Follicular development in cattle

◆ Follicular growth

Ovarian folliculogenesis is the process of forming mature follicles capable of ovulation from the pool of nongrowing primordial follicles in the ovary. As follicles grow, they progress through several distinct morphological stages of development, which include:
1) Primordial,
2) Primary,
3) Secondary,
4) Tertiary, and
5) Mature follicles (Figure 1).

Primordial follicles comprise an oocyte surrounded by a single layer of squamous epithelial cells, called pregranulosa cells (Peters, 1978; Greenwald and Terranova, 1988). Enlargement of the oocyte and initiation of granulosa cell division mark the beginning of follicular growth (Peters, 1978). Soon after initiation of growth, the pregranulosa cells, which form the simple squamous epithelium of the primordial follicle, become cuboidal and form the follicular granulosa cell layer or membrana granulosa (Peters, 1978; Greenwald and Terranova, 1988; Zoller, 1991). The oocyte begins to synthesize and secrete the zona pellucida, which surrounds and separates the oocyte from the adjacent granulosa cells soon after formation of the granulosa cell layer (Hirshfield, 1991). At this stage, the follicle is termed a primary follicle. As this primary follicle grows, ovarian stromal cells adjacent to the follicle differentiate to form a morphologically distinct thecal cell layer that is separated from the granulosa cell layer by a basement membrane (Moss et al., 1954; Greenwald and Terranova, 1988; Hsueh et al., 1989).

A follicle composed of a thecal cell layer and several layers of granulosa cells, but which has not yet formed a central cavity, or antrum, is classified as a secondary follicle (VanBlaricom and Motta, 1979). During secondary follicular growth, granulosa and thecal cells proliferate rapidly, and fluid begins to accumulate between the granulosa cells (Hirshfield, 1991). As development continues, the fluid between the granulosa cells coalesces to form a central cavity filled with follicular fluid (Hirshfield, 1991). Antrum formation heralds the tertiary, also called antral or vesicular, stage of follicular development (VanBlaricom and Motta, 1979).
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Follicular growth culminates with formation of a mature follicle capable of ovulation. A mature follicle comprises a developing oocyte, a follicular fluid-filled antrum, and a stromally-derived theca externa and richly vascularized theca interna separated from an avascular inner layer of epithelial-like granulosa cells by a basement membrane. The primary functions of the ovarian follicle are to:

1) Support and nurture a developing oocyte that is capable of fertilization after ovulation;
2) Biosynthesize and secrete the steroid hormone estrogen which regulates the morphology and function of the reproductive organs, induces mating behavior, and indirectly stimulates the endogenous surge of luteinizing hormone (LH); and
3) Provide the precursor cells that will luteinize and form the corpus luteum (CL) after ovulation (Iranni and Hodgen, 1992).

Follicular atresia

Atresia is the loss of follicles from an ovary other than by ovulation of an oocyte. Follicles can undergo atresia at any stage of follicular development in prenatal, neonatal, or mature females (Byskov, 1978; VanBlarikom and Motta, 1979; Greenwald and Terranova, 1988). In cattle, less than 1% of all ovarian follicles present at puberty will develop to maturity and ovulate. Thus, growth of follicles that culminates with ovulation is the exception rather than the rule during follicular development. Most remaining follicles never begin to grow or undergo atresia after initiation of follicular growth (Byskov, 1978; diZerega and Hodgen, 1981; Hsueh et al., 1994). The majority of follicular loss in cattle occurs early during follicular development as a wave of atresia reduces the number of primordial and primary follicles in the ovaries from several million to around 100,000. The majority of follicles that undergo atresia after puberty occurs later during follicular development in follicles that have undergone antrum formation (Byskov, 1978).

Follicular waves in cattle

Female reproductive tissues, including ovarian follicles and CL, are some of the fastest growing tissues in the adult female, and are also some of the few adult tissues to exhibit periodic and dynamic growth and regression (Reynolds et al., 1992; Luck and Zhao, 1995). For example, antral ovarian follicles can increase or decrease in diameter by more than two millimeters per day. Until recently, little was known of the temporal associations among growing and regressing follicles during an estrous cycle because of the difficulties of studying rapidly growing and regressing tissues in vitro. A technologic breakthrough using transrectal ultrasonic imaging was reported in 1984 (Pierson and Ginther, 1984) and has led to clarification of the nature of antral follicular development in cattle. Transrectal ultrasonic imaging provides a means for repeated, direct, noninvasive monitoring and measuring of ovarian follicles, regardless of their depth within the ovary. Transrectal ultrasonic imaging has revolutionized our understanding of follicular growth for antral follicles ≥ three mm in diameter, the smallest follicles that can

Figure 1. Schematic diagram of an ovary showing the sequence of events in the origin, growth, and ovulation of follicles and formation and regression of the corpus luteum. Follow clockwise around the ovary starting with the primary follicle. Adapted from Patten and Carlson, 1974. Foundations of Embryology (3rd ed) McGraw-Hill. Reproduced with permission.
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Studies using ultrasound revealed that follicular growth occurs in waves, each wave culminating with formation of a large follicle (Figure 2). A follicular wave begins with emergence of a group or cohort of small antral follicles just before the day of ovulation. During the next several days, one of the follicles in this cohort continues to grow and becomes dominant, thereby suppressing emergence of a new follicular wave. As the dominant follicle continues to grow, growth of the remaining follicles in the cohort ceases or slows, and these subordinate follicles eventually undergo atresia. A second wave of growth emerges on approximately Day 10 after ovulation and, for three-wave cycles, an additional wave emerges at Day 16 after ovulation. For both two and three-wave cycles, the ovulatory follicle arises from the final wave. Wave duration and the maximal size attained by the dominant follicle of the first wave is similar for both two- and three-wave cycles (Ginther et al., 1989). Wave duration is shorter and the dominant follicle is smaller for the second wave of a three-wave cycle compared with the first wave (Ginther et al., 1989).

The first reports using ultrasound indicated that the number of follicular waves occurring in cycling heifers varied among animals. Some heifers exhibit two, whereas others exhibit three successive waves of follicular growth during each estrous cycle (Savio et al., 1988; Sirois and Fortune, 1988; Ginther et al., 1989; Taylor and Rajamahendran, 1991). In general, primiparous and multiparous lactating dairy cows exhibit two-wave cycles more frequently, whereas nulliparous dairy heifers tend to exhibit three-wave cycles more frequently. However, an animal exhibiting a two-wave cycle may exhibit three waves during the subsequent cycle and vice versa, however the frequency with which this switchover in the number of waves per cycle occurs within an animal has not been well established. Several factors that influence the number of waves per estrous cycle in dairy cattle include dietary intake (Murphy et al., 1991), age, parity, and lactational status (Lucy et al., 1992).

Follicular waves are not limited to postpubertal cyclic cows, but are present in many physiologic states. The onset of follicular waves begins early in life, with prepubertal heifers as young as two weeks postpartum exhibiting wavelike patterns of follicular growth (Adams et al., 1994; Evans et al., 1994). Follicular waves continue throughout the prepubertal period.

Figure 2. Schematic diagram depicting two-wave (top panel) and three-wave (bottom panel) patterns of follicular growth during the bovine estrous cycle. Growing follicles before selection of the dominant follicle are depicted as black circles, the dominant follicles of each wave are depicted as gray circles, and atretic follicles are depicted as open circles.
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and are present in dairy and beef heifers at the onset of cyclicity (Savio et al., 1990). Pregnant cows exhibit follicular waves similar to those observed in nonpregnant cows throughout the first eight months of gestation (Ginther et al., 1996). Follicular waves in prepubertal and pregnant animals differ from those that occur in cyclic animals in two respects. 

1) The diameter of the dominant follicle of each wave is smaller and 
2) The duration of each follicular wave tends to be shorter in prepubertal and pregnant animals.

The physiologic role of dominant, nonovulatory follicles during the luteal phase of the bovine estrous cycle or pregnancy is uncertain. Administration of hCG in the presence of a luteal-phase dominant follicle results in ovulation and subsequent formation of a CL (Price and Webb, 1989; Fricke et al., 1993), indicating that dominant follicles present during the early and midluteal phases of the estrous cycle are capable of ovulation and formation of a luteal structure. Nonovulatory dominant follicles may play a role during luteal regression (Thatcher et al., 1989). Electrocautery of all visible follicles and x-irradiation of the ovary to arrest further follicular growth on Day 10 of the estrous cycle delays luteal regression in cows (Fogwell et al., 1985). Thus, absence of a dominant follicle during the mid- to late-luteal phase delays luteal regression. Increased secretion of estradiol 17-β by late-cycle dominant follicles may cause luteal regression by stimulating secretion of ovarian or uterine PGF2α (Fogwell et al., 1985).

Synchronization of estrus

Synchronization of estrus behavior has also been used to improve reproductive efficiency. Synchronization protocols using hormones approved for lactating dairy cows have primarily been limited to prostaglandin (PG) F2α (Lucy et al., 1986; Stevenson et al., 1987; Archibald et al., 1992; Stevenson and Pursley, 1994). This hormone is available commercially, and many studies have shown that use of PGF2α can reduce the interval between detected estrous cycles and improve estrus detection efficiency. However, PGF2α does not regress the early corpus luteum (less than six days after estrus); therefore, two injections of PGF2α, administered fourteen days apart, are required to effectively synchronize estrus in lactating cows. Also, PGF2α does not synchronize anestral cows, which constitute about 15% of all cows in the breeding group (Stevenson and Pursley, 1994).

Synchronization of estrus with PGF2α has been successful if cattle are bred at a detected estrus (Lucy et al., 1986; Stevenson et al., 1987; Larson and Ball, 1992), because estrus detection rates increase and management of AI is more efficient compared with daily estrus detection. However, estrus is not precisely synchronized with PGF2α in lactating dairy cows that respond to PGF2α because this treatment only regulates the life span of the corpus luteum and does not synchronize growth of follicles. Thus, cows with functional corpora lutea will come into heat over a 7-day period after treatment with PGF2α. Furthermore, when cows received a fixed-time AI 72-80 h after a second injection of PGF2α, pregnancy rate per AI was about half of that of cows bred at a detected estrus (Lucy et al., 1986; Stevenson et al., 1987; Larson and Ball, 1992).

Synchronization of ovulation

Reproductive physiologists have long searched to develop a synchronization program that could avoid the inherent problems and limitations associated with estrus detection. Such a program was developed at the University of Wisconsin in 1995 and is now commonly referred to as Ovsynch. Because Ovsynch synchronizes ovulation rather than estrus, managers no longer need to rely on estrus detection, which is inefficient on most dairy operations, to artificially inseminate their cows. Because ovulation is precisely timed using Ovsynch, lactating dairy cows can be bred by appointment while maintaining a conception rate similar to that of cows bred to an estrus.
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The Ovsynch protocol involves two hormones that are approved for use in lactating dairy cows. Figure 3 illustrates the injection protocol and the purpose of each injection. Administered at a random stage of the estrous cycle, the first injection of GnRH induces ovulation in 65% of cows and causes emergence of a new follicular wave in 100% of cows. The PGF$_2\alpha$ injection induces regression of the spontaneous and/or GnRH-induced corpora lutea, and the second GnRH injection synchronizes the time of ovulation of the dominant follicle of the follicular wave that began growing after the first GnRH injection. Ovulation of a dominant follicle in response to the second GnRH injection occurs in 85% of lactating cows receiving this protocol (Fricke et al., 1998), and ovulation occurs within 24 to 32 hours after the second GnRH injection in synchronized cows followed by growth of a new follicular wave (Pursley et al., 1996).

To determine the effectiveness of using Ovsynch for reproductive management of lactating cows, cows (n = 333) from three Wisconsin dairy herds were randomly assigned at parturition to one of two groups (Pursley et al., 1997b). Reproduction for control cows was managed using the typical reproductive management procedure in place on each farm (i.e., estrus detection, AM/PM breeding, and periodic use of PGF$_2\alpha$). Reproduction for Ovsynch-treated cows was managed by timed AI after the Ovsynch protocol on the same day each week. Pregnancy status was determined 32 days after AI for both groups by using transrectal ultrasonography. Nonpregnant cows were reinseminated using the same treatment until diagnosed pregnant or culled from the herd. Median days to first AI (Figure 4 left panel; 54 vs. 83 days) and average days open

![Figure 3. Timing and purpose of hormonal injections for synchronization of ovulation in lactating dairy cows (Ovsynch)](image)

![Figure 4. Survival curves for days to first AI (left panel) and days open (right panel) for cows that received AI after a detected estrus (Control) and cows that received appointment AI after synchronization of ovulation (Ovsynch). Median days to first AI and average days open were less for Ovsynch than for Control cows, and pregnancy rate to first AI was similar for both groups. Figures taken from Pursley et al., 1997b](image)
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(Figure 4 right panel; 99 vs. 118 days) were fewer for Ovsynch-treated cows than for control cows. Pregnancy rate to first AI was similar (37% vs. 39%) for both groups even though Ovsynch cows were bred earlier postpartum. Service rate is dramatically improved using Ovsynch because all eligible cows are routinely serviced on a given day of lactation regardless of estrus detection. Thus, Ovsynch improves reproductive performance of lactating dairy cows by increasing service rate, allows for timed AI, and eliminates reliance on estrus detection for AI compared with standard reproductive management.

Ovsynch improves reproductive efficiency of lactating dairy cows by increasing service rate; however, conception rate in response to timed AI after Ovsynch is similar to conception rate in response to AI after a detected estrus. Table 1 shows the results from two experiments comparing PR/AI of lactating cows receiving AI after a detected estrus (Control) or timed AI after synchronization of ovulation (Ovsynch; Pursley et al., 1997a).

For both experiments, PR/AI did not differ between groups. Thus, timed AI after Ovsynch results in normal fertility without the need for estrus detection. In addition, the effectiveness of Ovsynch for synchronization of ovulation in virgin dairy heifers was assessed in Experiment 2 (Table 1). Conception rate was greater (p<0.01) for heifers receiving AI after a detected estrus (Control) compared with heifers receiving timed AI after synchronization of ovulation (Ovsynch). Based on these results, Ovsynch is not recommended as a method for synchronizing and breeding dairy heifers. Although not fully understood, the difference in the efficacy of Ovsynch between lactating cows and heifers is related to differences in the patterns of follicular growth between lactating cows and heifers during the estrous cycle.

Table 2 shows days-in-milk (DIM) and PR/AI after first and second service for lactating cows receiving AI after a detected estrus (Control) or timed AI after synchronization of ovulation (Ovsynch). Reproduction for control cows was managed using the typical reproductive management procedure in place on each farm (i.e., estrus detection, AM/PM breeding, and periodic use of PGF$_2$α), and reproduction for Ovsynch-treated cows was managed by timed AI after the Ovsynch protocol on the same day each week. Pregnancy status was determined 32 days after AI for both groups by using transrectal ultrasonography, and nonpregnant cows were reinseminated using the same treatment until diagnosed pregnant or culled from the herd.

First and second service AI occurred earlier (p<0.01) for Ovsynch cows compared with Control cows, whereas PR/AI did not differ between groups. For this experiment, the voluntary waiting period was 50 days; however, PR/AI was 5 to 6% less for first service compared with second service AI. Thus, it is likely to be more profitable to breed cows with Ovsynch after 70 DIM because of the improved PR/AI and the extended length of lactation.

Another interesting observation from the data in Table 2 is the interval from first to second

<table>
<thead>
<tr>
<th>Service</th>
<th>Control</th>
<th>Ovsynch</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIM</td>
<td>PR/AI</td>
<td>DIM</td>
</tr>
<tr>
<td>1$^{st}$</td>
<td>83</td>
<td>39%</td>
</tr>
<tr>
<td>2$^{nd}$</td>
<td>128</td>
<td>45%</td>
</tr>
</tbody>
</table>

$^1$ Data adapted from Pursley et al., 1997a

$^2$ Differs from Control, p<0.01

Table 1. Pregnancy rate per AI (PR/AI) of lactating cows and heifers receiving AI after a detected estrus (Control) or timed AI after synchronization of ovulation (Ovsynch)$^1$

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Number of animals</th>
<th>PR/AI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lactating Cows</td>
<td>1</td>
<td>546</td>
</tr>
<tr>
<td>Heifers</td>
<td>2</td>
<td>311</td>
</tr>
<tr>
<td></td>
<td>Heifers</td>
<td>2</td>
</tr>
</tbody>
</table>

$^1$ Data adapted from Pursley et al., 1997a

$^2$ Differs from Control, p<0.01
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service between groups. Because cows in the Ovsynch group were not allowed to be bred to an estrus, the 42-day interval between first and second service was experimentally determined by the 32-day interval from AI to the pregnancy diagnosis using ultrasound plus the additional 10-day interval to resynchronize the cows using Ovsynch. In contrast, the interval between first and second service for Control cows was 45 days, despite the fact that these cows could be bred at any detected estrus. Thus, an average of one estrus period was not detected between services when managers relied on estrus detection alone to breed their cows.

Effect of day of the estrus cycle on synchronization of ovulation

To determine the effect of day of the estrous cycle on which synchronization of ovulation was initiated, lactating dairy cows (n=159) with a known estrus date within 22 days of initiation of the first GnRH injection of the protocol were examined by ultrasound on the day of each injection of the protocol, and 24 and 48 hours after the second GnRH injection. Cows were grouped by the day of the cycle on which synchronization was initiated as follows: Day 1-4 (n=31), Day 5-8 (n=38), Day 9-12 (n=39), Day 13-16 (n=24), and Day 17-22 (n=27). Based on the ultrasound examinations, the percentage of cows ovulating after the first GnRH injection and the second GnRH injection was determined. Cows that ovulated within 48 hours of the second GnRH injection were used to determine the synchronization rate.

Table 3 shows the effect of the day of the estrous cycle on the percentage of cows ovulating after each injection of the synchronization protocol. Ovulatory response to the first GnRH injection is lowest on days 1 to 4 of the cycle because a dominant follicle capable of ovulating is not present in most cows, whereas the greatest response occurs on day 5 to 8 of the cycle when nearly all cows, regardless of whether they exhibit two or three follicular waves, have an ovulatory follicle. Interestingly, the synchronization rate to the second GnRH injection is greatest when the first GnRH injection is administered on day 1 to 4 of the cycle, when the response to the first GnRH injection is lowest. Thus, cows do not necessarily need to respond to the first GnRH injection to synchronize to the second GnRH injection.

Table 4 shows the outcome of cows that either synchronized or failed to synchronize to the second GnRH injection of the protocol. Cows were classified into positive and negative responses to the first GnRH injection of the protocol, and further subdivided into the stage of the estrous cycle (first half, Day 1-12 vs. second half, Day 13-22) at the time they received the first GnRH injection. Of interest in this study were cows that failed to synchronize to the second GnRH injection of the protocol. Two primary groups of nonsynchronized cows emerged from these data. Nonsynchronized cows that responded to the first GnRH injection were primarily in the first half of the estrous cycle when the protocol was initiated. These cows likely initiate growth of a new follicular wave in response to ovulation of a dominant follicle; however, the follicle grows quickly and loses dominance during the nine-day interval between GnRH injections and fails to ovulate to the second GnRH injection. In contrast, nonsynchronized cows that failed to ovulate to the first GnRH injection were primarily in the

Table 3. Days in milk (DIM) and pregnancy rate per artificial insemination (PR/AI) after first and second service for lactating cows receiving AI after a detected estrus (Control) or timed AI after synchronization of ovulation (Ovsynch)¹

<table>
<thead>
<tr>
<th>Day of the cycle</th>
<th>n</th>
<th>% of cows ovulating in response to:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1st GnRH injection 2nd GnRH injection</td>
</tr>
<tr>
<td>1-4</td>
<td>31</td>
<td>23 94</td>
</tr>
<tr>
<td>5-8</td>
<td>38</td>
<td>95 90</td>
</tr>
<tr>
<td>9-12</td>
<td>39</td>
<td>56 87</td>
</tr>
<tr>
<td>13-16</td>
<td>24</td>
<td>63 78</td>
</tr>
<tr>
<td>17-22</td>
<td>27</td>
<td>74 80</td>
</tr>
</tbody>
</table>

¹Data adapted from Vasconcelos et al., 1997
second half of the estrous cycle when they received the first GnRH injection. These cows exhibited estrus during the protocol before the second GnRH injection, because the corpus luteum regresses and the cow naturally comes into heat.

**Modifications of Ovsynch**

Based on the variation in response due to the stage of the estrous cycle at which Ovsynch is initiated, several experiments have been conducted to determine the effect of presynchronizing dairy cattle before initiation of Ovsynch using single or double injections of PGF$_{2\alpha}$. A presynchronization strategy in which two injections of PGF$_{2\alpha}$ administered 14 days apart preceded initiation of Ovsynch by 12 days improved conception rate in lactating dairy cows in confinement-based dairies (Moriera et al., 2000). Although Ovsynch, and modifications of the Ovsynch protocol, have been extensively studied in confinement-based dairies in the United States, few studies have been conducted on lactating dairy cows managed in grazing-based dairy systems.

**Use of Ovsynch in U.S. grazing-based dairy systems**

Recently, my laboratory has investigated the efficacy of Ovsynch in grazing-based dairies in the United States (Cordoba and Fricke, 2000; Cordoba and Fricke, 2001). These studies were conducted as field trials on several grazing-based dairies in Wisconsin.

To determine the effect of Ovsynch and one modification of Ovsynch in grazing based dairies in the United States, lactating dairy cows (n = 142) from two grazing-based dairies located in south central Wisconsin were randomly assigned to one of three treatment groups.

1) Cows in the first group (Ovsynch) received

- 50 µg GnRH (Day –10);
- 25 mg PGF$_{2\alpha}$ (Day –3); and
- 50 µg GnRH (Day –1)

Followed by timed AI on Day 0.

2) Cows in the third group (control) received standard reproductive management in place on each farm.

Average milk production for both farms was between 10,000 and 11,000 kg based on bulk tank milk records collected during the study period. Thus, these farms are not typical of most grazing-based dairies in that milk production is similar to that of many confinement-based dairies.

Synchronization rate (i.e., ovulatory response at 48 hours after the second GnRH injection), conception rate at Day 32 and pregnancy rate at Day 60 was similar for cows in the Ovsynch and PGF$_{2\alpha}$ + Ovsynch groups. Cumulative pregnancy rate was greater for cows receiving TAI compared to control cows at Day 32 (41.2% vs. 20.0%), but did not differ at Day 60 (54.9% vs. 60.0%). Based on these results, we concluded that administration of PGF$_{2\alpha}$ 12 days before initiation of Ovsynch did not improve synchronization, conception, or pregnancy rate compared with the standard Ovsynch protocol. We also concluded that synchronization of ovulation to initiate timed AI at the onset of the breeding season resulted in earlier establishment

<table>
<thead>
<tr>
<th>Ovulation to 1$^{st}$ GnRH</th>
<th>Ovulation to 2$^{nd}$ GnRH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Before</td>
<td>Synchronized</td>
</tr>
<tr>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>YES</td>
<td>100 (63%)</td>
</tr>
<tr>
<td>Day</td>
<td>(1-12)</td>
</tr>
<tr>
<td></td>
<td>(13-21)</td>
</tr>
<tr>
<td>NO</td>
<td>59 (37%)</td>
</tr>
<tr>
<td>Day</td>
<td>(1-12)</td>
</tr>
<tr>
<td></td>
<td>(13-22)</td>
</tr>
</tbody>
</table>

Adapted from Vasconcelos et al., 1997
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of pregnancy compared with standard reproductive management. Thus, it appeared from this first experiment that Ovsynch worked well in cows managed in this grazing-based dairy (Cordoba and Fricke, 2000).

To further investigate the efficacy of Ovsynch on cows in grazing-based dairies in the United States, lactating dairy cows (n = 228) managed in a seasonal grazing based dairy in southern Wisconsin were subjected to a 21 day artificial insemination (AI) breeding period beginning at the onset of the breeding season (Day 0) followed by introduction of natural service sires (Day 22). Beginning 10 days before the breeding season, cows were randomly assigned to receive synchronization of ovulation (50 µg GnRH, Day –10; 25 mg PGF$_{2\alpha}$, Day –3; 50 µg GnRH, Day –1) and fixed-time AI (Day 0) followed by estrus detection and AI for the remainder of the AI breeding period (Ovsynch; n = 114), or estrus detection and AI for the duration of the AI breeding period (Control; n = 114). Throughout the AI breeding period, cows in both treatment groups received AI based on tail paint removal, which was evaluated twice daily at milking. Average milk production for this farm was 7,200 kg based on bulk tank milk records collected during the study period. Thus, this farm is more representative of grazing-based dairies in that milk production is low compared with confinement-based dairy systems.

Although days to first AI was greater (P < 0.01) for Control vs. Ovsynch cows (12.0 ± 0.6 vs. 0.0 ± 0.0, respectively) and the 21-day AI service rate was greater for Ovsynch vs. Control cows (100% vs. 86%, respectively), conception rate to first AI service was greater (P < 0.01) for Control vs. Ovsynch cows (47% vs. 27%, respectively). Only 75.2% of Ovsynch cows underwent luteolysis after PGF$_{2\alpha}$ administration. No Control cows received a second AI service during the AI breeding period, compared to 47% of Ovsynch cows (mean d to second AI = 17.0 ± 5.8). Conception rate to second AI service for Ovsynch cows was 43.1%, which did not differ from that of Control cows at first AI service. Cumulative pregnancy rate for Control and Ovsynch cows was similar at Day 49 (47% vs. 46%, respectively) and Day 179 (80% vs. 83%, respectively). We concluded from this study that Ovsynch failed to synchronize lactating dairy cows managed in a grazing-based dairy system thereby resulting in lower first service conception rates than AI to spontaneous estrus, and that tail paint is an effective reproductive management tool for conducting AI in grazing-based dairies. Thus, Ovsynch may not be an effective method for conducting timed AI in grazing-based dairy systems (Cordoba and Fricke, 2001).

Conclusions

Basic research using transrectal ultrasonography has elucidated the nature of ovarian follicular development in cattle. Once understood, a protocol (Ovsynch) that precisely synchronizes follicular development and ovulation in lactating dairy cows was developed that allows for a timed artificial insemination that results in conception rates similar to those of cows artificially inseminated to a standing estrus for lactating dairy cows managed in confinement-based dairies in the United States. This protocol dramatically improves the pregnancy rate in a dairy herd by improving the artificial insemination service rate to 100 per cent of cows that begin the protocol. Although this protocol has had a major impact on improving reproductive efficiency in confinement-based dairies, our recent studies suggest that Ovsynch does not effectively synchronize lower-producing lactating dairy cows managed in grazing-based dairies in the United States. Future and ongoing research is focused on further improving synchronization and conception rates to timed artificial insemination using modifications of this protocol, and on understanding the underlying physiology that determines whether cows synchronize to the protocol.
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