Theriogenology 86 (2016) 907–913

Contents lists available at ScienceDirect

Theriogenology

journal homepage: www.theriojournal.com

Interactions of side (left and right ovary) with the number of follicles per ovary and with the intraovarian relationships between dominant follicle and corpus luteum in heifers

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ARTICLE INFO

Article history:
Received 18 December 2015
Received in revised form 7 March 2016
Accepted 8 March 2016

Keywords:
Corpus luteum
Dominant follicle
Intraovarian pattern
Luteolysis
Side of ovary

ABSTRACT

The interactions between side of ovary (left ovary [LO] and right ovary [RO]) and number of follicles per ovary and between side and intraovarian patterns were studied in heifers with two follicular waves (anovulatory wave 1 and ovulatory wave 2). Intraovarian patterns were on the basis of location of the dominant follicle (DF) and corpus luteum (CL) and were termed DF–CL, DF, CL, and devoid. The frequency of the DF–CL intraovarian pattern was greater for the RO than for the LO in wave 1 (80 of 121; $P < 0.0004$) and in wave 2 (54 of 83; $P < 0.006$). For each wave, the DF of the DF–CL and DF patterns was more often in the RO for the ipsilateral relationship (e.g., wave 1: 66% vs. 48%; $P < 0.01$) and in the LO for the contralateral relationship (52% vs. 34%; $P < 0.01$). An interaction between side and pattern ($P < 0.05$) for number of follicles in wave 2 that attained 6 mm was from a greater number in RO than in LO when a DF was present (DF–CL and DF patterns). An interaction of side and pattern for the number of wave 2 regressing subordinate follicles that recovered (increased in diameter) and became part of the subsequent wave 1 was greater ($P < 0.05$) for LO than for RO for the DF pattern but not for the CL pattern. An effect of side or an interaction that involved side was not found for the greater dimensions and blood flow for both the DF and CL of the DF–CL pattern. Results indicated that side interacted with ovarian pattern for number of DF–CL patterns, side of DF, number of follicles per ovary, and recovery of regressing wave 2 follicles. The hypothesis was supported that some aspects of follicle dynamics reflect an interaction of side and intraovarian pattern. Future studies on the effect of side on luteal or follicle dynamics could be incomplete or misleading if intraovarian patterns are ignored.

1. Introduction

Cattle develop either two or three follicular waves during an interovulatory interval [1–4]. Emergence of 4- or 5-mm follicles in the periovulatory or first wave of the interval (wave 1) in *Bos taurus* cattle occurs on the day of ovulation. Waves 2 and 3 emerge about 10 and 16 days after ovulation, respectively. A dominant follicle (DF; diameter $\geq$ 10 mm) develops during each follicular wave. The DF is anovulatory in wave 1. The DF of wave 2 can be ovulatory or anovulatory depending whether there are 2 or 3 waves per interval.

Follicle dynamics and luteal function in cattle are affected not only by number of waves per interval but also by intraovarian pattern for location of the DF and corpus luteum (CL) of a follicular wave and by side of the body for location of an ovary (left ovary [LO] and right ovary [RO]) [5]. The interovarian relationships between a pair of ovaries and intraovarian patterns in single ovulators are on the

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0093-691X/$ – see front matter © 2016 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.theriogenology.2016.03.013

basis of the location of the DF and CL in the two ovaries. In the ipsilateral interovarian relationship, the intraovarian pattern of DF and CL in the same ovary is described by the nomenclature DF–CL (Fig. 1). Necessarily, the opposite ovary has neither a DF nor a CL and is described as devoid. In contralateral interovarian relationships, the nomenclature for the intraovarian patterns is DF for one ovary and CL for the other.

The frequency of the ipsilateral relationship in wave 1 of cattle is greater than the frequency of the contralateral relationship (e.g., 68% vs. 32% [6]). The four intraovarian patterns of DF–CL, devoid, DF, and CL have a profound intraovarian effect on follicular and luteal dynamics. More medium-sized [7] and 2- and 3-mm follicles [8] are present in the ovary containing the CL. However, a subsequent study found that the positive effect on number of follicles is attributable to the intraovarian presence of the DF rather than the presence of the CL even when the DF is not included in the tally [6]. The diameter of DF and percentage of DF wall with color Doppler signals of blood flow are greater for the DF, and the cross-sectional area (cm^2) and blood-flow signals are greater for the CL when the intraovarian pattern is DF–CL than when the pattern is DF or CL [9]. The pattern and extent of ovarian vascular perfusion for the preovulatory portion of wave 1 affect the pattern and vascular perfusion for the postovulatory portion [10]. The intraovarian patterns of wave 1 affect the vascular perfusion and number of follicles for the patterns of wave 2 [11].

In addition to the reports on the effects of interovarian relationships and intraovarian patterns, other independent studies in cattle have shown that ovarian side (LO and RO) has a profound effect on follicle dynamics (reviewed in [12]). Greater follicle activity of the RO was first reported in calves by a greater follicular-fluid volume and a heavier ovary [13]. A greater frequency of ovulation from the RO has been well established in cattle [8,14]. In the original study that used ultrasonic imaging, there were more follicles 4 to 6 mm in the RO regardless of the presence of a CL [8]. Most reports have considered either the effect of side of ovary or the effect of the intraovarian mechanisms and have not considered potential confounding effects between side and location of the DF and CL.

The present study considered the effect of side of ovary on the number of follicles and on intraovarian patterns (DF–CL, devoid, DF, and CL) and the interaction between side and pattern for several intraovarian events. This was done by reexamining data from intraovarian experiments that were previously reported but did not include side in the analyses. The hypothesis was that some aspects of follicle dynamics reflect an interaction of intraovarian pattern and side.

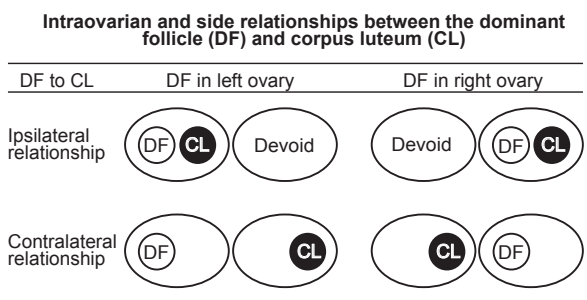

Fig. 1. Illustration of the spatial associations between ipsilateral and contralateral interovarian relationships and intraovarian patterns when the DF is in the left or right ovary. DF, dominant follicle.

2. Materials and methods

Data from previously reported studies on interovarian relationships and intraovarian patterns that did not consider the role of side (LO and RO) were reanalyzed. The reanalyses included the main effect and interactions of side on intraovarian follicular and luteal dynamics. The studies that were reconsidered were originally published in 2014 and 2015 and included the following: (1) effect of intraovarian pattern on number of follicles [6]; (2) blood flow to DF and CL during wave 1 [15]; (3) effect of intraovarian proximity between DF and CL on blood flow to each structure [9]; (4) conversion of follicular activity between the preovulatory and postovulatory portions of wave 1 [10] and conversion of intraovarian patterns between waves 1 and 2 [10,11]; (5) rescue of a regressing subordinate follicle of wave 1 to become the DF of wave 2 [16]; and (6) recovery of subordinate follicles of wave 2 to become growing follicles of the subsequent wave 1 [17]. When reference to a specific original report seems important for an individual analysis, the reference is cited in the Section 3. The heifers in each of the reported studies that provided records for the present studies were handled in accordance with the US Department of Agriculture Guide for Care and Use of Agricultural Animals in Research.

The handling and care of the Holstein heifers (*B. taurus)* and the equipment and methods of gray-scale transrectal ultrasonic imaging of the ovaries and color Doppler study of ovarian vascularity are given in detail in the original studies. Briefly, the heifers were never bred and ranged from 18 to 30 months of age. Heifers were not used if length of the interovulatory interval before a study was less than 18 days, double ovulations occurred, or abnormalities of the reproductive tract were observed during ultrasound examinations. Only heifers with two follicular waves (anovulatory wave 1 and ovulatory wave 2) were used to reduce the complexity of follicle dynamics [5]. Development of a third follicular wave was assumed if the largest growing follicle on Days 14 to 16 (Day 0 = ovulation) was less than 10 mm on Day 16 [4]. An ultrasound scanner with both gray-scale and color Doppler components and a transrectal 7.5-MHz transducer was used. Each follicle was tracked from examination to examination [18] until its outcome was known. The cursors were placed at the distinctive periphery of the antrum. Antral diameter was determined to the nearest 10th of a millimeter and was used to represent follicle diameter.

Data that were not normally distributed on the basis of the Shapiro–Wilk test were resolved by transformation to natural logarithms or ranks. The analyses used the Statistical Analysis System (SAS) by a MIXED procedure with a REPEATED statement to minimize autocorrelation (version 9.4; SAS Institute Inc, Cary, NC). The analyses of variance involved a three-way factorial for the factors of day,