Journal of Reproduction and Development, Vol. 66, No 5, 2020

—Original Article—

Relationship between sire predicted transmitting ability for daughter pregnancy rate and daughter's reproductive performance and milk production in Japanese dairy herds

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Abstract. Modern genetic improvement in dairy cattle is directed towards improvement of fertility; however, reproduction traits generally exhibit a genetic antagonism with milk yield. Herein, we aimed to clarify the effects of sire predicted transmitting ability (PTA) for daughter pregnancy rate (DPR) on the reproductive performance and milk yield of daughters in Japanese dairy herds. We conducted a retrospective cohort study on four dairy herds in eastern Hokkaido, Japan, using 1,612 records from 1,018 cows with first, second, or third calvings between March 2015 and September 2018. First, we classified sires into three groups based on the tertile value of their DPR estimate: ≤ −2.2 (low), −2.1 to −0.4 (intermediate), and ≥ −0.3 (high). Subsequently, we compared the sire PTA estimates, reproductive performance, and milk production among DPR groups for each parity of the daughters. In the first and second parity, the hazard of pregnancy by 200 days postpartum was highest in cows from the high-DPR group ($P < 0.05$); in the third parity, it was unaffected by DPR group. Although sire PTA for milk production in cows from the low-DPR group was highest, actual milk production was unaffected by DPR group regardless of parity. Our findings demonstrate that using sires with PTA for high fertility can enable farmers to improve reproductive performance without decreasing milk yield in Japanese dairy herds. However, it should be noted that sires with PTA for high fertility are at risk for reducing the genetic merit for milk production.

Key words: Daughter pregnancy rate (DPR), Fertility, Genetic selection, PTAM, Retrospective cohort study

(**J. Reprod. Dev. 66:** 445–452, 2020)

Good reproductive performance is essential for profitable dairy production systems; however, declines in the reproductive performance of dairy cattle have previously occurred in multiple regions worldwide [1]. Opposing this trend, recent data indicate that reproductive performance in the United States is improving, despite ongoing increases in milk production per cow [2, 3]. Underlying these data is the change in modern genetic selection programs that emphasize health and fitness traits, such as fertility, instead of milk production only [4].

Genetic evaluations for daughter pregnancy rate (DPR) —the fertility value defined for routine genetic evaluation by the Animal Improvement Programs Laboratory (US Department of Agriculture)— were introduced in the United States in 2003 [5]. A downward trend in fertility stabilized in the first year that these genetic evaluations became available, after which the selection response for DPR dramatically increased [6]. Reproduction traits generally exhibit low heritability in dairy cattle [7–9]; however, the coefficient of variation of reproductive traits is very large [8]. Indeed, several reports have indicated that genetic selection for improved daughter fertility is possible in dairy cattle [1, 8].

Unlike in the United States, the reproductive performance of dairy herds in Japan has not undergone recent improvement. According to data presented by the Livestock Improvement Association of Japan [10], the average calving interval of Japanese dairy herds has remained at more than 430 days. Genetic evaluation of "days open" in bulls was incorporated into the Nippon Total Profit index (NTP) as a fertility component in 2015 [11], thus, although behind other countries, genetic improvement of Japanese dairy cattle has been directed towards improvement of fertility. Nevertheless, reproductive performance in Japanese dairy cattle has not been improved, despite years having passed since the NTP was modified.

Reproductive performance in Japanese dairy cattle has not changed, in part, because many farmers are concerned that milk yields will decrease as a result of genetic improvement for fertility. Indeed, reproduction traits do generally exhibit genetic antagonism for milk yield [7–9]; however, conjoint improvement for milk yield and reproductive performance is possible [12]. Furthermore, Weigel (2006) indicated that the negative estimated genetic correlation between milk yield and female fertility is small enough to ensure an availability of sires with highly productive and highly fertile daughters [13]. To motivate Japanese dairy farmers towards genetic improvement for fertility, it must be shown (based on records of Japanese dairy herds) that it is possible to improve reproductive performance using sires with predicted transmitting ability (PTA)

Received: April 23, 2020
Accepted: June 8, 2020
Advanced Epub: June 28, 2020

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for high fertility without decreasing milk yield. As this relationship has not yet been examined in Japanese dairy herds, we carried out a retrospective cohort study to clarify the effects of sire PTA for DPR on the reproductive performance and milk yield of daughters.

Material and Methods

Study design

This was a retrospective cohort study conducted on four dairy herds in eastern Hokkaido, Japan. Herd sizes ranged from 90 to 213 milking cows. Herd-selection criteria included a free-stall facility for fresh cows, use of the same total mixed ration diet (TMR) center, quality of available records, subscription to the Hokkaido Dairy Milk Recording and Testing Association, and an established relationship with the local agricultural cooperative society to ensure the consistency and integrity of the data used.

Animals

Cows were fed a TMR consisting of corn silage, grass silage, soybean meal, corn grain, and concentrate, sourced from the same TMR center, and had free access to water. The TMR was formulated by professional nutritionists to meet the energy and protein requirements of cows producing 35 kg of milk with 4% fat each day; following the guidelines of the National Research Council Committee on Animal Nutrition [14]. Cows were milked twice daily. The 305-day milk yield ranged from 9,683 to 10,771 kg. Except for a few cases of embryo transfer (about 0.2%), artificial insemination (AI) was performed in all herds after a voluntary waiting period (VWP) that ranged from 50 to 60 days. The percentages of timed AI were about 80% and 30% of total AI numbers, in Herd A and Herds B–D, respectively. More specifically, timed AI was the main method for AI in Herd A; AI without hormone treatment was only performed in cases in which natural estrus was detected. In Herds B–D, timed AI was performed only when a veterinarian judged it to be necessary, by fresh check or pregnancy diagnosis. Prostaglandin F2α (PGF2α) or an analog, GnRH products, and progesterone releasing devices were used for estrus induction and timed AI.

Data collection

Data from milking cows were collected from the Hokkaido Dairy Milk Recording and Testing Association. For each cow, we collected information on herd, parity, calving date, production (milk, fat, and protein yield), first-service date and conception, calving to conception interval, culling date, and sire ID. For milking yield data, we used the estimated values of 305-day milk, fat, and protein yields, which were calculated from the monthly measured values, after days in milk first exceeded 200. We computed the 305 energy-corrected milk yield (ECM) using the following formula: (0.327 × milk in kg) + (12.95 × milk fat in kg) + (7.65 × milk protein in kg) [15]. The ECM expresses the amount of energy in milk, based on the weight of milk, fat, and protein standardized to 3.5% fat and 3.2% protein. The AI and pregnancy statuses of the surveyed cows were followed up until 200 days after calving or until the date of culling (if ≤ 200 days). Pregnancy diagnoses were made by non-return methods, and a cow was assumed to be pregnant if AI was not performed 70 days after a previous AI.

Sire PTA data for total performance index (TPI), DPR, and milk production (PTAM) were collected from the ST Genetics website (https://www.stgen.com/, accessed 31st March 2020) and the Council of Dairy Cattle Breeding website (https://www.uscdcb.com/, accessed 31st March 2020). We used the evaluated values of sire PTA released in December 2019.

Selection of data

Cow data for this study were collected for the first, second, or third calvings of cows from March 2015 to September 2018. If a cow had calved twice or three times during this period, the records from each parity were used. From an initially selected 1,713 records from first to third parity (Herd A, n = 262; Herd B, n = 716; Herd C, n = 453; Herd D, n = 282) of 1,065 cows (Herd A, n = 169; Herd B, n = 440; Herd C, n = 281; Herd D, n = 175), 83 records from cows that were culled within the first 50 days after calving were excluded. Also excluded were 18 records from 16 cows whose sire PTA estimates were not released in December 2019. Accordingly, 1,612 records (Herd A, n = 262; Herd B, n = 716; Herd C, n = 453; Herd D, n = 282) from 1,018 cows (Herd A, n = 161; Herd B, n = 421; Herd C, n = 265; Herd D, n = 171) were included in our study. For milking yield data, we used 1,459 records that included milking production data when days in milk exceeded 200.

Statistical analysis

The 1,018 cows in this study derived from 163 sires. We classified these sires into three groups based on their DPR estimate's tertile value: ≤ −2.2 (low), −2.1 to −0.4 (intermediate), and ≥ −0.3 (high). Reliabilities ranged from 0.41 to 0.99 (0.80 ± 0.17, mean ± SD), from 0.41 to 0.99 (0.72 ± 0.21), and from 0.47 to 0.99 (0.82 ± 0.19) for the low-, intermediate-, and high-DPR groups, respectively. We then compared several characteristics for each parity of the daughters among the groups; namely, sire PTA estimates, reproductive performance, and milk production.

A non-parametric Kruskal-Wallis test followed by Steel–Dwass test was used to compare sire PTA estimates among the groups and herds. Spearman's correlation coefficient was calculated between sire DPR and PTAM.

A generalized linear model (GLM) using a logit link function for binary data was used to quantify the association between sire DPR classification or herd (explanatory variable) and conception rate at first service, or pregnancy rate by 100 and 200 days postpartum (objective variable). We included calving month and year as explanatory variables in the model. If we set sire DPR classification as an explanatory variable, we added herd and the interaction effect between herd and DPR classification to the explanatory variables. A least significant difference (LSD) test served as a post-hoc test when a significant difference was detected due to DPR classification or herd.

We used survival analysis with Cox's proportional hazards model to determine the association of DPR classification or herd (explanatory variable) and calving to first service or conception intervals (objective variable), thereby estimating the possible hazards associated with a cow being inseminated or pregnant at a given time. We used the interval in days between calving and first insemination or pregnancy as the time variable in the model. Cows were right-censored if not diagnosed as being inseminated or pregnant before 200 days postpartum. We included calving month and year as explanatory variables in the model. If we set sire DPR classification as an explanatory variable, we added herd and the interaction effect between herd and DPR classification to the explanatory variables. An LSD test served as a post-hoc test when a significant difference was detected due to DPR classification or herd.

A GLM using an identity link function for Gaussian traits was used to quantify the association between sire DPR classification or herd (explanatory variable) and 305-day milk yield or 305 ECM yield (objective variable). We included calving month and year as explanatory variables in the model. If we set sire DPR classification as an explanatory variable, we added herd and the interaction effect between herd and DPR classification to explanatory variables. An LSD test served as a post-hoc test when a significant difference was detected due to herd.

We performed all analyses using the software R, version 3.6.3 for Windows [16]. In all analyses, we considered a P-value of < 0.05 to be statistically significant.

Results

Sire DPR, TPI, and PTAM are summarized by herd in Table 1. While sire DPR was highest in Herd A, sire PTAM in Herd A was the lowest among the herds. Figure 1 shows the frequency distribution of sire DPR in the 1,018 cows enrolled in our study. The mean sire DPR was −1.7 ± 2.6. The percentage of cows with a sire DPR of more than zero was 23.2% (236/1,018). Figure 2 shows the DPR classification by herd. In Herd D, the percentage of cows in the low-DPR group was about 65%; the percentages of cows in the low-DPR group in the other herds were 40–50%. Figure 3 shows the distribution of herds by parity, and demonstrates that Herds A, B, C, and D were similarly represented in the parities analyzed.

Tables 2 to 4 summarize by parity the associations between several parameters— including sire PTA estimates, reproductive performance, and milk production— and DPR classification. Among the three DPR groups, sire TPI of cows from the high-DPR group was higher than that of cows from the low-DPR group (P < 0.01). Conversely, sire PTAM of cows was higher in the low-DPR group than in the high-DPR group (P < 0.01). In the first and second parities, conception rate at first service and pregnancy rates by 100 and 200 days postpartum were the highest in the high-DPR group (P < 0.05); however, reproductive performance values in the third parity were not different between DPR groups. Milk production was unaffected by DPR group regardless of parity. Moreover, an interaction effect between herd and DPR classification, on all objective variables, was not detected regardless of parity.

Figures 4 and 5 show survival curves for the interval to first insemination and pregnancy, respectively, in cows from the low-, intermediate-, and high-DPR groups. In the first and third parities, the probability of insemination by 200 days postpartum did not differ between DPR groups. In the second parity, DPR group had an effect (P < 0.05), but the hazard of the first insemination after calving in cows from the high DPR-group was similar to cows from other groups. In the first and second parities, the rate of pregnancy by 200 days postpartum was highest in cows from the high-DPR group (P < 0.05); it did not differ between DPR groups in the third parity.

Figure 6 shows the negative correlation found between sire DPR and PTAM (r = −0.204, P < 0.01). Around 36%, 25%, and 15% of sires in the low-, intermediate-, and high-DPR groups, respectively, had a high PTAM of more than 1,000.

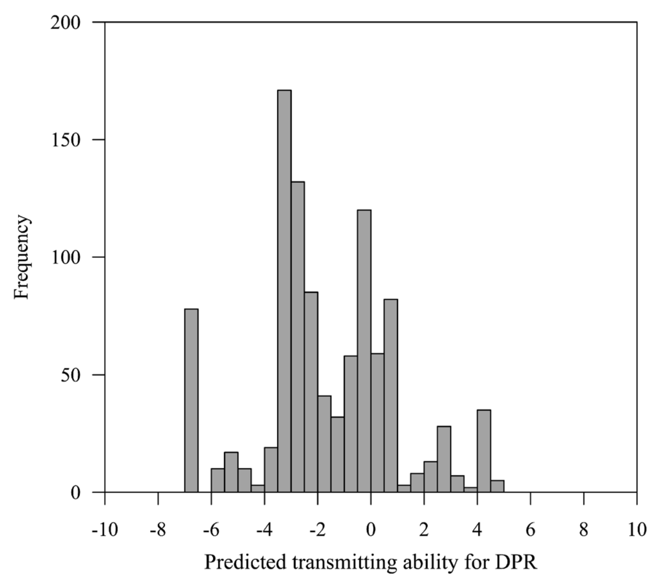


Fig. 1. The frequency distribution of sire predicted transmitting ability for daughter pregnancy rate (DPR) in 1,018 cows.

Table 1. Sire predicted transmitting ability (PTA) estimates for daughter pregnancy rate (DPR), total performance index (TPI), and milk production (PTAM) in lactating dairy cows by herd

Herds	Number of cows	Sire PTA estimates		
		DPR	TPI	PTAM
A	161	−1.3 [a] (−6.7 to 4.9)	1,748 [a] (1,374 to 2,366)	494 [b] (−1,047 to 2,051)
B	421	−2.2 [a] (−6.7 to 4.9)	1,705 [ab] (1,217 to 2,366)	719 [a] (−1,047 to 1,741)
C	265	−2.0 [a] (−6.7 to 4.9)	1,733 [a] (1,195 to 2,366)	494 [ab] (−808 to 1,917)
D	171	−2.7 [b] (−6.7 to 4.4)	1,673 [b] (1,348 to 2,228)	719 [ab] (−1,047 to 1,693)
P-value		< 0.01	< 0.01	< 0.01

Values of sire PTA estimates are medians (with minimum to maximum values in parentheses). [a, b] Values with different superscripts within the same column are significantly different (P < 0.05).

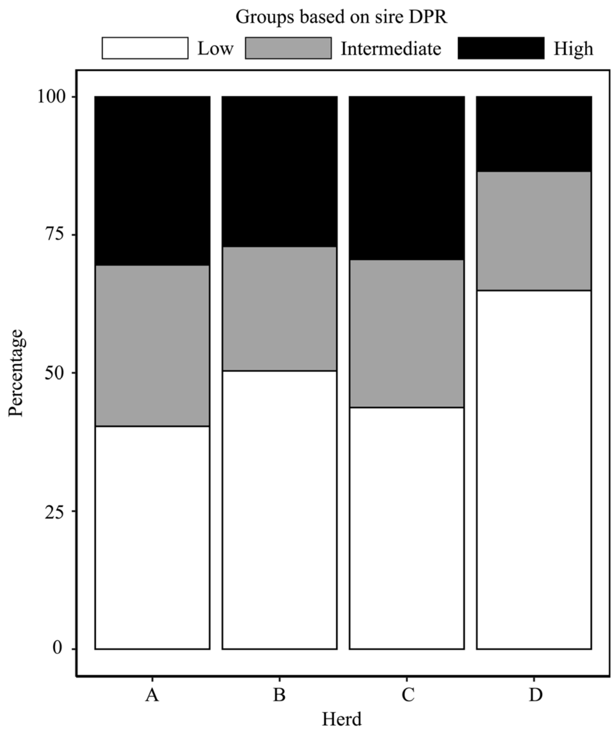


Fig. 2. The percentages in each herd of the groups based on sire predicted transmitting ability estimates for daughter pregnancy rate (DPR): ≤ −2.2 (low), −2.1 to −0.4 (intermediate), and ≥ −0.3 (high). Herd A, n = 161; Herd B, n = 421; Herd C, n = 265; Herd D, n = 171.

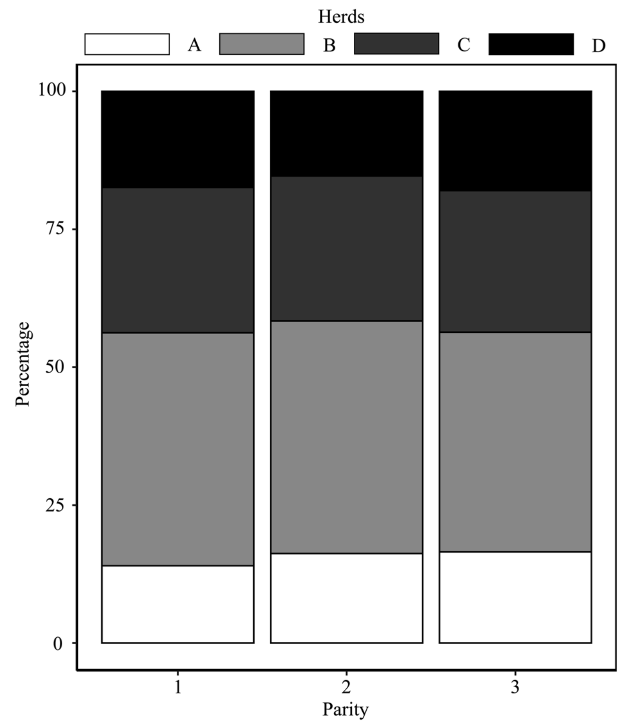


Fig. 3. The representation of each herd in each parity. First parity, n = 706; second parity, n = 567; third parity, n = 339.

Table 2. Characteristics of sire predicted transmitting ability (PTA) estimates for daughter pregnancy rate (DPR), total performance index (TPI), and milk production (PTAM), reproductive performance, and actual milk production in first-parity cows with low (≤ −2.2), intermediate (−2.1 to −0.4), or high (≥ −0.3) sire daughter pregnancy rates

Variable		Groups based on sire DPR		
		Low	Intermediate	High
Number of cows		404	91	211
Sire PTA estimates	DPR	−3.2 [c] (−6.7 to −2.2)	−1.3 [b] (−2.1 to −0.4)	−0.8 [a] (−0.3 to 4.9)
	TPI	1,658 [b] (1,217 to 2,208)	1,950 [a] (1,302 to 2,363)	1,893 [a] (1,551 to 2,366)
	PTAM	845 [a] (−808 to 2,051)	851 [a] (−946 to 1,917)	303 [b] (−638 to 1,645)
Reproductive performance	Calving to first service interval (days)	66 (22 to 183)	63 (32 to 145)	64 (27 to 137)
	Conception rate at first service (%)	21.4 [b]	15.9 [b]	29.7 [a]
	Pregnancy rate by 100 days postpartum (%)	32.4 [b]	25.2 [b]	52.1 [a]
	Pregnancy rate by 200 days postpartum (%)	66.6 [b]	68.1 [b]	79.6 [a]
	Calving to conception interval (days)	103 [a] (35 to 200)	115 [a] (32 to 195)	88[b] (27 to 200)
Number of cows obtained milking data		377	81	191
Actual milk production	305-day milk (kg)	9,688 (6,173 to 12,802)	9,581 (6,112 to 13,036)	9,410 (6,287 to 11,772)
	305-day energy-corrected milk (kg)	10,362 (6,927 to 13,363)	10,415 (6,816 to 14,086)	10,230 (6,644 to 12,422)

Values of sire PTA estimates, calving to first service or conception interval, and milking data are medians (with minimum to maximum values in parentheses). [a, b, c] Values with different superscripts within the same row are significantly different ($P < 0.05$).

Table 3. Characteristics of sire predicted transmitting ability (PTA) estimates for daughter pregnancy rate (DPR), total performance index (TPI), and milk production (PTAM), reproductive performance, and actual milk production in second-parity cows with low (≤ −2.2), intermediate (−2.1 to −0.4), or high (≥ −0.3) sire daughter pregnancy rates

Variable		Groups based on sire DPR		
		Low	Intermediate	High
Number of cows		256	150	161
Sire PTA estimates	DPR	−3.2 [c] (−6.7 to −2.2)	−0.5 [b] (−2.1 to −0.4)	0.8 [a] (−0.3 to 4.4)
	TPI	1,618 [c] (1,217 to 2,140)	1,721 [b] (1,195 to 2,325)	1,768 [a] (1,454 to 2,096)
	PTAM	719 [a] (−494 to 1,741)	44 [c] (−946 to 1,685)	303 [b] (−1,047 to 1,645)
Reproductive performance	Calving to first service interval (days)	72 (26 to 179) [a]	61 (26 to 156) [b]	67 (32 to 186) [ab]
	Conception rate at first service (%)	18.3 [b]	20.5 [ab]	30.3 [a]
	Pregnancy rate by 100 days postpartum (%)	25.4 [b]	32.7 [ab]	40.4 [a]
	Pregnancy rate by 200 days postpartum (%)	57.0 [b]	62.7 [ab]	72.7 [a]
	Calving to conception interval (days)	120 [a] (44 to 198)	102 [b] (26 to 200)	100 [b] (33 to 199)
Number of cows obtained milking data		227	136	150
Actual milk production	305-day milk (kg)	10,928 (5,878 to 15,053)	11,041 (6,514 to 15,118)	10,680 (5,285 to 13,734)
	305-day energy-corrected milk (kg)	11,646 (6,092 to 15,305)	12,007 (6,971 to 16,354)	11,555 (5,867 to 14,911)

Values of sire PTA estimates, calving to first service or conception interval, and milking data are medians (with minimum to maximum values in parentheses). [a, b, c] Values with different superscripts within the same row are significantly different ($P < 0.05$).

Table 4. Characteristics of sire predicted transmitting ability (PTA) estimates for daughter pregnancy rate (DPR), total performance index (TPI), and milk production (PTAM), reproductive performance, and actual milk production in third-parity cows with low (≤ −2.2), intermediate (−2.1 to −0.4), or high (≥ −0.3) sire daughter pregnancy rates

Variable		Groups based on sire DPR		
		Low	Intermediate	High
Number of cows		116	135	88
Sire PTA estimates	DPR	−3.2 [c] (−6.7 to −2.2)	−0.6 [b] (−2.1 to −0.4)	0.8 [a] (−0.3 to 4.4)
	TPI	1,618 [c] (1,217 to 2,140)	1,702 [b] (1,387 to 2,325)	1,768 [a] (1,454 to 2,096)
	PTAM	689 [a] (−494 to 1,741)	44 [b] (−367 to 1,685)	288 [b] (−1,047 to 1,645)
Reproductive performance	Calving to first service interval (days)	75 (33 to 175)	70 (33 to 160)	66 (25 to 199)
	Conception rate at first service (%)	17.6	19.7	13.8
	Pregnancy rate by 100 days postpartum (%)	22.4	25.2	25.0
	Pregnancy rate by 200 days postpartum (%)	58.6	61.5	61.4
	Calving to conception interval (days)	115 (41 to 197)	118 (37 to 198)	117 (39 to 200)
Number of cows obtained milking data		101	116	80
Actual milk production	305-day milk (kg)	11,243 (7,480 to 15,067)	11,444 (6,679 to 15,637)	11,333 (5,858 to 15,321)
	305-day energy-corrected milk (kg)	11,812 (8,191 to 15,784)	12,276 (7,331 to 16,349)	12,116 (6,201 to 15,795)

Values of sire PTA estimates, calving to first service or conception interval, and milking data are medians (with minimum to maximum values in parentheses). [a, b, c] Values with different superscripts within the same row are significantly different ($P < 0.05$).

Discussion

The objective of our study was to clarify the effects of sire DPR on the reproductive performance and milk production of cows in Japanese dairy herds. To the best of our knowledge, this is the first study to identify an obvious positive effect of sire DPR on reproductive performance until second parity in Japanese dairy herds. This result agrees with previous studies from the United States [17] and Canada [18]. Moreover, our analysis indicated that daughters in the high-DPR group produced a similar volume of milk to those in the low-DPR group. This concurs with previous reports demonstrating that the genetic capacity for fertility does not have an inhibitory effect on actual milk production [19,20]. Herein, sire DPR varied from −6.7 to 4.9. Although this variation is smaller than that in the Canadian report [18], it is in a similar range to the variation in the US report [17]. On the basis of these data, it is thus reasonable to assume that the reproductive performance of daughters can be improved using sires available in Japan, without reducing milk production.

Early resumption of cyclicity is associated with genetic merit for good fertility [20], and early postpartum ovulation enables farmers to perform prompt first service [21]. However, in our study the interval from calving to first insemination of cows in the high-DPR group was not shorter than that of cows in the low-DPR group. This result is also consistent with a previous report [17]. The timing of first

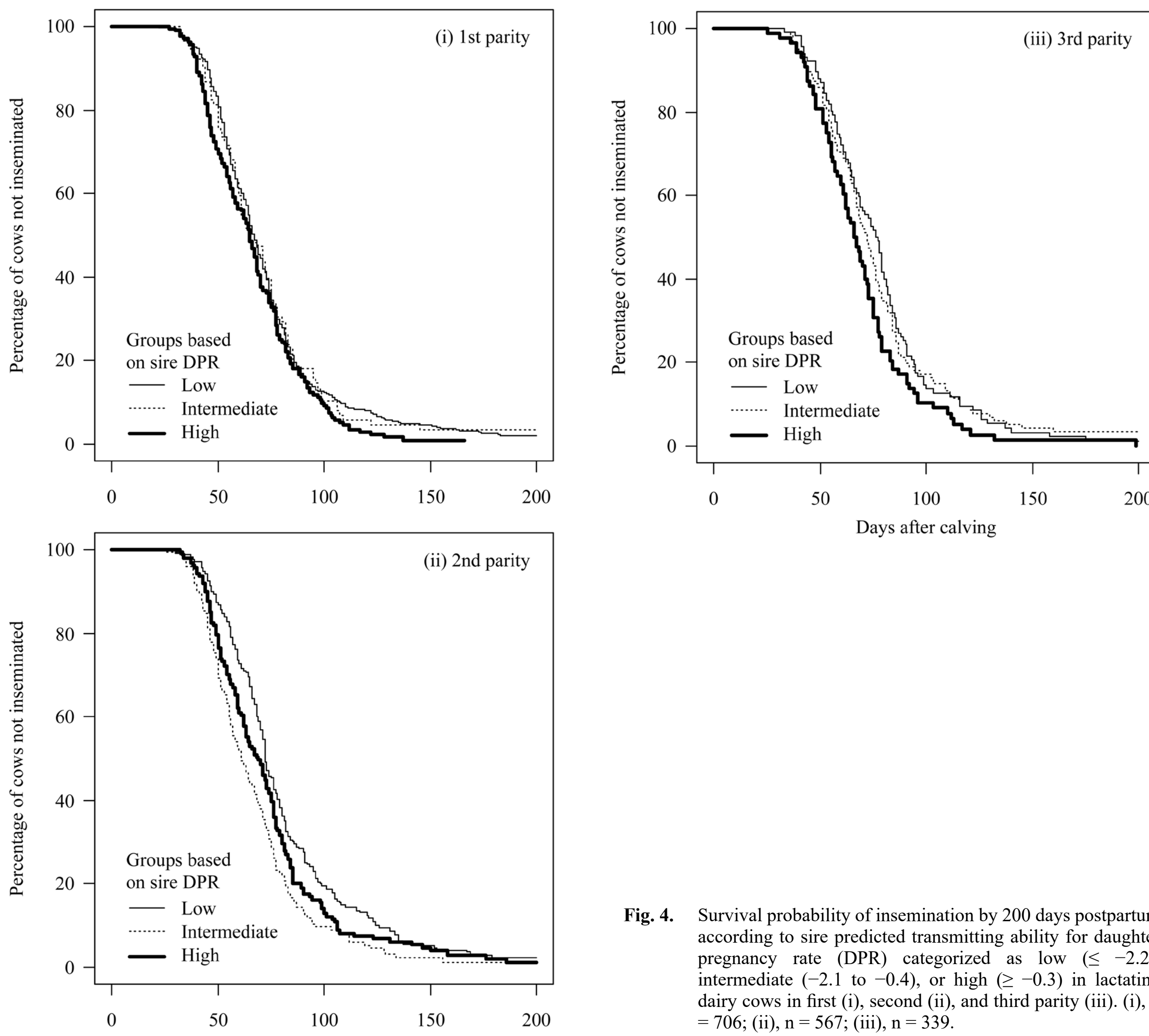
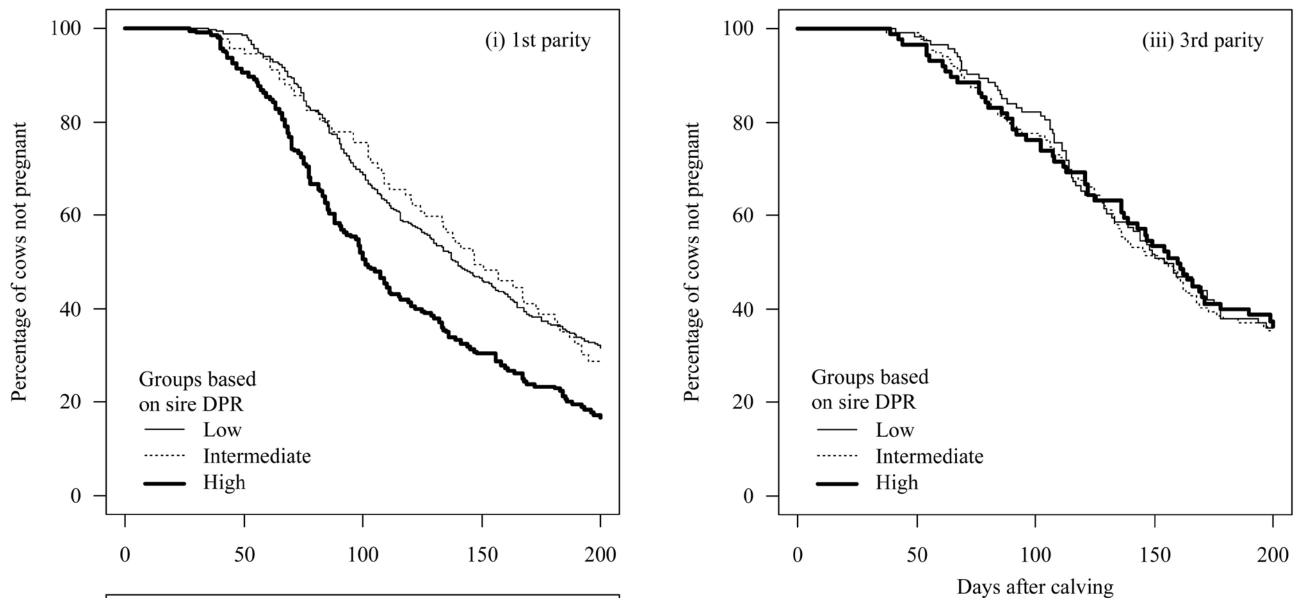


Fig. 4. Survival probability of insemination by 200 days postpartum according to sire predicted transmitting ability for daughter pregnancy rate (DPR) categorized as low (≤ −2.2), intermediate (−2.1 to −0.4), or high (≥ −0.3) in lactating dairy cows in first (i), second (ii), and third parity (iii). (i), n = 706; (ii), n = 567; (iii), n = 339.

insemination after calving depends on the reproductive management procedures of each herd [22]. The mean interval from calving to first insemination in Hokkaido herds from March 2019 to March 2020 was 87 days (Supplementary Table 1: online only), and the first insemination after calving in the herds enrolled in our study was performed earlier than this average. Therefore, the farmers of Herds A to D likely utilized aggressive reproductive management, and sire DPR may not have affected the timing of first insemination because of such activity. Active reproductive treatment, such as the frequent observation of estrus and the utilization of timed artificial insemination, may help hasten the first insemination after calving of cows from sires with low DPR.

Our results indicated that cows from sires with high DPR achieved pregnancy earlier than those from sires with low DPR. This could be due to differences in estrus expression [23], uterine health during early postpartum [20], and circulating estradiol and progesterone concentration [24]. However, in the case of third-parity cows, there was no difference in the interval from calving to conception among DPR groups. Hazard of pregnancy in lactating cows is dependent on the occurrence of disease before insemination [25], and advancing parity increases the risk of periparturient disorders [26]. Therefore, the more frequent occurrence of disease in third-parity cows might mask the impact of genetic merit for fertility on pregnancy, though we did not check disease occurrence data in our study. In contrast to our findings, Ortega *et al.* (2016) demonstrated that regardless of parity, there is a relationship between sire DPR and daughter fertility [17]. The reason for this inconsistency is unclear, thus future studies should be performed to elucidate the association between genetic merit for fertility and reproductive competence in cows with different parity.

Although the actual milk production of cows in the high-DPR group was similar to that of cows in other groups, sire PTAM in the high-DPR group was lower than that in the low-DPR group. Moreover,



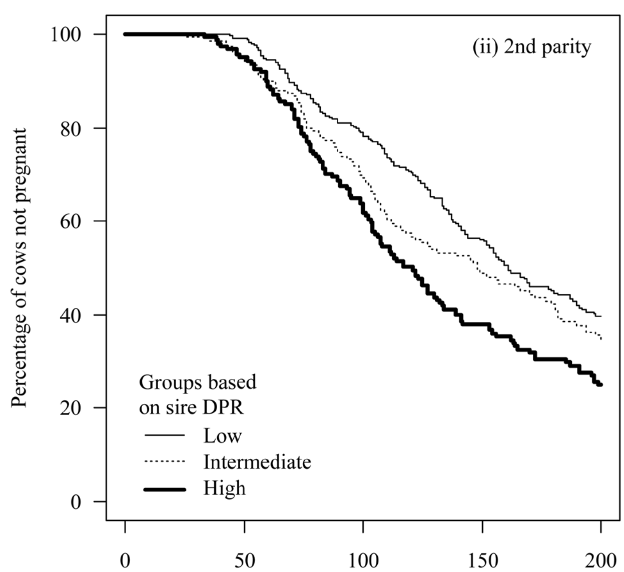


Fig. 5. Survival probability of pregnancy by 200 days postpartum according to sire predicted transmitting ability for daughter pregnancy rate (DPR) categorized as low (≤ −2.2), intermediate (−2.1 to −0.4), or high (≥ −0.3) in lactating dairy cows in first (i), second (ii), and third parity (iii). (i), n = 706; (ii), n = 567; (iii), n = 339.

we identified a negative correlation between sire DPR and PTAM —as also seen in a previous report [27]. This result indicates that selecting high-DPR sires risks the genetic merit for milk production; however, among the sires with high DPR, there were sires with high genetic merit for milk production. This indicates that it is possible to select sires that are superior for both milk production and fertility. Notably, sire DPR in Herd D was low, and reproduction performance in lactating cows of Herd D was relatively good (Supplementary Tables 2, 3, and 4: online only). Therefore, the farmer of Herd D would likely not have been focused on fertility as a direction for genetic improvement. The direction of herd improvement should be decided by each farmer, and some herds do not need genetic improvement for fertility; however, genetic improvement approaches should be one of the strategies used to improve reproductive performance in the whole herd because there is a clear positive effect of sire DPR on reproductive performance.

In conclusion, sire DPR affects the reproductive performance of daughters, and the actual milk production of cows from sires with high DPR is not reduced. Therefore, farmers can improve herd reproductive performance without a reduction in milk production by basing sire selection on sire DPR. Future studies are required to elucidate the relationship between genetic merit for fertility and reproductive competence in cows with different parity.

Acknowledgments

We thank the participating dairy producers, AI technicians, and Nakashibetsu Branch of Hokkaido Agriculture Cooperative Association for their cooperation.

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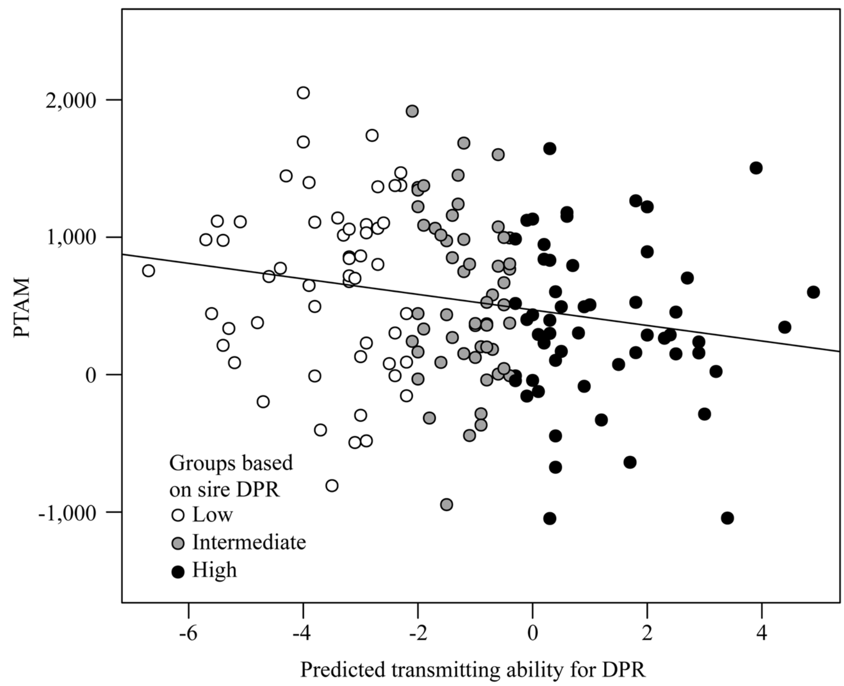

Fig. 6. Relationship between sire predicted transmitting ability for daughter pregnancy rate (DPR) and milk production (PTAM). White circles represent sires categorized as low DPR (≤ −2.2), grey circles represent sires categorized as intermediate DPR (−2.1 to −0.4), and black circles represent sires categorized as high DPR (≥ −0.3). Spearman's coefficient of rank correlation was −0.204 (P < 0.01).

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