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REVIEW
Reproductive Potential of Japanese High-producing Dairy Cattle

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Abstract

To establish sustainability in the dairy industry, it is important that cows become pregnant at a biologically optimal time and at an economically profitable interval after calving. In this review, the results obtained from Holstein cows in an experimental herd for dairy research are summarized. First, the postpartum follicular dynamics of lactating cows were traced in relation to their fertility. The premature initiation of ovarian activity does not always improve the fertility of cows, as indicated by the number of days open. Second, the occurrence of anestrous ovulations during the early postpartum period was analyzed with reference to the frequency of reversion to anestrus. The premature onset of estrous activity also failed to improve fertility, and relapse into anestrus after the onset of the estrous cycle often occurred during the breeding period. Third, both the emergence and fate of cystic ovarian follicles and repeated follicular waves during the early postpartum period were examined, and it was revealed that neither conditions exerted a significant impact on the cow's fertility, as indicated by days open. The importance of appropriate estrous detection was underlined and discussed as a major concern to improve the fertility of high-yield dairy cows.

Discipline: Animal industry
Additional key words: dairy cow, estrus, fertility, milk production, ovulation

Introduction

Rapid progress in genetics and management in the dairy industry has resulted in increased milk production per cow. Metabolic demands for more milk impair the reproductive function of postpartum cows[1,32]. Those with the greatest milk production also have the highest incidence of subfertility or infertility, but epidemiological studies indicate that, in addition to milk production, other factors probably contribute to decreasing reproductive efficiency in dairy herds[5,19].

In dairy cows, the resumption of ovarian activity plays an important role in their subsequent fertility[4,46], and many factors can influence the function of the postpartum ovaries[33]. Applying the ultrasound imaging technique to monitor bovine follicular dynamics[27,41,45], it has become clear that most postpartum follicular development occurs in a wave-like manner in normal cyclic cattle[29,41]. Recent studies have also revealed that postpartum anovulatory anestrus in dairy cows is attributable not to the lack of follicular development, but rather to the failure of a dominant follicle to ovulate[31]. The first dominant follicle is selected within 10 days of calving in nearly all dairy cows, regardless of their subsequent reproductive performance[22,41], and the first ovulation can be observed as early as 2 weeks after calving in dairy cows[22,29,42]. However, the average interval from parturition to postpartum first ovulation has been extended from 2 weeks in the 1960s[21,23] to 3 weeks during the 1970s-90s[4,6]; and recently to 4 weeks or more[19,31].

Postpartum anovulatory anestrus is regarded as a normal facet of bovine reproduction because the high concentrations of progesterone that prevail throughout pregnancy and the peripartum elevation of the estrogen level result in negative feedback suppression of the hypothalamo-pituitary axis, meaning that follicular activity in the ovaries of full-term pregnant cows is minimal. Fur-

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thermore, anestrous ovulations often occur during the early postpartum period[3,15], but only limited information on the frequency and timing of events occurring in modern high-yield dairy cows is available.

The use of ultrasound techniques has also improved the diagnostic accuracy for follicular cysts[12,48], and enabled their development and turnover to be accurately traced[9]. For postpartum dairy cattle, especially high-yield cows, the development of anovulatory ovarian cysts during the early lactation period is a significant cause of anestrus[8,10]. Anovulatory cysts have been further classified into follicular or luteal cysts, the former of which are more common than the latter. Follicular cysts are usually defined as fluid-filled, exceeding 25 mm in diameter and persisting for at least 10 days in the absence of a corpus luteum. The incidence of this condition has been reported at between 6 and 19 % in lactating dairy cows[8]. Ovarian follicular cysts in lactating dairy cattle were thought to be attributable to an extended calving interval[14], and follicular cysts that develop during the early postpartum period often recover spontaneously[2,17,23]. The ovaries of high-yield dairy cows frequently contain numerous large anovulatory follicles, which quickly become atretic during the early postpartum period[24]. The persistence of this condition is presumed to be observable as repeated waves of anovulatory large follicles and is believed to delay the resumption of ovulatory activity. Accordingly, the occurrence of repeated follicular waves has the potential to affect the fertility of postpartum cows. Information on these topics, including follicular dynamics and subsequent fertility, is also limited[22].

Resumption of Ovarian Activity after Parturition

Follicular dynamics during the normal estrous cycle have been extensively studied as an adjunct to developing effective estrus-synchronization strategies[11]. However, less information is available on postpartum follicular dynamics[29,43]. Moreover, the relationship between early follicular dynamics and subsequent fertility is unclear in modern dairy cows. Since it was reported that the occurrence of multiple estrous periods (up to 4) during the first 60 days postpartum was associated with an increased conception rate[49], the early resumption of cyclic ovarian activity and the occurrence of luteal concentrations of progesterone have been considered beneficial to fertility. However, whether the early resumption of ovarian activity improves the fertility of dairy cows remains controversial[4,13,18,26,51], and early ovulation could be associated with reduced pregnancy rates and prolonged calving to conception intervals in multiparous dairy cows[46,47].

To clarify the process for the resumption of ovarian activity, early postpartum follicular dynamics were characterized using 50 lactating Holstein cows, and the effect of the timing of the resumption of ovarian function on the subsequent reproductive performance of the cows, including the expression of estrus, pregnancy rate, and days open, was examined[34]. The ovaries and uterine horns of postpartum lactating cows were examined by ultrasonography three times weekly until the first services after a 45-d voluntary waiting period. Most of the cows regained normal ovarian follicular dynamics after the second ovulation. No fertility differences were detected between primiparous and multiparous cows.

The length of the ovarian cycle was restored to the normal range until the third ovulation. Table 1 shows the fertility and milk yield in cows with varying numbers of follicular waves before the first ovulation. The mean number of days until the first ovulation rose with increasing pre-ovulation follicular waves. Cows having the longest intervals from calving to the first ovulation produced the most milk and also showed prolonged intervals until the first estrous activity. Differences in follicular dynamics before the first ovulation altered the intervals until the first estrus, first service, and uterine involution, but these differences did not affect the pregnancy rate, number of services, or days open.

It has been suggested that early luteal activity impairs the involution of the uterus after calving[16] and reduces fertility in dairy cows[50]. From parturition until first ovulation, a period when the concentrations of progesterone are minimal, the uterus is resistant to infections, and purulent uterine infections seldom develop. After ovulation, when concentrations of progesterone increase, the uterine immune system becomes down-regulated, creating a uterus that is susceptible to infection[16]. Based on our results, the days required for uterine diameter involution in cows having one wave were greater than for those ovulating after two or more waves. Delayed uterine involution might be due to early exposure of the uterus to progesterone and might explain why no difference was detected in the number of days open among the four groups classified by the number of follicular waves before the first ovulation.

Anestrous Ovulation

It was speculated that the length of the postpartum anovulatory anestrus *per se* may not be a major factor causing infertility in cattle unless the anestrus period extends into the breeding period[20]. It was noted that the problematic noncycling condition can be a consequence of prolonged anovulation, ovulations without estrus, or

reversion to an anestrus state after previous detection of being in estrus[25]. This relapse into anestrus does significantly impair the reproductive performance of dairy cows, despite the resumption of the estrous cycle during the early postpartum period.

The frequency of anestrous ovulations during the early postpartum period in relation to their subsequent fertility was described using data from 92 lactations with 368 ovulations, and the frequency and timing of the occurrence of relapse into anestrus after the resumption of normal cycling activity was identified[40]. As summarized in Fig. 1, there were cows representing 4 different stages of ovulations at any one time (either the first to fourth or second to fifth respectively) during weeks 10 to 13. This finding that at a certain week postpartum the individual cows are at very different stages of ovulation could help in analyzing the possible causes of unexpected outcomes of hormonal treatment programs and developing successful hormonal programs in dairy herds.

In this study the cows that were observed standing to be mounted were considered in standing estrus, and those showing mounting activity accompanied by other signs but not observed standing were considered in mounting estrus. Of the total of 368 ovulations observed, 46% were accompanied by standing estrus, 17% by mounting estrus, and 37% were anestrous ovulations respectively. Only 10% of the first ovulations were accompanied by standing estrus behavior; while the percentage of ovulations that were accompanied by standing estrus increased in accordance with the advance of the ovulation stages (Fig. 2). The ratios of mounting estrus to the total number of estrus events (standing estrus + mounting estrus) increased from 11% in the first 4-week interval to 29% in the second, peaked at 34% in the third and then decreased to 24% in the fourth and 14% in the fifth or more 4-week intervals. These results suggest that intensive detection, for mounting estrus as well as standing estrus, can increase the submission rate to insemination.

Fourteen of 92 cows relapsing into anestrous ovulations after the onset of postpartum estrus were detected (either as standing estrus or mounting estrus). One cow relapsed three times, and another twice, resulting in a to-

Table 1. Fertility and milk yield in postpartum lactating dairy cows having various numbers of follicular waves before the first ovulation[34]

Item	Number of follicular waves before the first ovulation			
	1	2	3 or 4	More than four[1]
Intervals of days postpartum to				
First ovulation	18.1 ± 1.0^{a}	29.2 ± 1.5^{b}	38.5 ± 4.1^{c}	57.6 ± 4.4^{d}
First detected estrus	42.8 ± 2.3^{a}	50.4 ± 5.1^{a}	70.5 ± 4.1^{b}	79.6 ± 5.1^{b}
First service	63.1 ± 2.3^{a}	68.6 ± 6.5^{a}	74.7 ± 2.2^{ab}	92.2 ± 5.4^{b}
Uterine diameter involution	19.9 ± 0.9^{a}	15.9 ± 0.7^{b}	15.5 ± 1.7^{b}	16.3 ± 1.2^{b}
Number of services per conception				
By 100 days	1.44 ± 0.13	1.57 ± 0.20	1.00 ± 0.00	1.33 ± 0.33
By 180 days	1.68 ± 0.19	1.91 ± 0.25	1.40 ± 0.40	1.30 ± 0.23
Total	1.96 ± 0.23	1.91 ± 0.25	2.00 ± 0.68	1.30 ± 0.21
Days open				
By 100 days	72.6 ± 4.7	74.4 ± 6.7	72.3 ± 2.3	84.2 ± 4.1
By 180 days	79.5 ± 5.6	97.5 ± 11.0	90.6 ± 18.4	99.5 ± 8.7
Adjusted days open[2]	92.2 ± 8.2	97.5 ± 11.0	103.5 ± 19.8	99.5 ± 8.7
Number of cows (%)				
Total	23 (46)	11 (22)	6 (12)	10 (20)
Pregnant by 100 days	16 (70)	7 (63)	4 (67)	6 (60)
Pregnant by 180 days	19 (83)	11 (100)	5 (83)	10 (100)
Milk yield (kg)				
Daily (1 to 10 wks.)	32.7 ± 1.7^{a}	36.6 ± 2.1^{ab}	36.7 ± 3.2^{ab}	41.6 ± 2.0^{b}
305-d	8519 ± 402^{a}	9390 ± 516^{ab}	9553 ± 908^{ab}	10671 ± 515^{b}

Mean + SEM.

[1]Includes cows having developed follicular cysts.

[2]Cows without a positive pregnancy diagnosis by 180 DIM were assigned a days open value equal to 21 d after their last unsuccessful service.

$^{a, b, c, d}$ Values within rows with different superscripts differ ($P < 0.05$).

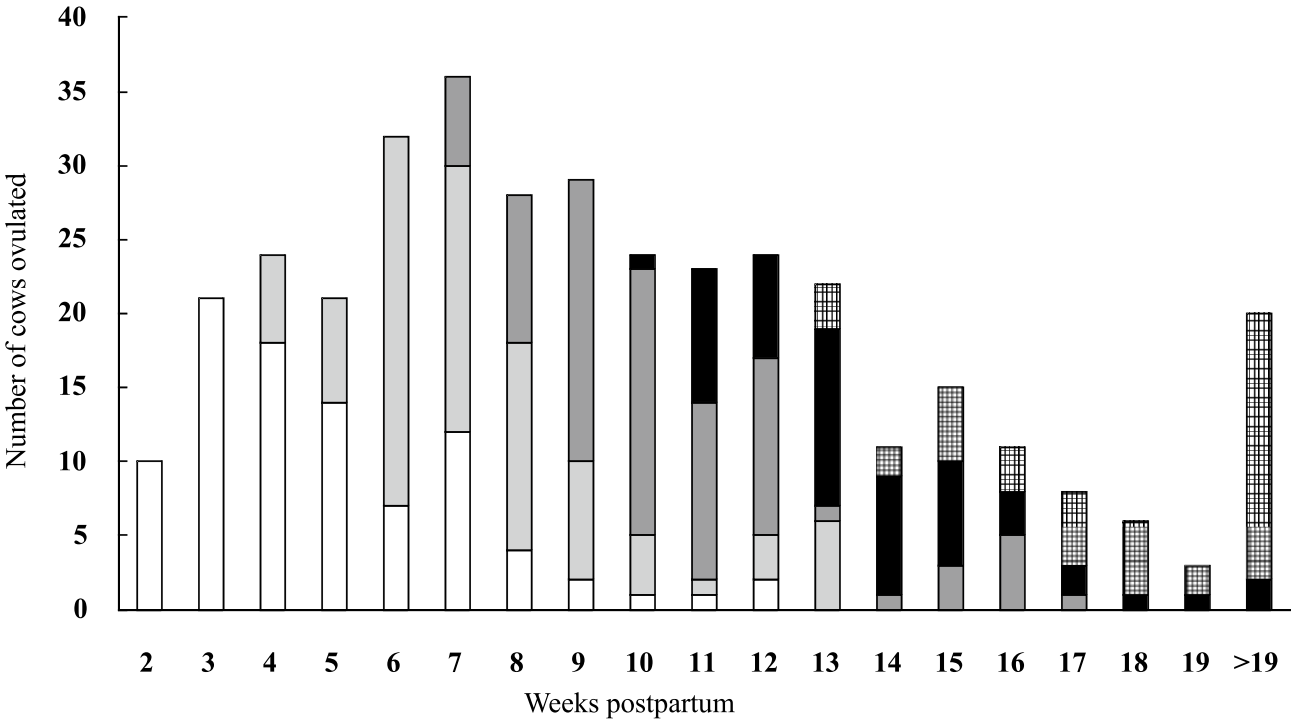

Fig. 1. Frequency distributions of the different times of each postpartum ovulation stage in fertile dairy cows[39]
▦ : ≧5th ovulations, ■ : 4th ovulation, ▩ : 3rd ovulation, ▨ : 2nd ovulation, □ : 1st ovulation.

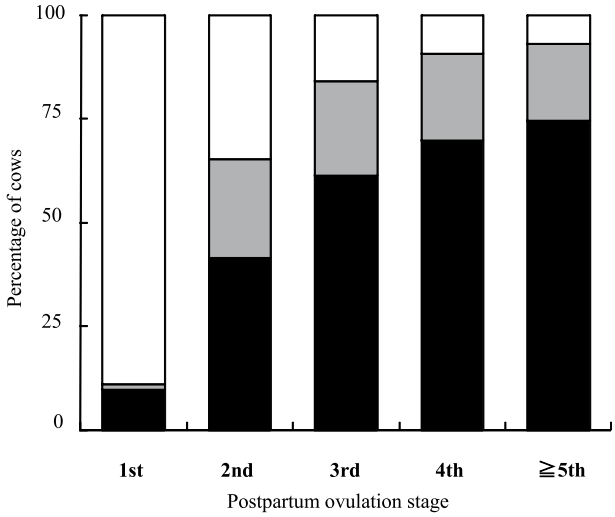

Fig. 2. Frequency distributions of estrous behavior at different ovulation stages[39]
□ : Anestrus, ▩ : Mounting, ■ : Standing.

tal of 17 relapses (13% of the total anestrous ovulations). Sixteen of the 17 relapses were observed during the second to fourth 4-week intervals (weeks 5-16). The mean number of days for which the cow's anestrus relapse lasted before reverting to estrus was 48.1 days. The early resumption of the estrous cycle with a relapse into anestrus may be a possible cause of the contradictory effect of the onset of estrous activity on reproductive performance.

The reproductive parameters of the cows resuming estrous activity at different ovulation stages are shown in Table 2. As would be expected, the number of days between parturition and the first detected estrus was lowest for the group that showed estrus at the first ovulation and increased as the ovulation stage of the first estrus was delayed. However, the lowest mean number of days open was recorded in the group that showed signs of estrus at the third ovulation, because of the relatively higher conception rate at the first service and the lower number of services required to become pregnant. The mean milk yield of the group that showed estrus at the first ovulation was lower than the pooled mean of the other three groups. These results indicate that the onset of estrous activity that is too early or late may increase the number of days open in high-yield dairy cows.

Follicular Cysts and Repeated Waves

Although extensive information exists on the dynamics of follicular cysts that have already developed or been induced and on the endocrine status of cows bearing cysts[8], very limited information exists on the developing and atretic processes of spontaneously occurring follicular cysts[42].

Among 50 cases where the early postpartum follicu-

lar dynamics were examined[34], 15 cases showing cystic follicles, some of which subsequently transitioned to follicular cysts, were observed before and after the first postpartum ovulation[35]. A cystic follicle was defined as one that had been observed as exceeding 25mm in diameter on at least two occasions but which had regressed or ovulated within 10 days after exceeding 25 mm. When the follicle remained > 25 mm for more than 10 days in the absence of a corpus luteum, it was clinically classified as a follicular cyst. Ten of the 15 cases were classified as cystic follicles, while the other 5 were diagnosed as follicular cysts. In 8 of the 10 cows, the cystic follicles emerged before the first ovulation and were ovulated or regressed. With the exception of one case, the ovulatory cystic follicles were the first detected dominant follicles. Both the mean maximum diameter of the 5 ovulated cystic follicles and the mean growth rate exceeded those of the 3 atretic follicles.

In 4 of the 5 cows that were diagnosed as having follicular cysts, the cysts emerged before the first postpartum ovulation; however, in the fifth cow, the cysts emerged after the first ovulation was completed. Ten cysts were observed in 5 cows, and their mean growth rate was 1.55 + 0.68 mm/day. None of the cows displayed nymphomaniacal behavior while the follicular cysts were present. In a typical case of follicular cyst, a single cyst developed on each ovary, followed by two additional cysts growing on the right ovary (Fig. 3). With 3 cysts on the right ovary, the first and second postpartum ovulations occurred on the left side without estrous activity. Before the third ovulation on the left side, the cow having shown its first estrous activity was inseminated and conceived.

Delayed first postpartum ovulations were observed in 6 different cows with 5 or more follicular waves, while second ovulations occurred during ovarian cycles lasting only 8 to 11 days[35]. A typical case with 13 repeated waves is shown in Fig. 4. The first postpartum estrus was detected at the first ovulation in one cow; at the second ovulation in three cows; and at the third ovulation in 2 cows. Each cow was inseminated at the third or fourth ovulation with no hormonal treatment and conceived.

The reproductive traits of these cows are summarized in Table 3. The mean milk yield of the cows having developed follicular cysts exceeded that of the cows with cystic follicles. The first postpartum ovulation was delayed by the development of follicular cysts and the repeated emergence of follicular waves, the latter causing a more severe delay in the resumption of the ovarian cycle. The mean duration of the first ovarian cycle was prolonged by the development of follicular cysts but shortened by repeated waves of follicles. The timing of the first detected estrus and the first insemination was delayed in cows with follicular cysts or repeated waves of follicles, but the number of services required for conception was lower in cows with repeated waves of follicles

Table 2. Reproductive parameters and milk yield in postpartum dairy cows that resumed estrous activity at the first to fifth ovulations and were subsequently pregnant[39]

Stage of ovulations	First	Second	Third	Fourth or Fifth	Total
Number of cows (%)					
Detected first postpartum estrus[1]	10 (11)	50 (54)	26 (28)	6 (7)	92(100)
Relapse into anestrus[2]	3 (30)	8 (16)	2 (8)	1 (17)	14 (15)
Pregnant at first service	4 (40)	28 (56)	17 (65)	1 (17)	50 (54)
Weeks to first ovulation[3]	5.4 ± 0.7	4.9 ± 0.3	4.7 ± 0.5	4.3 ± 0.9	4.8 ± 0.2
Days to first detected estrus	35.5 ± 5.4^{a}	49.3 ± 2.4^{b}	64.7 ± 3.3^{b}	96.3 ± 7.0^{c}	55.2 ± 2.3
Days to first service[4]	78.6 ± 5.6^{ab}	74.3 ± 2.5^{a}	71.2 ± 3.5^{a}	96.5 ± 7.2^{b}	75.3 ± 1.9
Number of services per pregnancy	2.30 ± 0.30	1.66 ± 0.14	1.46 ± 0.19	2.17 ± 0.39	1.71 ± 0.16
Days open	118.4 ± 10.4^{a}	92.4 ± 4.7^{ab}	85.0 ± 6.5^{b}	126.7 ± 13.5^{a}	95.4 ± 3.6
Milk yield (kg/305-day)[5]	8536 ± 542	9497 ± 242	9720 ± 336	9763 ± 700	9473 ± 179

Mean + SEM.

[1]Estrus was defined as observation of a cow standing to be mounted or observation of mounting activity accompanied by other symptoms with no standing activity and confirmed by subsequent ovulation within 2 days of the activity.

[2]An anestrous ovulation was observed after the resumption of the estrous cycle was detected.

[3]Ovulations were confirmed by rectal palpation or ultrasound scanning.

[4]Postpartum first service was initiated after the 45-day voluntary waiting period.

[5]The mean of the first estrus in the first ovulation group was lower than the pooled mean (9,587 ± 186 kg) of the other three groups ($P = 0.03$).

[a, b, c]Values within rows with different superscripts differ ($P < 0.05$).

than in those with cystic follicles. Consequently, there were no significant differences between the mean numbers of days open. The mean interval to uterine diameter involution was shorter in cows with repeated waves of follicles than in cows with cystic follicles or follicular cysts. When the cows were inseminated later due to the development of follicular cysts or repeated waves of follicles, the improvement in their conception rates at the first insemination tended to compensate for their prolonged postpartum interval to estrus.

Conclusions

At least at the experimental herd level, the premature initiation of ovarian and estrous activity did not improve the reproductive performance of postpartum dairy cows. The results reviewed in this paper were retrieved from a healthy herd with relatively sound management

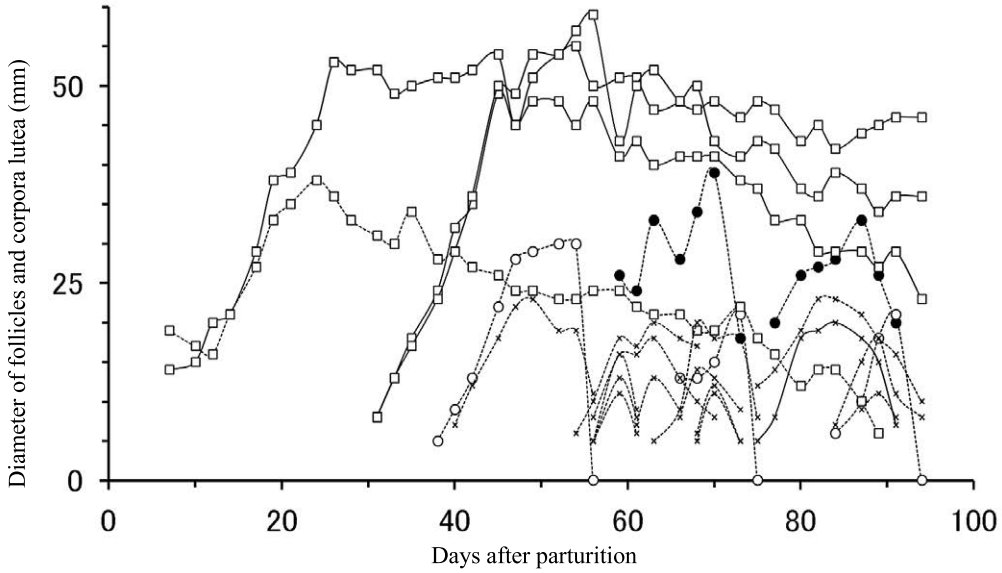

Fig. 3. Follicular dynamics and corpus luteum growth in a cow having developed follicular cysts
The diameters of the follicles and corpora lutea are plotted with solid lines for the right ovary and dotted lines for the left ovary[35].
□ : Anovulatory cyst, ○ : Ovulatory normal follicle, × : Other follicle, ● : Corpus luteum.

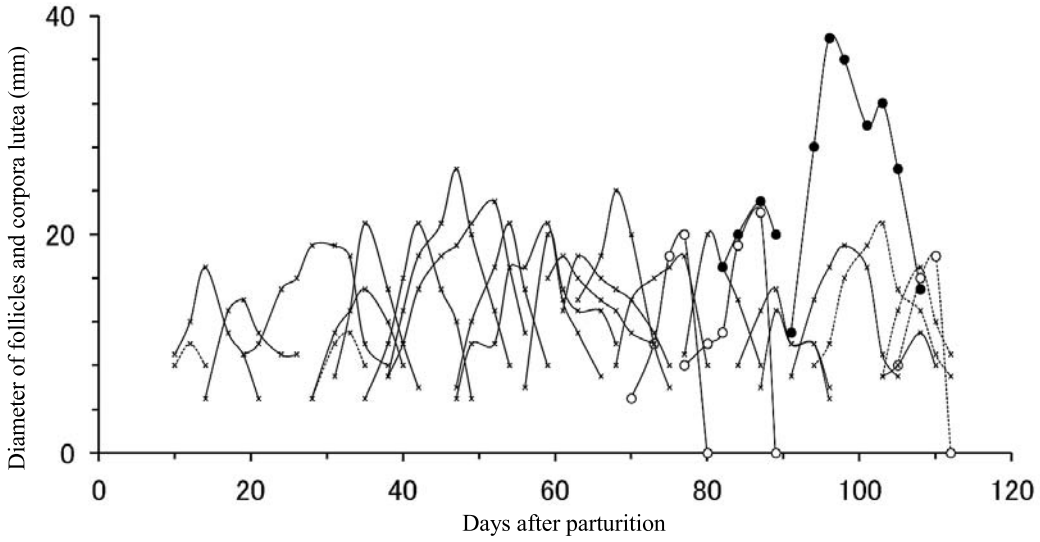

Fig. 4. Follicular dynamics and corpus luteum growth in a cow with repeated waves of follicles before the first postpartum ovulation
The diameters of the follicles and corpora lutea are plotted with solid lines for those emerging from the right ovary and dotted lines for those emerging from the left ovary[35].
○ : Ovulatory normal follicle, × : Other follicle, ● : Corpus luteum.

practice for experimental use, while the management factors under field conditions may affect these reproductive characteristics. Therefore, these results may not be directly applicable for understanding and improving farm-level reproductive performance. However, they represent the reproductive potential of modern high-yield dairy cows and provide a baseline to discuss their reproduction.

The summarized results in this review indicate that the exact detection of estrus, which often occurs during the late post-partum period, is an important factor for improving the reproductive performance of modern high-yield dairy cows. Measurement of the increase in an animal's activity around estrus using radiotelemetric pedometers will be one of the most reliable methods of detecting estrus[36,39]. The application of hormonal treatment programs, such as estrus or ovulation synchronization, is expected to be an effective means of overcoming the fertility problems of modern dairy herds. However, meta-analysis of hormonal synchronization datasets has demonstrated that the overall pregnancy rates are not improved by hormonal intervention[28]. It should be noted that the persistent employment of these techniques may hide deficiencies in the management of husbandry[44]. Furthermore, consumers have a growing interest in animal health and animal welfare issues, and ethical concerns regarding the use of hormones in addition to antibiotics, particularly if they are used as performance enhancers[30].

It is normal for mammals to store body fat during pregnancy and release it during early lactation regardless of the feeding level. A certain degree of negative energy balance in early lactation is inevitable, and this natural level of energy mobilization is presumed not to affect health and reproduction[7]. Although the negative energy balance that accompanies high milk production may be a cause of declining fertility directly or indirectly[37,38], it is important to determine the critical level of negative status as a threshold for declining fertility.

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Table 3. Productive and reproductive variables in cows with cystic follicles (CF), follicular cysts (FC) and repeated waves (RF)[35]

Variable	CF (n = 10)	FC (n = 5)	RF (n = 6)
305-day milk yield (kg)	9,241 ± 1,698[a]	11,693 ± 1,398[b]	10,038 ± 1,422[ab]
First ovulation (days postpartum)	27.4 ± 4.4[a]	45.4 ± 8.1[b]	64.2 ± 14.0[c]
First ovarian cycle (days)	17.8 ± 6.0[a]	28.3 ± 16.5[b]	9.5 ± 1.0[a]
Second ovarian cycle (days)	21.3 ± 1.2	23.5 ± 3.4[1]	19.2 ± 5.4
First estrus (days postpartum)	43.5 ± 5.0[a]	81.8 ± 7.0[b]	78.5 ± 6.4[b]
First insemination (days postpartum)	66.3 ± 6.2[a]	96.4 ± 26.6[b]	94.8 ± 14.0[b]
Number of services required to conceive (pregnancy rate, %)	2.10 ± 0.57[a] (100)	1.60 ± 0.89[ab] (100)	1.00 ± 0.00[b] (100)
Days open	98.0 ± 29.9	111.0 ± 38.4	94.8 ± 14.0
Uterine diameter involution (days postpartum)	19.3 ± 3.6[a]	18.6 ± 3.9[a]	14.3 ± 1.5[b]

Mean + SEM. [1]n= 4.
[a, b, c]Values within rows with different superscripts differ (P < 0.05).

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