicles of wave 1. *Hypothesis 2* was that the peak of an FSH oscillation is followed within 6 hours by the beginning of increased diameter of 3-mm follicles.

2. Materials and methods

2.1. Heifers and ultrasound scanning

Holstein (*Bos taurus*) dairy heifers aged between 20 and 26 months were used in the August to October period in the northern temperate zone ($n = 16$). The heifers were kept in an open shelter with natural light and *ad libitum* access to water, trace-mineralized salt, and primarily grass hay. The heifers were not bred and had no apparent abnormalities of the reproductive tract as determined by ultrasound examinations [18]. Length of the IOI was consistently greater than 17 days. Ovulations were not induced or synchronized with exogenous hormones. The animals were handled in accordance with the United States Department of Agriculture Guide for Care and Use of Agricultural Animals in Research.

A heifer was not used if two ovulations occurred at the end of the IOI or experimental period. Heifers that were developing a third follicular wave during the IOI also were not used. Development of a third wave was assumed if the largest growing follicle on Days 14 to 16 was less than 10 mm on Day 16 [19]. This was done to reduce the complexity of follicle dynamics relating to greater growth rate of the preovulatory follicle in wave 3 and differences between two- and three-wave IOIs in the number of follicles [11,20] during the ovulatory wave.

A duplex B-mode (gray scale) and pulsed-wave color Doppler ultrasound scanner (Aloka SSD 3500; Aloka America, Wallingford, CT, USA) with a linear-array transrectal 7.5-MHz transducer was used for follicle measurement. Each ovary was scanned in a slow continuous motion. The scanner's sine-memory function was used for controlled replay of the scanned images to reduce the length of heifer exposure to transrectal examination. Follicle diameter was determined to the nearest tenth of a millimeter. In this regard, the scanner's calipers move in 0.1-mm increments. The average of height and width of the follicle at the apparent maximal area from two separate frozen gray-scale images was used. Follicle diameter refers to antral diameter in that the cursors were placed at the distinctive periphery of the antrum [18]. Ultrasound scanning of the follicles that were 3.0 mm or larger was done every 6 hours from Day 14 to Day 0 (Day 0 = day of ovulation). The four examinations on Day 14, as an example, were designated Days 14.0 (8 AM), 14.25 (2 PM), 14.5 (8 PM), and 14.75 (2 AM).

Distinguishing between a follicle that is 2 mm or more in diameter from other structures and counting the number of follicles by transrectal ultrasonic imaging with a high-quality scanner, a 5-MHz transducer, and an experienced operator have been validated [21]. Validation involved the comparison of the results of *in vivo* ultrasonic imaging with the results of excising and slicing the ovaries in 2-mm widths in 23 heifers. Maintaining identity or tracking of individual follicles from examination to examination used sketches of the relative position of each follicle to other follicles as described [18]. Follicles smaller than 3.0 mm were not considered, thereby reducing heifer exposure to the transrectal procedure and the operator's workload. Tracking follicles was a crucial aspect of the protocol and was aided by the sine-memory function. Identity and measurement of follicles were done by the same operator at the 6-hour intervals throughout the study.

2.2. Persistent 3-mm follicles

A follicle that remained in the 3-mm range (3.0–3.9 mm) for at least 8 consecutive 6-hour intervals (2 days) was defined as a persistent 3-mm follicle (P3F). However, a transient increase into the 4-mm range was permitted, but the P3F definition required that the follicle was in the 3-mm range at the beginning and end of the period of persistence. The beginning of a transient increase in the diameter of a P3F was identified by an increase of 0.2 mm or more in 6 hours. Follicles that were classified as P3Fs were subdivided according to origin. The origin was defined as unknown for follicles that were in the 3-mm range at the first examination on Day 14.0. Follicles that were first detected or first reached 3.0 mm after Day 14.0 were assigned to a known origin. If a follicle persisted in the 3-mm range for at least 2 days, it was considered to be a follicle of wave 1 that emerged before Day 0 [11,13] or as part of the minor follicular wave that preceded or intermeshed with wave 1 follicles during preovulation [14,15].

The P3Fs were further subgrouped according to their diameter change during the period of persistence and according to their outcome (regressed or rescued) at the

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