Journal of Reproduction and Development, Vol. 69, No 1, 2023

Original Article

Seasonality in resumption of ovarian activity and reproductive performance of postpartum Holstein cows

Minoru SAKAGUCHI[1)], Hiromi KUSAKA[1)] and Takeshi YAMAZAKI[2)]

[1)]*Laboratory of Theriogenology, School of Veterinary Medicine, KITASATO University, Aomori 034-8628, Japan*
[2)]*Hokkaido Agricultural Research Center, National Agriculture and Food Research Organization (NARO), Hokkaido 062-0045, Japan*

Abstract. It has been suggested that domestication has turned cattle from seasonal breeders to annual breeders. This study examined the seasonal differences in early postpartum ovulation and subsequent reproductive performance in 542 Holstein cows. Cows displaying corpora lutea in the ovary at 26 days postpartum were defined as early ovulators. Factors affecting the occurrence of early ovulation were analyzed, and subsequent reproductive traits were compared between cows with and without early ovulation. During the summer season, 70.6% of calving cows showed early ovulation, whereas 48.7, 39.2, and 47.2% presented this condition in autumn, winter, and spring, respectively ($P < 0.01$). Third parity cows showed early ovulation more often than their first parity counterparts ($P < 0.05$). Cows with a 2.50 to 3.00 or > 3.00 body condition score (BCS) more frequently became early ovulators than those with BCSs < 2.50 ($P < 0.01$). Calving year was a risk factor, and uterine abnormalities were also often risk factors for early ovulation. The survival analysis showed that seasonal differences in the occurrence of early ovulation did not completely affect the time to first service and pregnancy. Proportional hazard regression analysis revealed that calving year, parity, and early ovulation were risk factors for the time to first service and that calving year was a risk factor for the time to pregnancy. In conclusion, domesticated dairy cows maintain seasonality in postpartum ovarian activity but not in subsequent fertility.

Key words: Early ovulation, Holstein, Parity, Reproductive performance, Seasonality

(**J. Reprod. Dev. 69:** 25–31, 2023)

The ancestor of domestic cattle, which is now extinct, was a seasonal breeder that calved in late spring [1], but domestication has turned cattle into annual breeders; however, some seasonality persists [2–4]. To enhance the conservation of wild Bovini cattle species, such as yak, water buffalo, gaur, and banteng, the reproductive seasonality of these species has been reviewed using assisted reproductive technologies and they have been defined as short-day breeders [5]. Concerning seasonality in cattle, Tucker (1982) reported that several physiological changes occur in response to two major climatic variables, ambient temperature and photoperiod [6]. Winter calving, high milk yield, and high parity are epidemiologically confirmed risk factors for reproductive disorders that delay insemination and conception in dairy cows [7]. Increasing parity in lactating dairy cows has also been reported to decrease fertility without significant changes to progesterone concentrations [8].

Postpartum resumption of ovarian activity, indicated by the occurrence of the first ovulation and estrus activity, is influenced by seasonality. A study in the 1950s indicated that dairy cows calving during summer (June 21 to September 20) tended to enter estrus earlier than those calving in the other seasons. In contrast, those calving during winter (December 21 to March 20) showed the longest intervals from parturition to the first estrus [9]. Winter-calving (October to March) cows had significantly longer intervals from parturition to first ovulation and estrus than summer-calving (April to September) cows [10]. These seasonal differences are considered a consequence of seasonal differences in gonadotropin secretion [11]. The prolonged anestrus period (later first estrus) in winter-calving cows is considered to lengthen the interval from parturition to insemination and conception [10]. Concerning the seasonal effects on reproductive performance, North Carolina Holstein cows that calved in summer (June to August) were two-thirds as likely to become pregnant compared to cows that calved in autumn (September to November) [12]. Another study from the southeast area of the United States showed that cows that calved during spring had the greatest number of days to first service and conception, whereas autumn-calving cows had the fewest. The highest pregnancy rate was observed during winter and the lowest during summer [13]. The seasonality of the interval from calving to conception in Holstein cows in the United States has been related to the extent of heat stress, which differs regionally [14]. In contrast, epidemiological results from Norway, which is located in the higher latitudes of the Northern hemisphere, show that the 60-day non-return rate of Norwegian Red cattle after single inseminations was higher in the summer than in the winter, suggesting higher reproductive performance in summer season when this breed is located at a higher latitude [15].

A negative relationship between parity and the number of days from calving to the first ovulation was reported in Holstein cows in Japan [16]. Those results showed that cows at greater than 3 parity ovulated approximately 2 weeks earlier than cows at first parity (mean 17.3 *vs*. 31.8 days, $P < 0.05$). No similar significant differences in the resumption of ovarian activity were observed in Uruguay between Holstein cows of different parities [17]. In combination with parity, the body condition of dairy cows at parturition influences the resumption of ovarian activity and subsequent reproductive

Received: August 31, 2022
Accepted: November 8, 2022
Advanced Epub: December 2, 2022

Correspondence: M Sakaguchi (e-mail: saka99@vmas.kitasato-u.ac.jp)

performance [18]. A negative relationship between milk yield and reproductive performance has been reported [12], and uterine infection could be an important cause of perturbed ovarian function during the postpartum period in dairy cows [19].

In our previous studies, delayed resumption of ovarian activity (first ovulation and estrus) had no detrimental effects on the subsequent reproductive performance of postpartum dairy cows in an experimental herd [20, 21]. We hypothesized that seasonality, parity at calving, year, BCS, number of calves, and uterine abnormality influence the occurrence of early postpartum ovulation in lactating dairy cows without affecting reproductive performance. This study aimed to identify the factors affecting early postpartum ovulation and analyze the relationship between early ovulation and subsequent reproductive performance.

Materials and Methods

Animals

This retrospective study was conducted at the Hokkaido Agricultural Research Center, National Agriculture and Food Research Organization (NARO, Sapporo, Japan, latitude 41.28 degrees north, with a subarctic climate), between October 1999 and June 2012 (annual average temperature; 8.3–9.8ºC). A total of 542 lactations (203 primiparous and 339 multiparous) of 248 Holstein dairy cows were examined. The average heifer age at the first service was 12–15 months.

All cows were housed in the same free-stall barn with a free-access soil paddock throughout the experimental period. The cows were fed a diet that met all maintenance, growth, and lactation requirements throughout the experimental period, following Japanese feeding standards (Agriculture, Forestry and Fisheries Research Council Secretariat, 1999). During summer (May to September), cows were pastured for 3–4 h per day, with the amount of food reduced to meet the nutritional requirements necessary for this period. The cows were milked twice daily (0900 and 1900 h). The rolling herd average amount of milk for sequential parities was 8,000 kg (first), 9,800 kg (second), 10,500 kg (third), and 10,700 kg (fourth and higher) per cow. The management of the cows and all procedures in the present study were performed in accordance with the Animal Experimental Guidelines of the National Agricultural Research Center for Hokkaido Region.

Ultrasound examination and measurement of BCS

The ovaries of all cows were monitored using a real-time linear array ultrasound scanner (SSD-620 with a 5 MHz probe or SSD-900 with a 7.5 MHz probe; ALOKA, Tokyo, Japan). The presence or absence of corpora lutea (CL) was confirmed for each cow at 26 days postpartum (D26: mean ± SD: 26.0 ± 0.7 days). In our previous study, the mean interval from calving to first ovulation was 30.9 days [20], with a median of 26 days in Holstein cows (Sakaguchi *et al*. unpublished data). Thus, the cow with CL (diameter ≥ 10 mm) at D26 was defined as an early ovulator in the present study. The uteri of all cows were monitored ultrasonographically concurrent with ovarian monitoring. When uterine fluid was confirmed or purulent vaginal discharge from the vulva was visualized, the cow was defined as having uterine dysfunction [22].

The average BCS was assessed by two or three independent observers based on a 5-point scale (where 1 = thin and 5 = fat) [23] simultaneously with ovarian monitoring.

Reproductive management

After a 45-day voluntary waiting period, cows exhibiting estrus were artificially inseminated using frozen-thawed bull semen for which normal fertility had been confirmed. The cows were observed twice daily for at least 30 minutes before milking. Those exhibiting standing estrus or mounting activity accompanied by other symptoms such as vaginal mucus discharge and swelling of the vulva were considered in estrus. When necessary, during the breeding period (46 to 300 days postpartum), prostaglandin F2 alpha (PGF2α) and gonadotropin-releasing hormone (GnRH) were used to treat reproductive dysfunctions such as delayed ovulation, persistent CL, developing cystic follicles, and uterine endometritis. No hormonal treatment, such as the Ovsynch program, was applied for the insemination of cows without reproductive dysfunction. Conception was confirmed by detecting a fetal heartbeat using ultrasonography 35–40 days after each artificial insemination (AI). The interval from calving to the first service of over 200 days and the interval from calving to conception of over 300 days were censored. The following reproductive performance outcomes were collected after calving: total submission rate to AI, interval from calving to first service, first service conception rate, final conception rate, number of AIs per conception, and interval from calving to conception. Table 1 presents the reproductive performance of the 542 lactations included in this analysis.

Statistical analysis

All statistical analyses were performed using the JMP statistical software (JMP Pro Statistics and Graphics Guide ver. 16.2.0; SAS Inst. Inc., Cary, NC). Statistical significance was set at $P \leq 0.05$, and continuous variables were presented as mean ± SD.

To analyze the factors contributing to the occurrence of early ovulation, a multivariate logistic regression model was used to calculate the odds ratio with a 95% confidence interval for various risk factors. The selection of explanatory variables was based on previous studies and included calving season, parity, BCS, calf number, and uterine dysfunction [10, 12, 17–19]. Calving season and parity

Table 1. Reproductive performance for 542 lactations

Item	Primiparous cows (203)	Multiparous cows (339)	Total (542)
Summation rate of AI, % (n)	84.7 (172)	82.6 (280)	83.4 (452)
Interval from calving to first service, mean ± SD (days)	85.6 ± 23.8	90.3 ± 27.0	88.5 ± 25.9 ranging from 45 to 220
First service conception rate, % (n)	56.4 (97/172)	58.2 (163/280)	57.5 (260/452)
Final conception rate, % (n)	93.0 (160)	93.6 (262)	93.4 (422)
Number of AIs per conception, mean ± SD	1.61 ± 0.94	1.60 ± 0.95	1.60 ± 0.94
Interval from calving to conception, mean ± SD (days)	107.4 ± 44.9	110.5 ± 42.0	109.3 ± 43.1 ranging from 45 to 296

were classified into four categories: calving season: spring (April to June, n = 144), summer (July to September, n = 136), autumn (October to December, n = 119), and winter (January to March, n = 143); and parity: 1 (n = 203), 2 (n = 141), 3 (n = 104), and ≥ 4 (n = 94). The recent mean lactation number of Holstein cows at removal was 3.23–3.45 in Japan [24]. To examine the association between postpartum energy status and the occurrence of early ovulation, BCS on D26 was grouped into three categories: < 2.50 (n = 78), 2.50–3.00 (n = 422) and > 3.00 (n = 42). Additionally, twin births could affect the resumption of postpartum reproductive activity; therefore, the number of calves delivered per cow was categorized into two grades: single (n = 521) and twin (n = 21). To consider genetic changes throughout the experimental period, the year was included in this analysis, which was grouped into four categories: period 1 (1999–2002, n = 143), period 2 (2003–2005, n = 153), period 3 (2006–2008, n = 121), and period 4 (2009–2012, n = 125). According to a previous report [22], uterine function was defined and categorized into two grades at D26: normal (n = 467) or abnormal (n = 75). Data on the presence or absence of CL at D26 were used to indicate early postpartum ovulation. The frequency of early ovulation was used as an outcome variable.

To analyze the impact of early ovulation on reproductive performance, survival curves were generated for the time to first service and time to pregnancy between cows with and without early ovulation using the Kaplan-Meier analysis. Curves of the cows displaying early ovulation were constructed relative to the cows without ovulation by plotting the values of time to first service and pregnancy against the proportion of cows in each group left to complete the calving conception period at each time point. A generalized Wilcoxon test was used to compare survival curves. Furthermore, Cox proportional hazard regression analyses were performed to evaluate the factors affecting the probability of insemination to 100 and 200 days postpartum and pregnancy to 200 and 300 days postpartum. All variables were applied to the models as mentioned above: calving season (spring, summer, autumn, and winter), years (period 1, 2, 3, and 4), parity (1, 2, 3, and ≥ 4), BCS (< 2.50, 2.50 to 3.00, and > 3.00), number of calves (single and twin), early ovulation (the presence or absence of CL at D26), and uterine function (normal and abnormal). The Wald test was performed, and if significance was detected, the HR and 95% confidence interval were calculated between the categories for each variable.

Results

Descriptive analysis

Figure 1 shows monthly histograms of the frequency of cows with early ovulation. The mean (SD) diameter of the detected CL was 27.9 (5.9) mm. The number of cows with early ovulation was higher in July, August, and September (71.4, 69.0, and 71.1%, respectively), whereas lower frequencies were observed in December, February, and April (34.3, 27.3, and 37.1%, respectively). The distribution of cows with early ovulation was significantly different between the seasons (P < 0.01). Cows that calved in summer had higher frequencies of early ovulation than those that calved in the other seasons. Figure 2 shows the histograms of the frequency of cows with early ovulation by parity. Cows in the third parity had the highest frequency of early ovulation; however, the distribution of cows with early ovulation did not differ among parities (P = 0.21).

Factors contributing to the occurrence of early ovulation

Table 2 presents the results of the multinomial logistic regression analysis of various risk factors for the occurrence of early ovulation. Compared to animals that calved in summer, the frequency of early ovulation was significantly lower in cows that calved in winter, spring, and autumn (P < 0.0001). Additionally, the cows in the third parity had 1.8 times higher frequencies of early ovulation (59.6%) than those in the first parity (46.8%, P < 0.05). As compared to period 1, the frequency of early ovulation was significantly higher in period

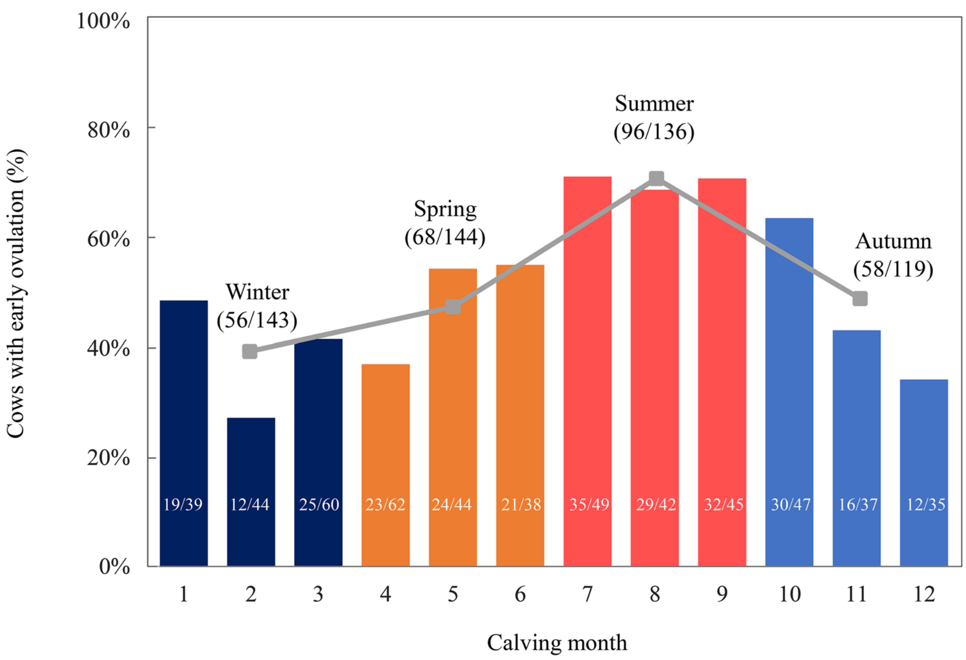

Fig. 1. Monthly histograms with seasonal variations[a] for the frequency of calving cows with early ovulation. [a] Winter calving: January to March, spring calving: April to June, summer calving: July to September, autumn calving: October to December.

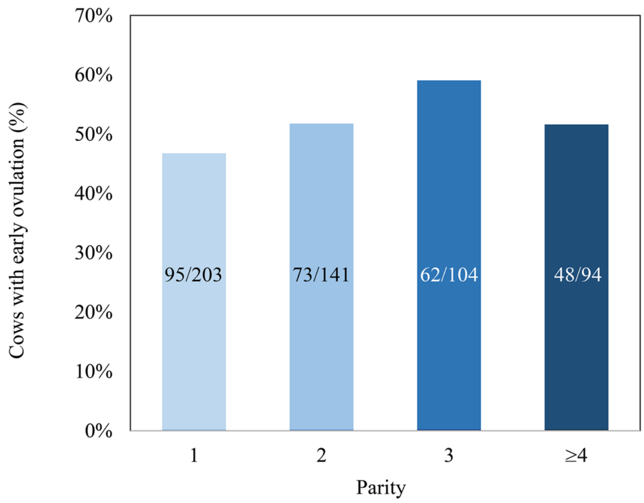

Fig. 2. Histogram for the frequency of cows with early ovulation by parity.

3 (49.7% *vs*. 61.2%, P < 0.05). The cows with BCSs of 2.50 to 3.00 and > 3.00 at calving became early ovulators more frequently than the cows with a BCS < 2.50 (P < 0.01). No significant differences were observed between groups in terms of the number of calves. The cows with abnormal uterine function tended to have a lower frequency of early ovulation compared with those with normal function (40.0% *vs*. 53.1%, P = 0.10).

Impact of early ovulation on reproductive performance

Figure 3 presents the Kaplan-Meier curves for the proportions of non-serviced and non-pregnant cows. Survival analysis demonstrated that the proportion of non-serviced and non-pregnant cows did not differ significantly between cows with and without early ovulation.

Table 3 shows the results of the Cox proportional hazard regression (HR) models for the time to first service to 100 and 200 days postpartum. Calving year and early ovulation were identified as risk factors for the time to first service (P < 0.01 and P < 0.05, respectively). Parity of the dams tended to be a risk factor for the time to first service to 100 days postpartum (P = 0.05) but not to 200 days postpartum. The other features did not appear to be risk factors. Compared to cows that calved in period 1, those that calved in periods 2, 3, and 4 had significantly higher HRs of time to first service to 100 and 200 days postpartum (HR = 1.9 and 1.7; 2.8 and 2.5; and 2.7 and 2.5, respectively, P < 0.01). Cows with early ovulation had significantly higher HRs for the time to first service to 100 and 200 days postpartum than those without early ovulation (HR=1.3 and 1.3, respectively, P < 0.05). This HR = 1.3 means that a cow with early ovulation had a chance of first service (true first service rate) of 130% relative to a cow without early ovulation. Compared to cows in the first parity, cows in the second and fourth parities had higher HRs of time to first service to 100 and 200 days postpartum (HR = 1.3 and 1.3, P = 0.06 and 0.05; and HR = 1.5 and 1.3, P = 0.03 and 0.07, respectively), but cows in the third parity showed no similar trend (HR = 1.0 and 1.1, P = 0.98 and 0.40, respectively).

Table 3 also presents the results of the Cox proportional hazard regression models for the time to pregnancy to 200 and 300 days postpartum. Calving year was identified as a risk factor for the time to pregnancy (P < 0.05); however, the other factors were not. Compared to cows that calved in period 1, those that calved in periods 2, 3, and 4 had a significantly higher HR of time to pregnancy to 200 and 300 days postpartum (HR = 1.4 and 1.3; 1.6 and 1.6; and 1.4 and 1.3, respectively, P < 0.05).

Table 2. Results of the multinomial logistic regression analysis for risk factors of 278 early ovulating cows

Factor	Category	% (n)	Odds ratio	95% CI [f]	P-value
Calving season [a]	Summer	70.6 (96/136)	Reference		
	Autumn	48.7 (58/119)	0.3368	0.1948–0.5822	< 0.0001
	Winter	39.2 (56/143)	0.2284	0.1334–0.3908	< 0.0001
	Spring	47.2 (68/144)	0.3161	0.1866–0.5354	< 0.0001
Parity of dam	1	46.8 (95/203)	Reference		
	2	51.8 (73/141)	1.3334	0.8330–2.1345	0.2306
	3	59.6 (62/104)	1.8466	1.0892–3.1309	0.0228
	≥ 4	51.1 (48/94)	1.3963	0.7947–2.4533	0.2457
Year [b]	Period 1	49.7 (71/143)	Reference		
	Period 2	54.9 (84/153)	1.4121	0.8666–2.3010	0.1660
	Period 3	61.2 (74/121)	1.9369	1.1462–3.2729	0.0135
	Period 4	39.2 (49/125)	0.7673	0.4538–1.2974	0.3230
BCS [c]	< 2.50	37.2 (29/78)	Reference		
	2.50 to 3.00	53.3 (225/422)	2.7892	1.5634–4.9763	0.0005
	> 3.00	57.1 (24/42)	3.4255	1.4207–8.2593	0.0061
Number of calves [d]	Single	52.0 (271/521)	Reference		
	Twin	33.3 (7/21)	0.5803	0.2059–1.6352	0.3032
Uterine function [e]	normal	53.1 (248/467)	Reference		
	abnormal	40.0 (30/75)	0.6356	0.3700–1.0917	0.1006

[a] Spring: April to June, summer: July to September, autumn: October to December, and winter: January to March. [b] Period 1: 1999 to 2002, period 2: 2003 to 2005, period 3: 2006 to 2008, and period 4: 2009 to 2012. [c] < 2.50, 2.50 to 3.00, and > 3.00 at D26. [d] Single and twin. [e] Abnormal: cows had either uterine fluid or purulent vaginal discharge from the vulva; normal: cows other than abnormal. [f] 95% confidence interval.

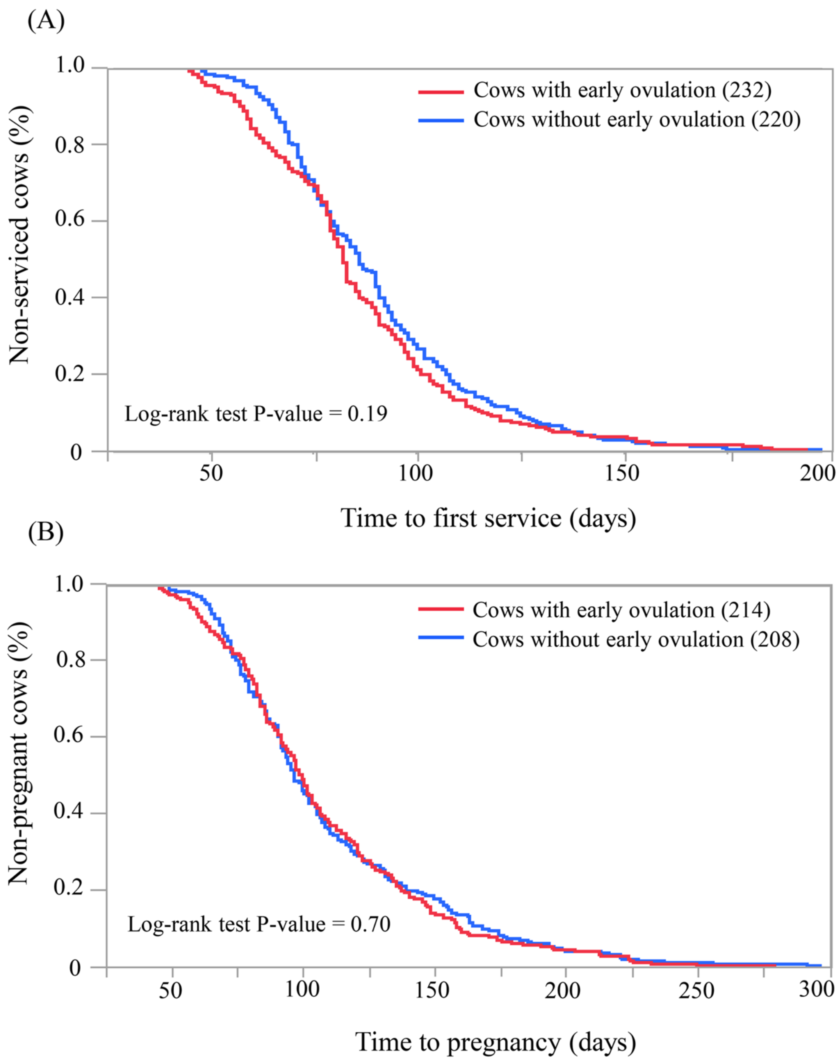

Fig. 3. Kaplan-Meier curves for proportions of non-serviced cows (A) and non-pregnant cows (B) with or without early ovulation.

Discussion

This study demonstrated that calving season and parity influence the resumption of ovarian activity, as indicated by the frequency of early postpartum ovulation. Seventy percent of summer-calving cows ovulated within D26, while 40 percent of winter-calving cows and less than half of spring- and autumn-calving cows ovulated within this period. This means that summer-calving cows are more likely to ovulate earlier than cows calving in other seasons. This is consistent with the results reported by Hansen and Hauser (1983) and suggests that the postpartum resumption of ovarian activity is still regulated via seasonal mechanisms [10]. A study conducted in New Zealand using cyclic beef cows showed that plasma concentrations of luteinizing hormone and prolactin differed by season, resulting in seasonal differences in ovarian activities, such as the pattern of follicular atresia and the diameter of healthy antral follicles [11]. Plasma prolactin concentration positively correlates with day length and ambient temperature, and high prolactin concentrations during spring and summer increase the frequency of luteinizing hormone pulses [6, 11].

Cows in third parity showed early ovulation the most frequently with approximately 1.8 times that of cows in first parity. Piñeyrúa *et al*. (2018) reported that the interval from calving to first ovulation in primiparous cows was not different from those in multiparous cows (parity = 3.3 ± 1.0) [17]. No information regarding the effect of parity sequence on postpartum ovarian activity was included in that study. According to the results concerning parity sequence [16], the days to first ovulation after calving in ≥ 3rd parity cows (17.3 ± 6.3 days) were significantly less than those in first parity cows (31.8 ± 8.3 days). However, they were not significantly different from those of the second-parity cows. Although that study analyzed data from a small number of cows (n = 16), the findings support our results. Generally, the body growth of Holstein cows terminates before their third calving when they have reached complete physiological maturity [25, 26]. Higher ovarian activity indicated by early ovulation may reflect fully mature ovarian function, as indicated by the developmental competence of oocytes in third parity cows [27]. Both mature body size and ovarian function in third lactation cows could accelerate the timing of postpartum ovulation.

Researchers at the University of Nottingham (latitude 52.95 degrees north) reported that beef cows calving in winter (November to April) were acyclic, which was defined as the time to the first rise in milk progesterone concentration of ≥ 3 ng/ml followed by a regular progesterone cycle, and this was significantly longer (70.8 days) than

Table 3. Hazard regression models of time to first service to 100 days ($P < 0.001$) and 200 days postpartum ($P < 0.001$), and time to pregnancy to 200 days ($P = 0.09$) and 300 days postpartum ($P = 0.10$)

Variable	Wald, χ^2	P-value
Time to first service to 100 days postpartum		
Calving season	6.0246	0.1104
Parity of dam	7.6957	0.0527
Years	53.375	< .0001
BCS	1.5005	0.4722
Number of calves	1.4375	0.2305
Uterine function	0.1727	0.6777
Early ovulation	4.8332	0.0279
Time to first service to 200 days postpartum		
Calving season	1.7085	0.6350
Parity of dam	5.3424	0.1484
Years	53.069	< .0001
BCS	1.4893	0.4749
Number of calves	0.8228	0.3644
Uterine function	0.1747	0.6760
Early ovulation	4.5310	0.0333
Time to pregnancy to 200 days postpartum		
Calving season	3.4122	0.3323
Parity of dam	0.5554	0.9066
Years	11.486	0.0094
BCS	2.7125	0.2576
Number of calves	1.0931	0.2958
Uterine function	0.6593	0.4168
Early ovulation	0.3227	0.5700
Time to pregnancy to 300 days postpartum		
Calving season	2.9042	0.4066
Parity of dam	0.3419	0.9520
Years	10.473	0.0149
BCS	3.2045	0.2014
Number of calves	1.5628	0.2112
Uterine function	0.3508	0.5537
Early ovulation	0.4743	0.4910

those calving in summer (May to October, 35.9 days) [2, 3]. Those authors suggested that both nutritional status and photoperiod may be important in determining the length of the acyclic period in beef cows. In the present study, while the number of cows with a low BCS (< 2.50) was small (78/542), low nutritional status may have affected the incidence of early ovulation.

Although differences in the seasonal feeding quality and nutritional status, such as grazing during the summer season, could influence certain reproductive traits, our results suggest that photoperiod mainly causes seasonal differences in early ovulation, as shown in beef cows [2]. Although the number of cows with uterine abnormalities on day D26 was small (75/542), uterine abnormalities might be a potential risk factor that needs to be determined by further investigation.

These results imply that the calving season and parity of dams should be considered when evaluating the experimental or epidemiological results of dairy reproduction when the timing of postpartum ovulation is used as an indicator of the reproductive performance of dairy cows.

The survival analysis results for non-serviced and non-pregnant cows demonstrated that early ovulators (within D26) were not serviced earlier and did not conceive earlier. In other words, early postpartum ovulation, which is influenced by seasonality, may have no significant impact on the subsequent reproductive performance of modern dairy cows, as previously reported [20]. Seasonal changes in postpartum ovarian activity of domesticated cows resulted in no seasonal changes in their reproductive potential. Gröhn and Rajala-Schultz (2000) also reported that the calving season had no significant effect on conception in New York Holstein cows [7], whereas North Carolina Holstein cows calving in winter or spring were more likely to become pregnant [12]. The experimental herd where the present results were obtained is located in Sapporo, in the northern part of Japan, at a latitude of 43°, which is similar to that of New York. At relatively high latitudes, it is speculated that the domestication process neutralized the seasonality of fertility of Holstein cows with the remaining seasonality of ovarian activities. However, proportional hazard regression analysis demonstrated that calving year, parity, and early ovulation were risk factors for the time of first service, and that calving year was a risk factor for the time to pregnancy. Large-scale studies analyzing trends and seasonality of reproductive performance have demonstrated that the calving year influences the fertility traits of dairy cattle [13, 15]. Although genetics, nutrition, climate, and other factors might have synergistic effects on yearly fertility traits in the present study, our results could not determine the details of these complex impacts.

These results indicate that the differences in the early resumption of ovarian activity have no significant impact on the reproductive performance of postpartum dairy cows but could be a risk factor for the timing of the first service in combination with parity differences.

In conclusion, the frequency of early postpartum ovulation differed seasonally in modern dairy cows and did not influence the time to first service or the time to pregnancy after calving. Domesticated dairy cows maintain seasonality in postpartum ovarian activity but not in subsequent fertility.

Conflict of interests: The authors declare that they have no conflict of interest.

Acknowledgement

This study did not receive any specific grants from funding agencies in the public, commercial, or not-for-profit sectors.

References

1. **Phillips CJC.** The development of the world's cattle production. *In:* Phillips CJC, editor. Principles of cattle reproduction. 2nd ed. Cambridge, UK: Cambridge University Press; 2010. p. 1–10.
2. **Peters AR, Riley GM.** Milk progesterone profiles and factors affecting postpartum ovarian activity in beef cows. *Anim Prod* 1982; **34**: 145–153.
3. **Peters AR, Riley GM.** Is the cow a seasonal breeder? *Br Vet J* 1982; **138**: 533–537. [Medline] [CrossRef]
4. **Setchell BP.** Domestication and reproduction. *Anim Reprod Sci* 1992; **28**: 195–202. [CrossRef]
5. **Mastromonaco GF, Gonzalez-Grajales AL.** Reproduction in female wild cattle: Influence of seasonality on ARTs. *Theriogenology* 2020; **150**: 396–404. [Medline] [CrossRef]
6. **Tucker HA.** Seasonality in cattle. *Theriogenology* 1982; **17**: 53–59. [CrossRef]
7. **Gröhn YT, Rajala-Schultz PJ.** Epidemiology of reproductive performance in dairy cows. *Anim Reprod Sci* 2000; **60–61**: 605–614. [Medline] [CrossRef]
8. **Balendran A, Gordon T, Pretheeban T, Singh R, Perera R, Rajamahendran R.** Decreased fertility with increasing parity in lactating dairy cows. *Can J Anim Sci* 2008; **88**: 425–428. [CrossRef]
9. **Buch NC, Tyler WJ, Casida LE.** Postpartum estrus and involution of the uterus in an experimental herd of Holstein-Friesian cows. *J Dairy Sci* 1955; **38**: 73–79. [CrossRef]
10. **Hansen PJ, Hauser ER.** Genotype x environmental interactions on reproductive traits of bovine females. III. Seasonal variation in postpartum reproduction as influenced by genotype, suckling and dietary regimen. *J Anim Sci* 1983; **56**: 1362–1369. [Medline]

[CrossRef]
11. **McNatty KP, Hudson N, Gibb M, Henderson KM, Lun S, Heath D, Montgomery GW.** Seasonal differences in ovarian activity in cows. *J Endocrinol* 1984; **102**: 189–198. [Medline] [CrossRef]
12. **Farin PW, Slenning BD, Correa MT, Britt JH.** Effects of calving season and milk yield on pregnancy risk and income in North Carolina Holstein cows. *J Dairy Sci* 1994; **77**: 1848–1855. [Medline] [CrossRef]
13. **de Vries A, Risco CA.** Trends and seasonality of reproductive performance in Florida and Georgia dairy herds from 1976 to 2002. *J Dairy Sci* 2005; **88**: 3155–3165. [Medline] [CrossRef]
14. **Oseni S, Misztal I, Tsuruta S, Rekaya R.** Seasonality of days open in US Holsteins. *J Dairy Sci* 2003; **86**: 3718–3725. [Medline] [CrossRef]
15. **Refsdal AO.** Reproductive performance of Norwegian cattle from 1985 to 2005: trends and seasonality. *Acta Vet Scand* 2007; **49**: 5. [Medline] [CrossRef]
16. **Tanaka T, Arai M, Ohtani S, Uemura S, Kuroiwa T, Kim S, Kamomae H.** Influence of parity on follicular dynamics and resumption of ovarian cycle in postpartum dairy cows. *Anim Reprod Sci* 2008; **108**: 134–143. [Medline] [CrossRef]
17. **Morales Piñeyrúa JT, Fariña SR, Mendoza A.** Effects of parity on productive, reproductive, metabolic and hormonal responses of Holstein cows. *Anim Reprod Sci* 2018; **191**: 9–21. [Medline] [CrossRef]
18. **Meikle A, Kulcsar M, Chilliard Y, Febel H, Delavaud C, Cavestany D, Chilibroste P.** Effects of parity and body condition at parturition on endocrine and reproductive parameters of the cow. *Reproduction* 2004; **127**: 727–737. [Medline] [CrossRef]
19. **Williams EJ, Fischer DP, Noakes DE, England GCW, Rycroft A, Dobson H, Sheldon IM.** The relationship between uterine pathogen growth density and ovarian function in the postpartum dairy cow. *Theriogenology* 2007; **68**: 549–559. [Medline] [CrossRef]
20. **Sakaguchi M, Sasamoto Y, Suzuki T, Takahashi Y, Yamada Y.** Postpartum ovarian follicular dynamics and estrous activity in lactating dairy cows. *J Dairy Sci* 2004; **87**: 2114–2121. [Medline] [CrossRef]
21. **Sakaguchi M.** Oestrous expression and relapse back into anoestrus at early postpartum ovulations in fertile dairy cows. *Vet Rec* 2010; **167**: 446–450. [Medline] [CrossRef]
22. **Kusaka H, Hasegawa R, Nishimoto N, Kawahata M, Miura H, Kikuchi M, Sakaguchi M.** Comparison of diagnostic methods for uterine health in dairy cattle on different days postpartum. *Vet Rec* 2020; **186**: 91. [Medline] [CrossRef]
23. **Edmonson AJ, Lean J, Weaver LD, Farver T, Webster G.** A body condition scoring chart for Holstein cows. *J Dairy Sci* 1989; **72**: 68–78. [CrossRef]
24. **Sasaki O, Takeda H, Nishiura A.** Estimation of the economic value of herd-life length based on simulated changes in survival rate. *Anim Sci J* 2019; **90**: 323–332. [Medline] [CrossRef]
25. **Coffey MP, Hickey J, Brotherstone S.** Genetic aspects of growth of Holstein-Friesian dairy cows from birth to maturity. *J Dairy Sci* 2006; **89**: 322–329. [Medline] [CrossRef]
26. **Kawakami J, Baba T, Gotoh Y, Oka T, Kawahara T.** Annual phenotypic and genetic changes of growth pattern for body measurement traits in Holstein females. *Nihon Chikusan Gakkaiho* 2021; **92**: 149–158. (In Japanese). [CrossRef]
27. **Snijders SEM, Dillon P, O'Callaghan D, Boland MP.** Effect of genetic merit, milk yield, body condition and lactation number on in vitro oocyte development in dairy cows. *Theriogenology* 2000; **53**: 981–989. [Medline] [CrossRef]