



# Genetic correlations among fertility traits and lactation persistency within and across Holstein herds with different milk production during the first three lactations?

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1 **Genetic correlations among fertility traits and lactation persistency within and**  
2 **across Holstein herds with different milk production during the first three**  
3 **lactations**

4

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18 **Abstract**

19 Genotype by environment interaction ( $G \times E$ ) effects for lactating cows' fertility traits may differ with  
20 lactation number when accounting for herd production level. Our objective here was to investigate the  
21 genetic correlations among three fertility traits in cows and lactation persistency within and across  
22 herds with different milk-production levels by using lactation records of Japanese Holstein cows  
23 (475,446 records for first lactation, 378,540 for second, and 265,560 for third). Herds with data were  
24 categorized into three groups (**LOW**, **MID**, and **HIGH**) based on the average herd-year effects in each  
25 herd for 305-day milk yield at the first lactation. The fertility traits evaluated were conception rate at  
26 first insemination (**CR**); number of inseminations (**NI**); and days open (**DO**). Lactation persistency  
27 (**PER**) was defined as the difference between milk yields at 240 and 60 days in milk. Genetic  
28 parameters were estimated within each lactation by using a multiple-trait model that considered the  
29 traits of different herd milk-production groups (**HPGs**) as separate traits. The genetic correlations  
30 among fertility traits were estimated by using a three **HPG**  $\times$  three-trait animal model; for those  
31 between fertility traits and **PER** we used a three **HPG**  $\times$  two-trait (each fertility trait and **PER**) animal  
32 model. The genetic correlations among fertility traits were strong, whereas those between fertility traits  
33 and **PER** were weak and undesirable; most of the values did not differ significantly among **HPGs** or  
34 lactations. Some of the genetic correlations of **CR** or **NI** among different **HPGs** for the second and  
35 third lactations were lower than those for the first lactation. These findings suggest that  $G \times E$  effects  
36 on a cow's ability to conceive with respect to herd production level are larger in later lactations than  
37 in the first lactation.

38 **Highlights**

- 39 • We examined G×E effects for Holstein cow fertility among herd production levels.
- 40 • Herd production level did not affect genetic correlations among fertility traits.
- 41 • Nor did it affect the genetic correlations of fertility with lactation persistency.
- 42 • G×E effects for fertility after the first lactation were relatively large.

43

44 Differences in herd-average milk production affect the expression of genotype effects in terms of a  
45 cow's ability to conceive after the second calving.

46

47 **Keywords**

48 Dairy cattle, fertility, genotype by environment interaction, herd milk production

## 49 **Introduction**

50 Female fertility is an important factor for improving the lifetime production of dairy cattle. Because  
51 antagonistic genetic relationships between female fertility and milk production traits have been found  
52 (e.g., Abe et al., 2009; Hagiya et al., 2013), the emphasis on fertility in the dairy cattle selection indices  
53 of many countries is greater now (Egger-Danner et al., 2015) than in the past (Miglior et al., 2017). A  
54 cow's ability to conceive is commonly evaluated by using conception rate (**CR**) or non-return rate for  
55 first insemination, and number of inseminations (**NI**). Days open (**DO**; days from calving to  
56 pregnancy) and calving interval are defined as combined traits representing a cow's abilities to recycle  
57 and to conceive after calving (ICAR, 2018). The genetic correlations among these fertility traits are  
58 strong: absolute values of more than 0.7 have been reported (e.g., Ghiasi et al., 2011; Yamazaki et al.,  
59 2014).

60 The existence of a genotype by environment interaction ( $G \times E$ ) for fertility traits has been examined  
61 by considering differences in environmental descriptors such as region, herd size, temperature-  
62 humidity index, and herd-average production (Calus et al., 2005; Haile-Mariam et al., 2008; Ismael et  
63 al., 2016; Strandberg et al., 2009). Low genetic correlations among different environmental descriptors  
64 might suggest that the effect of  $G \times E$  is not negligible. For traits with large  $G \times E$ , individual farmers  
65 could choose bulls that were more appropriate to their environments if information on bulls' genetic  
66 evaluations in different environments were available. Some  $G \times E$  effects for fertility traits during first  
67 lactation have been found when production was considered (Haile-Mariam et al., 2008; Strandberg et  
68 al., 2009). However, to our knowledge there have been no reports of these effects in lactations beyond  
69 the first. According to Yamazaki et al. (2014), **CR** in later lactations is lower, and **DO** is longer, than  
70 in the first lactation. Those findings suggest the hypothesis that the strength of genotype  $\times$  herd  
71 production effects for fertility traits in later lactations may differ from those in the first lactation.

72 To our knowledge, there have been few studies of the genetic correlations among fertility traits and  
73 production traits such as milk yield or lactation persistency (**PER**) under different levels of herd  
74 production (Haile-Mariam et al., 2008; Togashi et al., 2016). **PER** is generally defined as the ability to  
75 maintain a high level of milk production after peak milk yield (Togashi and Lin, 2003). It has been  
76 suggested that genetic improvement of **PER** should help increase milk production without increasing  
77 mastitis susceptibility (Hagiya et al., 2014b) or somatic cell score (Yamazaki et al., 2013). However,  
78 some poor, or slightly undesirable, genetic correlations between fertility traits and **PER** have been  
79 reported (Albarrán-Portillo and Pollott, 2013; Yamazaki et al., 2014). Togashi et al. (2016) reported  
80 desirable genetic correlations between **PER** and conception until 180 days in milk (**DIM**) in a high-  
81 level reproductive management and milk-production environment. Information on genetic  
82 relationships in different environments is important for individual farmers in choosing bulls with the  
83 optimum breeding values for each trait to improve their cows' productivity.

84 Therefore, our objective here was to investigate the genetic relationships among three fertility traits  
85 and **PER** during the first three lactations of Holstein cows by using a multiple trait model that  
86 considered the trait values of herds with different milk-production levels as separate traits.

87

88

## 89 **Materials and Methods**

90

### 91 ***Data***

92 Insemination records during the first three lactations of Holstein cows with first inseminations from  
93 20 to 200 **DIM** recorded between 2007 and 2011 were obtained from the Livestock Improvement  
94 Association of Japan (Tokyo, Japan). Monthly test day (**TD**) milk records within 305 **DIM** were  
95 collected through the Dairy Herd Improvement program. The original data set included records for

96 475,446, 378,540 and 265,560 first, second, and third parity cows, respectively. Each cow had at least  
97 eight **TD** records. Age at first insemination ranged from 20 to 46 months in the first lactation (i.e., for  
98 the second calving), from 32 to 66 months in the second, and from 44 to 86 months in the third. The  
99 minimal size of the contemporary groups (herd year for first insemination and that for calving) was  
100 two cows for each data set, in accordance with the official genetic evaluation model for female fertility  
101 traits in Japan (National Livestock Breeding Center, 2017). The pedigree was traced back five  
102 generations and included 1,211,559, 1,035,440, and 798,595 animals for first-, second-, and third-parity  
103 cows, respectively.

104 The average milk production of each herd (**Herd production**) was defined as the average of the  
105 herd-year solution for 305-day milk yield at first lactation. Herd-year solutions for 305-day milk yield  
106 were obtained from the following single-trait animal model:

$$107 \quad y_{ijkl} = HY_i + M_j + A_k + u_l + e_{ijkl},$$

108 where  $y_{ijkl}$  is the 305-day milk yield at first lactation of cow  $l$ ;  $HY_i$  is the fixed effect of herd year  $i$   
109 (41,328 levels);  $M_j$  is the fixed effect of calving month  $j$ ;  $A_k$  is the fixed effect of calving age group  
110  $k$ , with 15 levels (18 to 20, 21 to 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, and  $\geq 35$  months);  
111  $u_l$  is the random additive effect of animal  $l$ ; and  $e_{ijkl}$  is a random residual effect associated with  
112  $y_{ijkl}$ . The 305-day milk yield was estimated by using multiple-trait prediction (Schaeffer and Jamrozik,  
113 1996) according to Wilmink's function (Wilmink, 1987). Solutions for fixed effects of 305-day milk  
114 yield were obtained by using the BLUPF90 program (Misztal et al., 2002), which uses the  
115 preconditioned conjugate gradient algorithm with iteration on data (Tsuruta et al. 2001). The variance  
116 components estimated by Yamazaki et al. (2014) were used to solve the fixed effects. Herds were  
117 classified into three groups based on the deviations of their **Herd production**, namely **LOW** (lower  
118 than  $-1$  standard deviation [SD] of Herd production), **MID** ( $\pm 1$  SD), and **HIGH** (higher than  $+1$  SD).

119 The numbers of cows, herds, and means of 305-day milk yield for each **Herd production group**  
120 (**HPG**) in the first three lactations are shown in Table 1.

121 The female fertility traits were **CR**, **NI**, and **DO**. **CR** = 1 indicated that the first insemination  
122 achieved pregnancy, 0 otherwise. **NI** was classified into five levels (1, 2, 3, 4 or 5, and  $\geq 6$  times). **DO**  
123 greater than 365 days were set to 365 days (Oseni et al., 2004). The number of cows whose pregnancy  
124 could not be confirmed by the insemination records was 17,367, 20,721 and 17,437 in the first, second  
125 and third lactations, respectively; **DO** for these cows were treated as missing (Yamazaki et al., 2014).  
126 **PER** were estimated by using the same method as that for 305-day milk yield. **PER** was defined as  
127 the difference between milk yields at 240 and 60 **DIM** (Yamazaki et al., 2014). Summary statistics of  
128 each trait for the three **HPGs** are given in Table 2.

129

### 130 *Models*

131 The data were analyzed within each lactation by using a multiple-trait linear model that took into  
132 account the genetic covariance among records for the three **HPGs**. Threshold models theoretically are  
133 more appropriate for the analysis of binary (e.g., **CR**) or categorical (e.g., **NI**) data (Gianola, 1982).  
134 However, most routine national genetic evaluations of categorical fertility traits (including those in  
135 Japan) are based on linear models (Jamrozik et al., 2005; Liu et al., 2008; Mark, 2004), because  
136 analyses that use threshold models require excessive amounts of calculation time.

137 The model used for reproductive traits, in accordance with Japan's official genetic evaluation model  
138 (National Livestock Breeding Center, 2017), was:

$$139 \quad y_{ijklmn} = FHY_i + FM_j + FA_k + s_n + u_{lm} + e_{ijklmn},$$

140 where  $y_{ijklmn}$  is the fertility trait of cow  $m$ ;  $FHY_i$  is the fixed effect of herd year  $i$  for first  
141 insemination (the levels were 38,906 for the first lactation, 37,464 for the second, and 34,534 for the  
142 third);  $FM_j$  is the fixed effect of region (two levels) – month  $j$  at first insemination;  $FA_k$  is the fixed



143 effect of age group  $k$  at first insemination, with seven levels (18, 19, 20, 21 to 25, 26 to 30, 31 to 40,  
 144 and  $\geq 41$  months);  $S_n$  is the random effect of service sire  $m$  at first insemination (the levels were 9819  
 145 for the first lactation, 8660 for the second, and 7313 for the third);  $u_{lm}$  is **HPG**  $l \times$  the random additive  
 146 effect of animal  $m$ ; and  $e_{ijklmn}$  is a random residual effect associated with  $y_{ijklmn}$ . The age effect at  
 147 first insemination was not considered in the third lactation record.

148 The model for **PER** was:

$$149 \quad y_{ijklm} = HY_i + M_j + A_k + u_{lm} + e_{ijklm},$$

150 where  $y_{ijklm}$  is the **PER** of cow  $l$ ;  $HY_i$  is the fixed effect of herd year  $i$  (the levels for the first, second,  
 151 and third lactations were 41,328, 39,405, and 35,767, respectively);  $M_j$  is the fixed effect of calving  
 152 month  $j$ ;  $A_k$  is the fixed effect of calving age group  $k$ , with 30 levels (18 to 20, 21 to 22, 23, 24, 25,  
 153 26, 27, 28, 29, 30, 31, 32, 33, 34, and  $\geq 35$  months for first lactation;  $\leq 35$ , 36 to 37, 38 to 39, 40 to 41,  
 154 42 to 43, 44 to 45, 46 to 47, and 48 to 49, and  $\geq 50$  months for second lactation; and  $\leq 45$ , 46 to 50, 51  
 155 to 55, 56 to 60, 61 to 65, and  $\geq 66$  months for third lactation); and  $u_{lm}$  and  $e_{ijklm}$  are defined as in  
 156 the previous model.

157 Genetic parameters for **CR**, **NI**, and **DO** were estimated by using a three-**HPG**  $\times$  three-trait animal  
 158 model. Genetic correlations between fertility traits and **PER** were estimated by using a three-**HPG**  $\times$   
 159 two-trait (each fertility trait and **PER**) animal model. The covariance structure was defined as

$$160 \quad \text{Var} \begin{bmatrix} \mathbf{s} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{S} \otimes \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G} \otimes \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$$

161 for the three-**HLG**  $\times$  three-trait (fertility traits) animal model,

$$162 \quad \mathbf{S} = \begin{bmatrix} \sigma_{s(f_1)}^2 & \sigma_{s(f_1)s(f_2)} & \sigma_{s(f_1)s(f_3)} \\ & \sigma_{s(f_2)}^2 & \sigma_{s(f_2)s(f_3)} \\ \text{Symme} & & \sigma_{s(f_3)}^2 \end{bmatrix},$$

$$163 \quad \mathbf{G} = \begin{bmatrix} \sigma_{u(Lf_1)}^2 & \sigma_{u(Lf_1)u(Lf_2)} & \sigma_{u(Lf_1)u(Lf_3)} & \sigma_{u(Lf_1)u(Mf_1)} & \sigma_{u(Lf_1)u(Mf_2)} & \sigma_{u(Lf_1)u(Mf_3)} & \sigma_{u(Lf_1)u(Hf_1)} & \sigma_{u(Lf_1)u(Hf_2)} & \sigma_{u(Lf_1)u(Hf_3)} \\ & \sigma_{u(Lf_2)}^2 & \sigma_{u(Lf_2)u(Lf_3)} & \sigma_{u(Lf_2)u(Mf_1)} & \sigma_{u(Lf_2)u(Mf_2)} & \sigma_{u(Lf_2)u(Mf_3)} & \sigma_{u(Lf_2)u(Hf_1)} & \sigma_{u(Lf_2)u(Hf_2)} & \sigma_{u(Lf_2)u(Hf_3)} \\ & & \sigma_{u(Lf_3)}^2 & \sigma_{u(Lf_3)u(Mf_1)} & \sigma_{u(Lf_3)u(Mf_2)} & \sigma_{u(Lf_3)u(Mf_3)} & \sigma_{u(Lf_3)u(Hf_1)} & \sigma_{u(Lf_3)u(Hf_2)} & \sigma_{u(Lf_3)u(Hf_3)} \\ & & & \sigma_{u(Mf_1)}^2 & \sigma_{u(Mf_1)u(Mf_2)} & \sigma_{u(Mf_1)u(Mf_3)} & \sigma_{u(Mf_1)u(Hf_1)} & \sigma_{u(Mf_1)u(Hf_2)} & \sigma_{u(Mf_1)u(Hf_3)} \\ & & & & \sigma_{u(Mf_2)}^2 & \sigma_{u(Mf_2)u(Mf_3)} & \sigma_{u(Mf_2)u(Hf_1)} & \sigma_{u(Mf_2)u(Hf_2)} & \sigma_{u(Mf_2)u(Hf_3)} \\ & & & & & \sigma_{u(Mf_3)}^2 & \sigma_{u(Mf_3)u(Hf_1)} & \sigma_{u(Mf_3)u(Hf_2)} & \sigma_{u(Mf_3)u(Hf_3)} \\ & & & & & & \sigma_{u(Hf_1)}^2 & \sigma_{u(Hf_1)u(Hf_2)} & \sigma_{u(Hf_1)u(Hf_3)} \\ & & & & & & & \sigma_{u(Hf_2)}^2 & \sigma_{u(Hf_2)u(Hf_3)} \\ & & & & & & & & \sigma_{u(Hf_3)}^2 \end{bmatrix},$$

$$164 \quad \text{and } \mathbf{R} = \begin{bmatrix} \sigma_{e(Lf_1)}^2 & \sigma_{e(Lf_1)e(Lf_2)} & \sigma_{e(Lf_1)e(Lf_3)} & 0 & 0 & 0 & 0 & 0 & 0 \\ & \sigma_{e(Lf_2)}^2 & \sigma_{e(Lf_2)e(Lf_3)} & 0 & 0 & 0 & 0 & 0 & 0 \\ & & \sigma_{e(Lf_3)}^2 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & & \sigma_{e(Mf_1)}^2 & \sigma_{e(Mf_1)e(Mf_2)} & \sigma_{e(Mf_1)e(Mf_3)} & 0 & 0 & 0 \\ & & & & \sigma_{e(Mf_2)}^2 & \sigma_{e(Mf_2)e(Mf_3)} & 0 & 0 & 0 \\ & & & & & \sigma_{e(Mf_3)}^2 & 0 & 0 & 0 \\ & & & & & & \sigma_{e(Hf_1)}^2 & \sigma_{e(Hf_1)e(Hf_2)} & \sigma_{e(Hf_1)e(Hf_3)} \\ & & & & & & & \sigma_{e(Hf_2)}^2 & \sigma_{e(Hf_2)e(Hf_3)} \\ & & & & & & & & \sigma_{e(Hf_3)}^2 \end{bmatrix},$$

165 and for the three-HPG × two-trait (fertility trait and PER) animal model,

$$166 \quad \mathbf{S} = \begin{bmatrix} \sigma_s^2 & 0 \\ 0 & 0 \end{bmatrix},$$

$$167 \quad \mathbf{G} = \begin{bmatrix} \sigma_{u(Lf)}^2 & \sigma_{u(Lf)u(Lp)} & \sigma_{u(Lf)u(Mf)} & \sigma_{u(Lf)u(Mp)} & \sigma_{u(Lf)u(Hf)} & \sigma_{u(Lf)u(Hp)} \\ & \sigma_{u(Lp)}^2 & \sigma_{u(Lp)u(Mf)} & \sigma_{u(Lp)u(Mp)} & \sigma_{u(Lp)u(Hf)} & \sigma_{u(Lp)u(Hp)} \\ & & \sigma_{u(Mf)}^2 & \sigma_{u(Mf)u(Mp)} & \sigma_{u(Mf)u(Hf)} & \sigma_{u(Mf)u(Hp)} \\ & & & \sigma_{u(Mp)}^2 & \sigma_{u(Mp)u(Hf)} & \sigma_{u(Mp)u(Hp)} \\ & & & & \sigma_{u(Hf)}^2 & \sigma_{u(Hf)u(Hp)} \\ & & & & & \sigma_{u(Hp)}^2 \end{bmatrix},$$

168 and  $\mathbf{R} = \begin{bmatrix} \sigma_{e(Lf)}^2 & \sigma_{e(Lf)e(Lp)} & 0 & 0 & 0 & 0 \\ & \sigma_{e(Lp)}^2 & 0 & 0 & 0 & 0 \\ & & \sigma_{e(Mf)}^2 & \sigma_{e(Mf)e(Mp)} & 0 & 0 \\ & & & \sigma_{e(Mp)}^2 & 0 & 0 \\ & & & & \sigma_{e(Hf)}^2 & \sigma_{e(Hf)e(Hp)} \\ & \text{Symme} & & & & \sigma_{e(Hp)}^2 \end{bmatrix}$

169 where  $\mathbf{S}$  is a (co)variance matrix of random service-sire effects for first insemination;  $\mathbf{G}$  is a  
 170 (co)variance matrix of random additive genetic effects;  $\mathbf{R}$  is a residual (co)variance matrix;  $\mathbf{A}$  is the  
 171 additive genetic relationship for animals;  $\mathbf{I}$  is the identity matrix; subscripts ( $Lf$  (or  $Lp$ )), ( $Mf$  (or  $Mp$ )),  
 172 and ( $Hf$  (or  $Hp$ )) are the fertility traits (or **PER**) for the **LOW**, **MID**, and **HIGH HPGs**, respectively;  
 173 and  $\otimes$  is the Kronecker product. The residual covariances between different **HPGs** were fixed at  
 174 zero. The GIBBS3F90 program (Misztal, 2008) was used for Gibbs sampling to estimate the variance  
 175 components. For Gibbs sampling, the first 300,000 samples were discarded as burn-in. The subsequent  
 176 200,000 samples were saved to calculate posterior means and standard deviations for the (co)variance  
 177 components. Convergence was verified through the inspection of graphical data by using the  
 178 POSTGIBBSF90 program (Misztal, 2008).

179 We calculated Spearman's rank correlations for the bulls' estimated breeding values (EBVs) for  
 180 each fertility trait among different **HPGs** by using our estimated variance components. EBVs were  
 181 estimated by using a three-**HPG**  $\times$  one-trait animal model and a preconditioned conjugate gradient  
 182 algorithm with iteration on data (Tsuruta et al. 2001) in a program developed for national evaluation  
 183 in Japan by the National Livestock Breeding Center (Nishigo-mura, Japan). Bulls selected for  
 184 calculating rank correlations had at least 10 daughters' records in every **HPG** for each lactation data  
 185 set: 349, 319, and 273 bulls for the first, second, and third lactations, respectively. Spearman's rank  
 186 correlations were calculated by using the CORR procedure of the SAS software package (SAS Institute  
 187 Inc., 2015).

188

## 189 **Results and Discussion**

190 **CR** decreased and average **NI** increased, with increasing **HPG** level, especially in the second and third  
191 lactations (Table 2); **CRs** for **HIGH HPG** were 11% lower than those for **LOW HPG** in the second  
192 and third lactations. There were only small differences among the averages of **DO** in each of the  
193 different **HPGs** in each lactation. Weak and undesirable phenotypic correlations between milk yield  
194 traits and fertility traits have been reported in the same lactation (Hagiya et al., 2013; Yamazaki et al.,  
195 2014). The differences we found here in **CR** and **NI** among the different **HPGs** may have been the  
196 result of several interactions between breeding timing decision or milk production level and fertility  
197 of the cows in each herd.

198 Average **PER** increased in the first lactation and decreased in the second and third lactations with  
199 rising **HPG** level. The standard deviation of **PER** increased with rising **HPG** level in each lactation.  
200 Weak and positive phenotypic correlations between 305-day milk yield and **PER** have been reported  
201 (Yamazaki et al., 2014). These relationships thus likely affect the variance of **PER** in each **HPG**,  
202 because the standard deviation of 305-day milk yield increased with increasing **HPG** level (Table 1)  
203 as a result of heterogeneous variance due to differing production level.

204

## 205 **Heritabilities and genetic correlations within each HPG**

206 The variances of service-sire effect as proportions of the total variances were very small for fertility  
207 traits and ranged from 0.0020 to 0.0042 (not shown). Most of the heritability estimates for **CR** and **NI**  
208 did not differ significantly ( $P \geq 0.05$ ) within **HPGs** among lactations or among **HPGs** for the same  
209 lactation; they ranged from 0.022 to 0.044 for **CR** and from 0.035 to 0.056 for **NI** (Table 3). **CR**  
210 showed significant differences between the values in **MID** (0.022) and **HIGH** (0.041) **HPG** for the  
211 second lactation and between those in **LOW** (0.044) and **MID** (0.022) **HPG** for the third lactation. For

212 **NI**, the value in **MID HPG** (0.035) for the second lactation was significantly ( $P < 0.05$ ) lower than  
213 that in **HIGH HPG** for the second (0.056) and first (0.054) lactations. The heritabilities of **DO** ranged  
214 from 0.065 to 0.172; the values for the third lactation (0.116 to 0.172) were significantly higher than  
215 those for the first and second lactations (0.065 to 0.101) within the same **HPGs**, with the exception of  
216 the difference between the first (0.084) and third (0.116) lactations in **HIGH HPG**. The heritability  
217 values for **LOW HPG** tended to be higher than those for the other **HPGs** in the same lactation,  
218 although the differences were not significant. Our heritability estimates for these fertility traits were in  
219 line with previous findings (e.g., Abe et al., 2009; Ghiasi et al., 2011; Hagiya et al., 2013; Jamrozik et  
220 al., 2005), except that those of **DO** for the third lactation were higher than in these studies. Some  
221 reports have stated that the heritability estimates of **DO** for later lactations are higher than those for  
222 the first lactation (Dematawewa and Berger, 1998; Menendez-Buxadera et al., 2013). Dematawewa  
223 and Berger (1998) suggested that intense selection may contribute to more homogeneity (smaller  
224 phenotypic variance) among cows in later parities and lead to higher heritability estimates for later  
225 parities than for first parity. Our heritability estimates of fertility traits for the third lactation may have  
226 been affected by selection in former lactations, because cows with poor fertility are culled.

227 The reason for the higher heritabilities of **DO** for **LOW HPG** than in the other **HPGs** in the same  
228 lactations in our study was that the genetic variances were higher than those for the other **HPGs** (not  
229 shown): the genetic variances of **DO** for **LOW HPG** were 37%, 38%, and 33% higher than those of  
230 **MID** and also 19%, 25%, and 64% higher than those of **HIGH** for the first, second, and third lactations,  
231 respectively. Ismael et al. (2016) similarly reported that the heritability and genetic variance of the  
232 interval from calving to first peak estrus activity in low-producing herds were higher than those in  
233 high-producing herds. Haile-Mariam et al. (2008) and Strandberg et al. (2009) also reported that the  
234 heritability of the interval from calving to first insemination in low-producing herds was higher than  
235 that in high-producing herds. The differences in our heritability estimates for **DO** agreed with these

236 previous findings, because **DO** is strongly genetically correlated with the interval from calving to first  
237 insemination (Yamazaki et al., 2014).

238 The heritability estimates for **PER** increased significantly with rising **HPG** level in each lactation  
239 (Table 3), except in the case of the difference between **MID** (0.185) and **HIGH** (0.238) in the second  
240 lactation and that between **LOW** (0.115) and **MID** (0.145) in the third lactation. Those for **MID HPG**  
241 were consistent with the estimates of Yamazaki et al. (2014). An increase in heritabilities for **PER** with  
242 rising **Herd production** has been reported by Togashi et al. (2016). Differences in the variance of **PER**  
243 among **HPGs** likely affected our heritability estimates, because the phenotypic standard deviations of  
244 **PER** increased with rising **HPG** level (Table 2) as a result of heterogeneous variance due to differing  
245 production level.

246 Most of the genetic correlations among fertility traits (Table 4) and those between each fertility trait  
247 and **PER** (Table 5) did not differ significantly within **HPGs** among lactations or among **HPGs** for the  
248 same lactation. The genetic correlations between **CR** and **NI** were the strongest (from  $-0.985$  to  $-$   
249  $0.903$ ). Those of **DO** with **CR** or **NI** were also strong (from  $-0.885$  to  $-0.714$  and from  $0.760$  to  $0.908$ ,  
250 respectively). That of **DO** with **NI** in **LOW HPG** for the first lactation ( $0.908$ ) was significantly  
251 stronger than that for the second lactation ( $0.798$ ) (Table 4). Those of **PER** with the fertility traits were  
252 weak and undesirable (Table 5), although there were large posterior standard deviations ( $0.033$  to  
253  $0.100$ ); the values of **PER** with **CR**, **NI**, and **DO** ranged from  $-0.266$  to  $-0.121$ , from  $0.161$  to  $0.363$ ,  
254 and from  $0.233$  to  $0.439$ , respectively. The only significant difference in the genetic correlations  
255 between **PER** and **DO** was for **MID HPG**, between the first ( $0.251$ ) and third ( $0.439$ ) lactations. Our  
256 genetic correlation estimates among fertility traits were similar to previous findings (e.g., Abe et al.,  
257 2009; Ghiasi et al., 2011; Kadarmideen et al., 2003; Yamazaki et al., 2014), and those between fertility  
258 and **PER** were similar to the estimates of Yamazaki et al. (2014). The genetic correlation between **NI**  
259 and **DO** for the second lactation was significantly weaker than that for the first lactation in **LOW HPG**

260 (see Table 4); however, that correlation was still moderate to strong. Our results suggest that differences  
261 in herd milk production do not affect the genetic relationships among fertility traits and lactation  
262 persistency.

263

#### 264 **Genetic correlations of each trait across different HPGs**

265 Positive and moderate to strong genetic correlations (greater than 0.7) were estimated for each trait  
266 across different **HPGs**, except in the case of those of **CR** for the **LOW–MID** and **LOW–HIGH HPGs**  
267 in the third lactation (Table 6). The genetic correlations of **CR** for the **MID–HIGH** (0.754) and **LOW–**  
268 **HIGH** (0.706) **HPGs** in the second lactation, and those for the **LOW–MID** (0.527) and **LOW–HIGH**  
269 (0.509) **HPGs** in the third lactation, were significantly weaker than that for the **MID–HIGH HPG** in  
270 the first lactation (0.906). Those of **CR** for the **LOW–MID** and **LOW–HIGH HPGs** in the third  
271 lactation were also significantly weaker than that for the **LOW–MID HPG** in the first lactation (0.837).  
272 The genetic correlations of **NI** for the **LOW–HIGH** (0.808) **HPG** in the second lactation and those  
273 for the **LOW–MID** (0.821) and **LOW–HIGH** (0.733) **HPGs** in the third lactation were significantly  
274 weaker than that for the **MID–HIGH HPG** in the first lactation (0.935). Most of the genetic  
275 correlations of **DO** did not differ among **HPGs** or lactations, with the exception of the difference  
276 between the **MID–HIGH HPG** in the first lactation (0.952) and the **LOW–HIGH HPG** in the second  
277 lactation (0.830). Genetic correlations of 0.74 for calving interval between low and high herd-average  
278 production groups have been reported for the first lactation (Haile-Mariam et al., 2008; Strandberg et  
279 al., 2009). Some of our genetic correlations for **CR** in the third lactations across the different **HPGs**  
280 were lower than these previous estimates for the first lactation. Spearman’s rank correlations of bulls’  
281 EBVs for each analyzed trait within each **HPG** are shown in Table 7. **CR** and **NI** showed lower  
282 correlations between different **HPGs** in the second and third lactations than in the first, suggesting that  
283 the genotype × environment effect was not negligible.

284 Our findings indicate that differences in herd-average milk production affect the expression of  
285 genotype effects in terms of a cow's ability to conceive after the second calving. These results imply  
286 that the appropriate bulls for female fertility after the second calving may differ with the production  
287 system (e.g., the housing management system or feeding system) related to herd production. Hagiya  
288 et al. (2014a) examined the effects of housing type  $\times$  feeding system on milk yield and reported that  
289 milk yield in later parity cows was more susceptible to difference in the feeding system than was milk  
290 yield in first lactation cows. Here, we were unable to take these systems into account in relation to herd  
291 production level. Revealing the effects of genotype  $\times$  production system on female fertility after the  
292 second calving would help to inform us of the appropriate bulls for improving cow fertility in  
293 individual farming systems, for example, by notifying us of those bulls with high EBVs for fertility in  
294 each system.

295

296

## 297 **Conclusions**

298 We examined the genetic relationships among female fertility traits and lactation persistency during  
299 the first three lactations of Holstein cows with regard to herd milk-production level. The genetic  
300 correlations among fertility traits and those between fertility and lactation persistency did not differ  
301 significantly among herd production levels. The genetic correlations and bulls' rank correlations for  
302 conception rate and number of inseminations between herds with low and high milk-production levels  
303 were lower in later lactations than in the first lactation. This suggests that the appropriate bulls for  
304 improving a cow's ability to conceive after the second calving are different among herd milk-  
305 production levels.

306

307



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311

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393 lactations of Japanese Holstein cows. *Livest. Sci.* 168, 26-31.  
394

395 Table 1. Numbers of cows, herds, and average 305-day milk yield in each herd production group (**HPG**)  
 396 for the first three lactations

	Lactation	<b>HPG</b>			Overall
		<b>LOW</b>	<b>MID</b>	<b>HIGH</b>	
Number of cows	First	53,505	320,851	101,090	475,446
	Second	46,583	255,825	76,132	378,540
	Third	36,363	179,752	49,445	265,560
Number of herds	First	1533	6470	1407	9410
	Second	1468	6219	1353	9040
	Third	1427	6020	1292	8739
305-day milk yield (SD), kg	First	6466 (1015)	8193 (1249)	9610 (1369)	8300 (1522)
	Second	7485 (1245)	9389 (1549)	10,948 (1708)	9469 (1824)
	Third	7887 (1304)	9774 (1610)	11,393 (1784)	9817 (1885)

397 **HPG** was categorized on the basis of the milk production of each herd, i.e., the average herd-year  
 398 solution for 305-day milk yield in the first lactation: **LOW** (lower than  $-1$  standard deviation (SD)  
 399 from the mean value), **MID** ( $\pm 1$  SD from the mean value), and **HIGH** (higher than  $+1$  SD from the  
 400 mean value).

401 Table 2. Summary statistics of fertility traits and lactation persistency (**PER**) in each herd production  
 402 group (**HPG**) for the first three lactations

	Lactation	<b>HPG</b>			Overall
		<b>LOW</b>	<b>MID</b>	<b>HIGH</b>	
<b>CR</b>	First	0.38	0.38	0.37	0.38
	Second	0.37	0.34	0.33	0.34
	Third	0.36	0.34	0.32	0.34
<b>NI (SD), times</b>	First	2.4 (1.8)	2.5 (1.9)	2.6 (2.0)	2.5 (1.9)
	Second	2.4 (1.8)	2.6 (1.9)	2.7 (1.9)	2.6 (1.9)
	Third	2.5 (1.8)	2.6 (1.8)	2.7 (1.9)	2.6 (1.9)
<b>DO (SD), days</b>	First	146 (83)	144 (83)	144 (82)	144 (83)
	Second	151 (83)	151 (83)	151 (81)	151 (83)
	Third	153 (85)	154 (83)	154 (81)	154 (83)
<b>PER (SD), kg</b>	First	-7.2 (2.7)	-6.3 (2.9)	-5.7 (3.1)	-6.3 (2.9)
	Second	-9.3 (3.3)	-9.9 (3.7)	-10.7 (4.3)	-10.0 (3.8)
	Third	-10.1 (3.5)	-10.8 (3.9)	-11.7 (4.6)	-10.9 (4.0)

403 **HPG** is as defined in the footnote to Table 1.

404 Fertility traits: **CR**, conception rate at first insemination; **NI**, number of inseminations; and **DO**, days  
 405 open. **PER** is defined as the difference between the milk yields at 240 and 60 days in milk.

406

407 Table 3. Posterior means (posterior SDs) of heritability for fertility traits and lactation persistency  
 408 (**PER**) in each herd production group (**HPG**) for the first three lactations

	Lactation	<b>HPG</b>		
		<b>LOW</b>	<b>MID</b>	<b>HIGH</b>
<b>CR</b>	First	0.034 (0.006) <sup>abc</sup>	0.026 (0.002) <sup>abc</sup>	0.035 (0.003) <sup>ab</sup>
	Second	0.033 (0.005) <sup>abc</sup>	0.022 (0.002) <sup>c</sup>	0.041 (0.005) <sup>a</sup>
	Third	0.044 (0.006) <sup>a</sup>	0.022 (0.003) <sup>bc</sup>	0.031 (0.008) <sup>abc</sup>
<b>NI</b>	First	0.051 (0.007) <sup>ab</sup>	0.044 (0.003) <sup>ab</sup>	0.054 (0.005) <sup>a</sup>
	Second	0.041 (0.004) <sup>ab</sup>	0.035 (0.003) <sup>b</sup>	0.056 (0.005) <sup>a</sup>
	Third	0.049 (0.008) <sup>ab</sup>	0.041 (0.005) <sup>ab</sup>	0.046 (0.006) <sup>ab</sup>
<b>DO</b>	First	0.101 (0.008) <sup>bcd</sup>	0.073 (0.005) <sup>de</sup>	0.084 (0.007) <sup>cde</sup>
	Second	0.090 (0.008) <sup>cde</sup>	0.065 (0.004) <sup>e</sup>	0.074 (0.006) <sup>de</sup>
	Third	0.172 (0.016) <sup>a</sup>	0.136 (0.008) <sup>ab</sup>	0.116 (0.009) <sup>abc</sup>
<b>PER</b>	First	0.116 (0.010) <sup>d</sup>	0.161 (0.007) <sup>bc</sup>	0.206 (0.009) <sup>a</sup>
	Second	0.129 (0.009) <sup>cd</sup>	0.185 (0.008) <sup>ab</sup>	0.238 (0.016) <sup>a</sup>
	Third	0.115 (0.008) <sup>d</sup>	0.145 (0.009) <sup>cd</sup>	0.202 (0.014) <sup>ab</sup>

409 **HPG** is as defined in the footnote to Table 1.

410 All traits are the same as those defined in the footnote to Table 2.

411 Heritabilities for **PER** were estimated by using a three-**HPG** × two-trait (**CR** and **PER**) animal model.

412 Values with different superscript letters across rows and down columns are significantly different:  $P <$

413 0.05 after Bonferroni correction.

414 Table 4. Posterior means (posterior SDs) of genetic correlations among fertility traits within each herd  
 415 production group (**HPG**) for the first three lactations

		<b>HPG</b>		
		<b>LOW</b>	<b>MID</b>	<b>HIGH</b>
	Lactation			
<b>CR - NI</b>	First	-0.903 (0.020) <sup>a</sup>	-0.965 (0.005) <sup>ab</sup>	-0.939 (0.012) <sup>ab</sup>
	Second	-0.936 (0.020) <sup>ab</sup>	-0.985 (0.007) <sup>b</sup>	-0.943 (0.014) <sup>ab</sup>
	Third	-0.908 (0.022) <sup>a</sup>	-0.952 (0.013) <sup>ab</sup>	-0.922 (0.023) <sup>ab</sup>
<b>CR - DO</b>	First	-0.841 (0.033)	-0.885 (0.027)	-0.846 (0.024)
	Second	-0.714 (0.049)	-0.815 (0.019)	-0.798 (0.026)
	Third	-0.774 (0.046)	-0.775 (0.033)	-0.812 (0.045)
<b>NI - DO</b>	First	0.908 (0.012) <sup>a</sup>	0.859 (0.017) <sup>ab</sup>	0.864 (0.016) <sup>ab</sup>
	Second	0.798 (0.031) <sup>b</sup>	0.801 (0.018) <sup>b</sup>	0.835 (0.021) <sup>ab</sup>
	Third	0.808 (0.034) <sup>ab</sup>	0.832 (0.019) <sup>b</sup>	0.760 (0.041) <sup>b</sup>

416 **HPG** is as defined in the footnote to Table 1.

417 All traits are as defined in the footnote to Table 2.

418 Values with different superscript letters across rows and down columns are significantly different:  $P <$   
 419 0.05 after Bonferroni correction.

420



421 Table 5. Posterior means (posterior SDs) of genetic correlations between fertility traits and lactation  
 422 persistency (**PER**) within each herd production group (**HPG**) for the first three lactations

		<b>HPG</b>		
		<b>LOW</b>	<b>MID</b>	<b>HIGH</b>
	Lactation			
<b>PER–CR</b>	First	–0.121 (0.083)	–0.220 (0.045)	–0.243 (0.058)
	Second	–0.222 (0.069)	–0.180 (0.061)	–0.181 (0.081)
	Third	–0.266 (0.100)	–0.192 (0.064)	–0.189 (0.089)
<b>PER–NI</b>	First	0.325 (0.081)	0.187 (0.044)	0.188 (0.049)
	Second	0.208 (0.062)	0.187 (0.052)	0.251 (0.064)
	Third	0.161 (0.081)	0.363 (0.053)	0.312 (0.075)
<b>PER–DO</b>	First	0.387 (0.047) <sup>ab</sup>	0.251 (0.042) <sup>b</sup>	0.275 (0.046) <sup>ab</sup>
	Second	0.387 (0.075) <sup>ab</sup>	0.361 (0.041) <sup>ab</sup>	0.317 (0.045) <sup>ab</sup>
	Third	0.233 (0.056) <sup>ab</sup>	0.439 (0.033) <sup>a</sup>	0.372 (0.078) <sup>ab</sup>

423 **HPG** is as defined in the footnote to Table 1.

424 All traits are as defined in the footnote to Table 2.

425 Values with different superscript letters across rows and down columns are significantly different:  $P <$   
 426 0.05 after Bonferroni correction.

427

428 Table 6. Posterior means (posterior SDs) of genetic correlations for each fertility trait and lactation  
 429 persistency (**PER**) across herd production groups (**HPGs**) for the first three lactations

		Genetic correlation between different <b>HPGs</b>		
	Lactation	<b>LOW–MID</b>	<b>MID–HIGH</b>	<b>LOW–HIGH</b>
<b>CR</b>	First	0.837 (0.031) <sup>ab</sup>	0.906 (0.028) <sup>a</sup>	0.759 (0.046) <sup>abc</sup>
	Second	0.743 (0.048) <sup>abc</sup>	0.754 (0.034) <sup>bc</sup>	0.706 (0.042) <sup>bc</sup>
	Third	0.527 (0.077) <sup>c</sup>	0.738 (0.082) <sup>abc</sup>	0.509 (0.071) <sup>c</sup>
<b>NI</b>	First	0.875 (0.023) <sup>ab</sup>	0.935 (0.012) <sup>a</sup>	0.803 (0.040) <sup>ab</sup>
	Second	0.871 (0.031) <sup>ab</sup>	0.894 (0.024) <sup>ab</sup>	0.808 (0.033) <sup>b</sup>
	Third	0.821 (0.033) <sup>b</sup>	0.845 (0.029) <sup>ab</sup>	0.733 (0.057) <sup>b</sup>
<b>DO</b>	First	0.944 (0.013) <sup>ab</sup>	0.952 (0.011) <sup>a</sup>	0.939 (0.010) <sup>ab</sup>
	Second	0.873 (0.023) <sup>ab</sup>	0.915 (0.016) <sup>ab</sup>	0.830 (0.035) <sup>b</sup>
	Third	0.907 (0.018) <sup>ab</sup>	0.941 (0.013) <sup>ab</sup>	0.848 (0.040) <sup>ab</sup>
<b>PER</b>	First	0.940 (0.010) <sup>bc</sup>	0.974 (0.006) <sup>ab</sup>	0.906 (0.015) <sup>c</sup>
	Second	0.953 (0.010) <sup>abc</sup>	0.978 (0.007) <sup>a</sup>	0.930 (0.013) <sup>bc</sup>
	Third	0.952 (0.011) <sup>abc</sup>	0.974 (0.007) <sup>ab</sup>	0.928 (0.015) <sup>abc</sup>

430 **HPG** is as defined in the footnote to Table 1.

431 All traits are as defined in the footnote to Table 2.

432 Genetic correlations for **PER** were estimated by using the three-**HPG** × two-trait (**CR** and **PER**)

433 animal model.

434 Values with different superscript letters across rows and down columns are significantly different;  $P <$   
435 0.05 after Bonferroni correction.  
436

437 Table 7. Spearman's rank correlations of bulls' estimated breeding values (**EBVs**) for each fertility  
 438 traits across herd production groups (**HPG**) for the first three lactations

		Rank correlation of <b>EBV</b> between different <b>HPGs</b>		
	Lactation	<b>LOW-MID</b>	<b>MID-HIGH</b>	<b>LOW-HIGH</b>
<b>CR</b>	First	0.78	0.84	0.70
	Second	0.69	0.74	0.60
	Third	0.58	0.65	0.46
<b>NI</b>	First	0.85	0.90	0.76
	Second	0.82	0.81	0.68
	Third	0.78	0.79	0.63
<b>DO</b>	First	0.88	0.89	0.82
	Second	0.84	0.85	0.71
	Third	0.89	0.90	0.81

439 **HPG** is as defined in the footnote to Table 1.

440 All traits are as defined in the footnote to Table 2.

441 Bulls selected for calculating rank correlations had at least 10 daughters' records in every **HPG** for  
 442 each lactation data set: 349, 319, and 273 bulls for the first, second, and third lactation, respectively.

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