

Genetic correlations between the cumulative pseudo-survival rate, milk yield, and somatic cell score during lactation in Holstein cattle in Japan using a random regression model

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1 Interpretive Summary

2 Relation between cumulative pseudo-survival rate and milk traits during lactation

3 Sasaki

4 Herd life of cows is affected by animal production and conditions. Using the cumulative
5 pseudo-survival rate, we found that cows with high production ability during the early
6 lactation stage had a low culling risk, even if they were in an energy deficit. The culling of
7 cows with low production ability occurred after the end of the current lactation. The risk of
8 culling for cows with high SCS was high during the lactation stage. The reliability of
9 longevity estimates increased when milk yield and SCS information were considered.

10 **Running head: RELATIONSHIPS AMONG LONGEVITY AND MILK TRAITS**

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12 **Genetic correlations between the cumulative pseudo-survival rate, milk yield, and**
13 **somatic cell score during lactation in Holstein cattle in Japan using a random regression**
14 **model**

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ABSTRACT

25
26 Trends in genetic correlations between longevity, milk yield, and SCS during lactation in
27 cows are difficult to trace. In this study, changes in the genetic correlations between milk
28 yield, SCS, and cumulative pseudo-survival rate (PSR) during lactation were examined, and
29 the effect of milk yield and SCS information on the reliability of EBV of PSR were
30 determined. Test day milk yield, SCS, and PSR records were obtained for Holstein cows in
31 Japan from 2004 to 2013. A random subset of the data was used for the analysis (825 herds,
32 205,383 cows). This dataset was randomly divided into 5 subsets (162–168 herds, 83,389–
33 95,854 cows), and genetic parameters were estimated in each subset independently. Data
34 were analyzed using multiple-trait random regression animal models including either the
35 residual effect for the whole lactation period (H0), the residual effects for five lactation
36 stages (H5), or both of these residual effects (HD). Milk yield heritability increased until
37 310–351 DIM and SCS heritability increased until 330–344 DIM. Heritability estimates for
38 PSR increased with DIM from 0.00 to 0.05. The genetic correlation between milk yield and
39 SCS increased negatively to under -0.60 at 455 DIM. The genetic correlation between milk
40 yield and PSR increased until 342–355 DIM (0.53–0.57). The genetic correlation between
41 the SCS and PSR was -0.82 to -0.83 at around 180 DIM, and decreased to -0.65 to -0.71 at
42 455 DIM. The reliability of EBV of PSR for sires with 30 or more recorded daughters was
43 0.17–0.45 when the effects of correlated traits were ignored. The maximum reliability of
44 EBV was observed at 257 (H0) or 322 (HD) DIM. When the correlations of PSR with milk
45 yield and SCS were considered, the reliabilities of PSR estimates increased to 0.31–0.76.
46 The genetic parameter estimates of H5 were the same as those for HD. The rank correlation
47 coefficients of the EBV of PSR between H0 and H5 or HD were greater than 0.9.
48 Additionally, the reliabilities of EBV of PSR of H0 were similar to those for H5 and HD.
49 Therefore, the genetic parameter estimates in H0 were not substantially different from those

50 in H5 and HD. When milk yield and SCS, which were genetically correlated with PSR, were
51 used, the reliability of PSR increased. Estimates of the genetic correlations between PSR and
52 milk yield and between PSR and SCS are useful for management and breeding decisions to
53 extend the herd life of cows.

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Key Words

56 dairy cattle, genetic evaluation, survivability, reliability

INTRODUCTION

57

58 Estimates of genetic correlations between longevity and milk yield in cows vary among
59 studies (e.g., Tsuruta et al., 2005; Pritchard et al., 2013; Tokuhisa et al., 2014), suggesting
60 variation in environmental factors. Genetic correlations between the length of herd life and
61 milk yield decrease yearly, from high positive values to low negative values (Tsuruta et al.,
62 2004; Hagiya et al., 2012a; Haile-Mariam and Pryce, 2015), indicating that correlations need
63 to be assessed periodically. Negative genetic correlations have been reported between
64 longevity and SCS and between longevity and mastitis (Hagiya et al., 2012b; Pritchard et al.,
65 2013; Weller and Ezra, 2015). In these studies, longevity traits have been estimated for the
66 whole productive life or at each parity. Therefore, trends in genetic correlations between
67 longevity and both milk yield and SCS during lactation could not be traced. The risk of
68 becoming ill for high-producing dairy cows increases as the energy deficit increases in the
69 early stage of lactation (Heuer et al., 1999; Čejna and Chládek, 2005; Toni et al., 2011).
70 Accordingly, the genetic correlation between longevity and milk production may differ among
71 lactation stages; specifically, genetic correlations may be higher during early stages than later
72 lactation stages. Using a random regression model, Sasaki et al. (2015) reported that the
73 cumulative pseudo-survival rate (**PSR**) could reflect changes in genetic parameters during
74 lactation. Therefore, it is possible to assess changes in genetic correlations during lactation
75 between PSR and milk production traits and SCS using random regression models. If these
76 genetic correlations are high, milk production traits and SCS are expected to increase the
77 reliability of the EBV of PSR (Tsuruta et al., 2005; Hagiya et al., 2012b).

78 In this study, our aim was to investigate changes in genetic correlations among PSR, milk
79 yield, and SCS during lactation and to determine the effect of milk yield and SCS information
80 on the reliability of EBV of PSR. These findings may inform management and breeding
81 decisions aimed at extending the herd life of cows.

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MATERIALS AND METHODS

84 *Data*

85 Datasets containing test day information from 2004 to 2013 were obtained from the
86 Livestock Improvement Association of Japan (<http://liaj.lin.gr.jp/>) and from the National
87 Livestock Breeding Center (<http://www.nlbc.go.jp/english/index.html>). The first calving ages
88 of cows in this dataset were between 18 and 35 mo. Data from 3,306 herds, containing 110 or
89 more test days from 2008 to 2013 and 25 or more cows per test day, were extracted from this
90 dataset and included in the analysis. All data for the first five lactation test-day records
91 between 6 and 455 DIM were collected from these herds. The entire dataset was randomly
92 divided into 2 subsets based on herds owing to computational limitations, and one was used
93 for the analysis. This subset was randomly divided into 5 subsets, using the same criteria as
94 before, and the genetic parameters were estimated in each subset independently (**Data1–5;**
95 **Table 1**). The data consisted of test day milk yield, SCS, and PSR records. Test-day SCS was
96 calculated as follows: $SCS = \log_2[(SCC)/100] + 3$ (Ali and Shook, 1980). The PSR value was
97 estimated according to the methods of Sasaki et al. (2015). The day of cow removal from her
98 herd was considered the last test day of the cow when the interval between the last test day of
99 the cow and the last test day of her herd was longer than 120 d. When the interval between the
100 last test day of the cow and the last test day of her herd was less than 120 d, the last test day of
101 the cow was considered the day of censoring. When a cow was alive until September 2013, or
102 when her herd was withdrawn from the herd test, the cow had a censored record. The calving
103 records of a cow that was removed before the first test day of lactation were not included in
104 the dataset. The removal day of this cow was the dry-off day of prior parity. The PSR value
105 was determined according to whether the cow was alive (1) or absent (0) in her herd on the
106 test day within the lactation period. The PSR record for the last test day before the removal

107 day of a cow was coded 0, and the subsequent test-day records in the same parity for the cow
 108 were coded 0 until 455 DIM. The PSR record of a cow in the parities prior to the parity at
 109 removal was coded 1, and the last test day before the dry-off day of a cow was considered the
 110 day of censoring. The PSR record for the day of censoring of a cow was coded as 1, and the
 111 subsequent test-day records in the same parity of the cow were considered missing. When a
 112 cow was dried off after 455 DIM, the last test day of the cow before 456 DIM was considered
 113 the day of censoring and it was coded 1. When a cow was removed after 455 DIM, the last
 114 test day of the cow before 456 DIM was considered the removal day, and it was coded 0. The
 115 PSR records in the parities subsequent to the removal parity were considered missing. Related
 116 animals in the pedigree record were defined as cows for which PSR records were available
 117 and the ancestors traced back 3 generations from the cows with test-day records (Table 1).

118 **Models**

119 Data were analyzed using the multiple-trait random regression animal model, with slightly
 120 different models for milk and SCS than for PSR. The following model was used for daily milk
 121 yield and SCS:

$$\begin{aligned}
 122 \quad y_{dijklmt} = & \text{HTD}_{it} + \sum_{s=0}^6 \text{RPA}_{jts} \varphi_s(d) + \sum_{s=0}^2 \text{HYS}_{kts} \varphi_s(d) + \sum_{s=0}^2 a_{lts} \varphi_s(d) \\
 123 \quad & + \sum_{s=0}^2 p1_{lts} \varphi_s(d) + \sum_{s=0}^2 p2_{lmts} \varphi_s(d) + e1_{wdijklmt} + e2_{dijklmt} \quad [1]
 \end{aligned}$$

124 The following model was used for PSR:

$$\begin{aligned}
 125 \quad y_{djklm} = & \sum_{s=0}^4 \text{RPA}_{js} \varphi_s(d) + \sum_{s=0}^2 \text{HYS}_{ks} \varphi_s(d) + \sum_{s=0}^2 a_{ls} \varphi_s(d) \\
 126 \quad & + \sum_{s=0}^2 p2_{lms} \varphi_s(d) + e1_{wdjklm} + e2_{djklm} \quad [2]
 \end{aligned}$$

127 where $y_{dijklmt}$ is the milk yield and SCS and y_{djklm} is the PSR of cow l exhibiting trait t at

128 DIM d . HTD_{it} is the fixed effect of the herd-test day i with trait t . RPA_{jts} is the s^{th} fixed
129 regression coefficient of the region-parity-age of calving group j with trait t . The region
130 classes were Hokkaido and other regions in Japan. The age groups at calving were divided
131 into 5 classes in each parity. HYS_{kts} is the s^{th} random regression coefficient of the
132 herd-year-season group k with trait t . The season was divided into 4 classes: from January to
133 March, April to June, July to September, and October to December. a_{lts} represents the s^{th}
134 additive genetic random regression coefficient of cow l exhibiting trait t . p1_{lts} represents the
135 s^{th} permanent environmental random regression coefficient of cow l between lactation with
136 trait t . p2_{lmts} represents the s^{th} permanent environmental random regression coefficient of
137 cow l within lactation m with trait t ($m = 1-5$). $\text{e1}_{wdijklmt}$ represents the residual random
138 effect of lactation stage w with trait t . Five groups were established according to lactation
139 stage: from 6 to 95, 96 to 185, 186 to 275, 276 to 365, and 366 to 455 DIM. e2_{ajklmt}
140 represents the residual random effect for the whole lactation. $\varphi_q(d)$ is the q^{th} Legendre
141 polynomial at DIM d . The variance and covariance were defined as follows:

$$142 \quad \text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{p1} \\ \mathbf{p2} \\ \mathbf{e1}_w \\ \mathbf{e2} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{Q1} \otimes \mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Q2} \otimes \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R1}_w \otimes \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R2} \otimes \mathbf{I} \end{bmatrix} \quad [3]$$

143 where \mathbf{a} , $\mathbf{p1}$, and $\mathbf{p2}$ are vectors of the regression coefficients for the additive genetic effect,
144 permanent environmental effect between lactation, and permanent environmental effect within
145 lactation, respectively. The dimensions of \mathbf{a} , $\mathbf{p1}$ and $\mathbf{p2}$ for milk yield and SCS were the same
146 as those in the model for routine evaluation work in Japan. The dimensions of \mathbf{a} and $\mathbf{p2}$ of
147 PSR were the same as those used in the model in Sasaki et al. (2015). $\mathbf{e1}_w$ is a vector of the
148 residual effect of lactation stage group w . $\mathbf{e2}$ is a vector of the residual effect of the whole
149 lactation period. \mathbf{G} , $\mathbf{Q1}$, and $\mathbf{Q2}$ are the (co)variance matrices for the additive genetic,
150 permanent environmental between lactation, and permanent environmental within lactation

151 regression coefficients, respectively. $\mathbf{R1}_w$ is the residual (co)variance matrix of the lactation
 152 stage group w . $\mathbf{R2}$ is the residual (co)variance matrix of the whole lactation period. The
 153 covariance elements between the lactation stage groups of $\mathbf{R1}_w$ were set to zero because the
 154 test day observations for each trait were only included in one lactation stage group. \mathbf{A} is the
 155 additive genetic relationship matrix between animals. \mathbf{I} is the identity matrix.

156 *Heterogeneity of Residual Variances*

157 Three models were used to evaluate the heterogeneity of residual variances in equations [1]
 158 and [2]. The first model (**H0**) included the e2 effect and ignored the e1 effect. The second
 159 model (**H5**) included the e1 effect and ignored the e2 effect. The third model (**HD**) included
 160 the e1 and e2 effects. These models were compared based on residual variances (**RV**;
 161 Bohmanova et al., 2009), which were estimated as follows:

$$162 \quad RV = \frac{\sum_{i=1}^m (y_i - \hat{y}_i)^2 - \frac{[\sum_{i=1}^m (y_i - \hat{y}_i)]^2}{m}}{m - 1} \quad [4]$$

163 where y_i is the i^{th} test day record. \hat{y}_i is the estimate of the i^{th} test day record and m is the
 164 number of records.

165 *Parameter Estimates*

166 The variances in Data1–5 were estimated separately using GIBBS3F90 (Misztal et al.,
 167 2002). The first 100,000 Gibbs samples were discarded as the burn-in. Convergence was
 168 checked by visually inspecting the graph of the next 100,000 samples, which were used to
 169 calculate the posterior means for (co)variance components and heritabilities at test days 6 to
 170 455 DIM. Post-Gibbs analysis was performed using POSTGIBBSF90 (Tsuruta and Misztal,
 171 2006). When $\Phi'_d = [\varphi_0(d) \quad \varphi_1(d) \quad \varphi_2(d)]'$, the matrices for daily additive genetic
 172 (co)variance ($\widehat{\mathbf{G}}_d$), permanent environmental (co)variance between lactation ($\widehat{\mathbf{Q1}}_d$), and
 173 permanent environmental (co)variance within lactation ($\widehat{\mathbf{Q2}}_d$) at d DIM were defined as
 174 $\widehat{\mathbf{G}}_d = \Phi'_d \widehat{\mathbf{G}} \Phi_d$, $\widehat{\mathbf{Q1}}_d = \Phi'_d \widehat{\mathbf{Q1}} \Phi_d$, and $\widehat{\mathbf{Q2}}_d = \Phi'_d \widehat{\mathbf{Q2}} \Phi_d$, respectively. Heritability at d DIM

175 (\hat{h}_d^2) was defined as follows:

$$176 \quad \hat{h}_d^2 = \frac{\hat{\sigma}_{g_d}^2}{\hat{\sigma}_{g_d}^2 + \hat{\sigma}_{p1_d}^2 + \hat{\sigma}_{p2_d}^2 + \hat{\sigma}_{r1_d}^2 + \hat{\sigma}_{r2_d}^2} \quad [5]$$

177 where $\hat{\sigma}_{g_d}^2$, $\hat{\sigma}_{p1_d}^2$, $\hat{\sigma}_{p2_d}^2$, $\hat{\sigma}_{r1_d}^2$, and $\hat{\sigma}_{r2_d}^2$ are the additive genetic variance, permanent
 178 environmental variance between lactation, permanent environmental variance within lactation,
 179 residual variance of the corresponding lactation stage group, and residual variance of the
 180 whole lactation period at d DIM, respectively. The daily genetic correlations between trait 1
 181 and trait 2 at d DIM (\hat{r}_{g1g2_d}) were estimated according to equation [6].

$$182 \quad \hat{r}_{g1g2_d} = \frac{\widehat{Cov}_{g1g2_d}}{\sqrt{\hat{\sigma}_{g1_d}^2 \times \hat{\sigma}_{g2_d}^2}} \quad [6]$$

183 where \widehat{Cov}_{g1g2_d} is the genetic covariance between trait 1 and trait 2 at d DIM. $\hat{\sigma}_{g1_d}^2$ and
 184 $\hat{\sigma}_{g2_d}^2$ are the genetic variances of trait 1 and 2 at d DIM, respectively.

185 ***EBV and Reliability of PSR***

186 The EBV of PSR at 305 DIM was predicted for Data1–5 using GIBBS3F90 (Misztal et al.,
 187 2002). These analyses were performed using the genetic parameter estimates for each dataset.

188 The EBV of PSR obtained by linear model was compared to the EBV of the relative risk
 189 (**RR**) of the Weibull proportional hazard model (**PHM**) to confirm whether the EBV of PSR
 190 reflects longevity. The ETA of the RR of PHM was estimated using The Survival Kit version
 191 6.1 (Ducrocq et al., 2010). This analysis was performed using the analytical model and
 192 parameters reported in Sasaki et al. (2015). The model for PHM was as follows:

$$193 \quad \lambda(\delta) = \lambda_{0,p}(\delta) \exp[RPA_i + hys_j(\delta') + sire_k + 0.5mgs_l] \quad [7]$$

194 where $\lambda(\delta)$ is a hazard function of a cow at d DIM ($\delta = d - 5$). $\lambda_{0,p}(\delta) = \lambda_p \rho_p (\lambda_p \delta)^{\rho_p}$ is
 195 the Weibull baseline hazard function featuring the scale parameter λ_p and the shape
 196 parameter ρ_p specific to the region-parity-lactation stage group p . The lactation stage was

197 divided into 2 classes: from 6 to 255 DIM and from 266 to 455 DIM. RPA_i is the fixed effect
198 of region-parity-age for calving group i . $hys_j(\delta')$ is the time-dependent random effect of
199 herd-year-season group j at date δ' ; this effect is assumed to follow a log-gamma distribution
200 (γ_{hys}), where $\sigma_{hys}^2 = \Psi^{(1)}(\gamma_{hys})$, and $\Psi^{(1)}(\gamma_{hys})$ is a trigamma function of γ_{hys} . $sire_k +$
201 $0.5mgs_l$ is the additive genetic effect of the cow's sire and maternal grandsire, which follows
202 a multivariate normal distribution with mean zero and variance $\mathbf{A}\sigma_s^2$, where σ_s^2 is the
203 variance among sires and \mathbf{A} is the additive genetic relationship matrix between sires. Twice
204 the ETA of the RR was considered the EBV of the RR.

205 The EBV of PSR at 305 DIM and the EBV of RR for sires with 30 or more recorded
206 daughters (**Sire30**) in Data1–5 were selected. The EBV of RR for these same sires were
207 selected in each dataset. The Spearman's correlation coefficients for all pairs of EBV were
208 calculated using the CORR procedures of SAS (SAS Institute Inc. 2006).

209 In Data1, the reliabilities of the EBV of daily PSR of Sire30 were estimated using the
210 method of Liu et al. (2001, 2004). This reliability approximation method is based on the
211 concept of the multiple-trait effective daughter contribution for the random regression model.
212 The reliabilities of the EBV were estimated in four cases, i.e., using PSR information, PSR
213 and milk yield, PSR and SCS, and PSR, milk yield, and SCS.

214

215 **RESULTS AND DISCUSSION**

216 *Parameter Estimates*

217 The additive genetic variance, the permanent environmental variance among parities, and
218 the permanent environmental variance within parities for milk yield increased rapidly after
219 300 DIM (Figure 1a, b, c). Because the data points decreased from 3000 to 400 during the
220 period from 250 to 455 DIM, the variance in regression estimates is expected to increase.
221 The additive genetic variance and permanent environmental variance among parities for milk

222 yield in H0 were slightly smaller than those in H5 and HD. The permanent environmental
223 variance within parities for milk yield was larger than other variance components of milk
224 yield. The permanent environmental variance within parities of milk yield in H0 was larger
225 than the variances in H5 and HD until 301 DIM, after which those in H5 and HD were larger.
226 In the first lactation stage group, the residual variances of milk yield in H5 and HD were
227 larger than that in H0 (Figure 1d). The magnitude of the residual variance of milk yield in
228 H0 overtook those in H5 and HD after the first lactation stage. The heritability estimates of
229 milk yield increased with DIM and peaks were observed at 351 DIM in H0 and 310–311
230 DIM in H5 and HD (Figure 1e). The heritability of milk yield in H0 was lower than the milk
231 yield heritability in H5 and HD until 402 DIM. The heritability estimates of milk yield were
232 within the range of previous estimates (Muir et al., 2007; Savegnago et al., 2013; Hagiya et
233 al., 2013, 2014). The additive genetic variance (Figure 2a) and the permanent environmental
234 variance among parities of SCS (Figure 2b) peaked at 235 and 205 DIM, respectively. The
235 additive genetic variance of SCS in H0 was smaller than that in H5 and HD in the late
236 lactation stage. In the middle lactation stage, the permanent environmental variance among
237 parities of SCS in H0 was larger than that in H5 and HD. The permanent environmental
238 variance within parities was larger than the other variance components of SCS (Figure 2c).
239 This variance was large in the early and late lactation stages. This variance in H0 was larger
240 in the early lactation stage than the variance in H5 and HD, but the variances in H5 and HD
241 exceeded that of H0 in the late lactation stage. The residual variances of SCS in H5 and HD
242 decreased as the lactation stage increased (Figure 2d). These variances in H5 and HD were
243 smaller than that in H0 after the second lactation stage. The heritability of SCS increased
244 until 330–344 DIM, and then decreased (Figure 2e). The heritability estimates of SCS in H5
245 and HD were almost the same. The heritability of SCS in H0 was smaller than those in H5
246 and HD after the second lactation stage. The heritability estimates of SCS were within the

247 range of previous estimates (Mrode et al., 2012; Yamazaki et al., 2013; Hagiya et al., 2014).

248 The additive genetic variance (Figure 3a) and the permanent environmental variance
249 within parities (Figure 3b) of PSR increased with advancing lactation stages. These
250 variances in H0 were smaller than those in H5 and HD until 371 and 380 DIM, respectively.
251 The residual variances of PSR in H5 and HD increased as lactation advanced (Figure 3c).
252 These were larger than that in H0 after the third lactation stage. The heritability of PSR in
253 H0 increased with advancing lactation stages until 396 DIM (Figure 3d). The trends in
254 heritability estimates of PSR in H5 and HD during lactation were similar to those in H0, but
255 heritability was lower in the fifth lactation stage than in H0 (Figure 3e). The trend in the
256 heritability of PSR during lactation in this study was the same as that reported by Sasaki et al.
257 (2015), who used data from 2001 to 2010. The heritability of PSR was slightly lower than
258 that of the previous study, and this difference might reflect differences in herd size. A herd in
259 the previous study included five or more third-lactation cows on every test-day; different
260 lactations were treated as correlated traits in the multiple-trait model. The average herd size
261 of 70.9 in the previous study was larger than that of this study, i.e., 54.4. Therefore, the
262 differences in results among studies reflect differences in the conditions of herds. Longevity
263 is expressed by various traits, including herd life, life span score, mortality, and so on. The
264 heritability estimates of these longevity traits in previous reports are low (0.04–0.11:
265 Pritchard et al., 2013; Tokuhisa et al., 2014; Weller and Ezra, 2015).

266 ***Genetic Correlations***

267 Small, negative genetic correlations between milk yield and SCS were detected after
268 parturition, and they became more negative as the lactation stage increased (Figure 4a). The
269 values were below -0.6 at 455 DIM. The genetic correlations between milk yield and SCS in
270 H0, H5, and HD were very similar. A small, positive genetic correlation between milk yield
271 and SCS has been observed in the first parity, and negative correlations have been observed

272 thereafter (Miglior et al., 2007; Yamazaki et al., 2013). In these reports, the genetic
273 correlation between milk yield and SCS in the late lactation stage ranged from -0.4 to -0.5 .
274 The genetic correlation between milk yield and SCS in this study using the first five
275 lactation records agrees with the results obtained for multiparous cows. The genetic
276 correlations between milk yield and PSR increased until 342–355 DIM (Figure 4b). This
277 genetic correlation in H0 was stronger than those in H5 and HD from the third lactation
278 stage. The SCS and PSR showed a genetically strong negative relationship (Figure 4c). The
279 peak genetic correlation coefficients ranged from -0.82 to -0.83 around 180 DIM. After 180
280 DIM, the correlations observed in H0, H5, and HD decreased to -0.65 , -0.71 , and -0.69 at
281 455 DIM, respectively. The genetic correlation between longevity and milk yield varies
282 among studies. Previous studies have reported that the genetic correlation between longevity
283 and milk yield is positive (Haile-Mariam et al., 2003; Holtsmark et al., 2008; Pritchard et al.,
284 2013), negative (González-Recio and Alenda, 2007; Onyiro et al., 2008; Tokuhisa et al.,
285 2014), or weak (Tsuruta et al., 2005; Fujita and Suzuki, 2006; Hagiya et al., 2012b). These
286 differences suggest that the genetic correlation between longevity traits and milk yield is
287 dependent on the conditions of individual populations. Hagiya et al. (2012b) reported that
288 the milk yield in the first lactation is not genetically correlated with the length of herd life.
289 However, the genetic correlation of the milk yield between the first lactation and later
290 lactations was not strong (0.76 – 0.85 : Miglior et al., 2007; Yamazaki et al., 2013). Therefore,
291 the milk yield in later lactations may be genetically correlated with longevity traits. Tokuhisa
292 et al. (2014) reported that the genetic correlation between the milk yield and dairy cow
293 mortality differed with respect to parity and region in the US. Many previous reports have
294 indicated that the culling risk of cows with high SCS records is high (Hagiya et al., 2012b;
295 Pritchard et al., 2013; Weller and Ezra, 2015), in agreement with the results of this study.

296 ***Comparisons of Models***

297 The genetic parameter estimates in H5 were the same as those in HD. This result indicated
298 that the error variance separation methods used in this study did not affect the genetic
299 parameter estimates. The error variance estimates in H0 were different from those in H5 and
300 HD, but the heritability estimates and the genetic correlation estimates in H0 were similar to
301 those in H5 and HD. The differences in the error variance estimates between H0 and H5 or
302 HD are covered by the difference in the permanent environmental variance within parity.
303 Therefore, part of the error variance during lactation in H0 would be explained by the
304 variance in the permanent environmental effect within lactation. The heritability estimates in
305 the late lactation stage of H0 were higher than those in H5 and HD. These results indicated
306 that the error variance estimates in the late lactation stage of H0 may be underestimated.
307 Almost all effective sample sizes of the variance estimates were over 10, but the residual
308 variance estimates in HD were small (2.6 to 34.8). These results are common for complex
309 models (Varona et al., 1999). The variance estimates for the three models considered in this
310 study were reliable and not substantially different among the five datasets. However, the
311 variance estimates for HD should be verified using another model or multiple data sets. The
312 RV for milk yield and SCS in H0 was smaller than those in H5 and HD (Table 2). The RV of
313 milk yield and SCS in H5 was almost the same as that in HD. The RV of PSR was similar for
314 all three models. In Data1–5, the time required to estimate the EBV in H0 was 70% of the
315 time required in H5 and 65% of that for HD, indicating an advantage of H0 over H5 and HD
316 with respect to estimation time.

317 ***Reliability of Estimated Breeding Value***

318 Carlén et al. (2006) reported that the correlation coefficients for the comparison between
319 the true breeding value and the predicted breeding value from a linear model, threshold
320 model, and survival analysis were similar. Additionally, they reported that the accuracy of

321 the ranking of sires by predicted breeding value was similar for these three models. In this
322 study, the results obtained using the linear model were compared with those obtained in a
323 survival analysis because previous studies have reported that survival analyses can be used
324 to determine the correct analytical models to fit herd life data (Ducrocq, 2005; Sewalem et
325 al., 2010; Zavadiluv et al., 2011). Additionally, the correlation coefficient between the true
326 breeding value and estimated breeding value in a survival analysis was higher than that of a
327 linear model in a simulation study of herd life (Jamrozik et al., 2008). The Spearman's rank
328 correlation coefficients among the EBV of PSR at 305 DIM of Sire30 and the EBV of RR
329 are shown in Table 3. The rank correlation coefficients of EBV of PSR between H5 and HD
330 were high (0.97–1.00) for Data1–5. The rank correlation coefficients of EBV of PSR
331 between H0 and H5 and between H0 and HD were 0.87–0.95 and 0.86–0.96, respectively.
332 These were weaker than those between H5 and HD. The rank correlation coefficients of
333 EBV between PSR and RR were –0.60 to –0.80. The PSR and RR exhibited opposite trends;
334 accordingly, the genetic correlation between the PSR and RR was negative. Sasaki et al.
335 (2015) reported that the rank correlation coefficient of EBV between the H5 and RR was
336 –0.90. The lower rank correlation coefficient than that in the previous study can be
337 explained by the smaller dataset and the lower heritabilities in this study than in the previous
338 study. Jamrozik et al. (2008) reported that the absolute values of correlation coefficients of
339 EBV of sires with at least 20 daughters for the comparison between a random regression
340 model and PHM ranged from 0.57 to 0.81. These results were similar to those of this study.
341 The rank correlation coefficients of EBV between PSR and RR increased in the following
342 order: HD, H5, H0. Additionally, the rank correlation coefficients of the EBV of RR were
343 higher in H5 and HD than H0; accordingly, the EBV of PSR in H5 and HD were more
344 suitable than those in H0. However, the differences in the heritability estimates and the RV
345 between H0 and H5 or HD were small. The rank correlation coefficients of the EBV of PSR

346 between H0 and H5 or HD were greater than 0.9.

347 The reliabilities of the PSR of Sire30 were 0.26–0.45 in H0, 0.20–0.43 in H5, and 0.17–
348 0.43 in HD when the effects of other correlated traits were ignored (Figure 5a, b, c). The
349 maximum value was obtained at 329 DIM in H0 and 320 DIM in H5 and HD. When the
350 correlations of the PSR with the milk yield and SCS were considered, the reliability of PSR
351 was 0.36–0.76 in H0, 0.33–0.76 in H5, and 0.31–0.76 in HD. These values were 1.3 to 3.5
352 times higher than those obtained without including the effects of milk yield and SCS in each
353 DIM. The reliability of PSR in H5 and HD was slightly higher than that in H0 in the late
354 lactation stage (Figure 5b). When the milk yield and SCS were considered, the increment of
355 the reliability of PSR in H5 and HD was similar to that in H0. Because the size of Data1 is
356 one-tenth the size of the original dataset, the reliability of PSR of the original dataset is
357 higher than that of Data1.

358 We assumed that the genetic correlation between the PSR and the milk yield in the early
359 lactation stage is negative because high-yielding cows in the early lactation stage have a risk
360 of culling owing to the energy deficit. However, the genetic correlation between the PSR and
361 the milk yield was positive, but weak in the early lactation stage, and it was strong in the late
362 lactation stage. These results indicate that cows with high production ability remain in their
363 herd, even if they have trouble during the early lactation stage. Cows with low production
364 ability are culled during the dry period. The genetic correlation between the PSR and the SCS
365 was highly negative in all lactation stages. This result indicated that the cows with high SCS
366 had high culling risks at all lactation stages. Because the genetic correlation between the milk
367 yield and the SCS in the early lactation stage was weak, the culling of the high SCS cow in
368 the early lactation stage was not affected by the milk yield. The reliability of the EBV of PSR
369 based on the PSR record was low because one PSR record was available for each daughter.
370 When milk yield and SCS, which were genetically correlated with the PSR, were used, the

371 reliability estimate of the EBV of PSR increased. Because the SCS was genetically correlated
372 with the PSR from the early lactation stage, the reliability of EBV of PSR increased from the
373 early lactation stage. Therefore, SCS data were important for improving the reliability of EBV
374 of PSR. The genetic correlation between the milk yield and the PSR in the late lactation stage
375 increased the reliability of EBV of PSR in the late lactation stage. Milk yield information was
376 important because many cows were culled during the late lactation stage. When the breeding
377 value of longevity was estimated, the daughters of young sires remained in the herd, and
378 longevity data were not available. In some longevity studies (Cruickshank et al., 2002;
379 Tsuruta et al., 2005; Hagiya et al., 2012b), the genetic evaluations were based on production
380 traits, SCS, and type traits for accurate estimation.

381

382

CONCLUSIONS

383 The high genetic correlation in the late lactation stage indicated that the persistency of milk
384 yield is an effective parameter for extending the herd life. Additionally, because the genetic
385 correlation between PSR and SCS is high in all lactation periods, a reduction in the SCS at
386 any time point is effective to extend the herd life. When an elder sire has daughters with
387 longevity records, the reliability of EBV of PSR using milk yield and SCS information is high.
388 Because the reliability of young sires lacking daughters with longevity records is lower,
389 additional information, e.g., production trait data, should be considered.

390

391

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508

Table 1. Summary of raw data used to estimate genetic parameters for each dataset (Data1–5)

| Dataset | No. of herds | No. of cows | No. of related animals | No. of cows removed | Milk yield | | | SCS | | |
|---------|--------------|-------------|------------------------|---------------------|----------------|------|-----|----------------|------|------|
| | | | | | No. of records | Mean | SD | No. of records | Mean | SD |
| Data1 | 166 | 39,388 | 83,486 | 23,663 | 1,005,547 | 29.1 | 8.8 | 1,002,073 | 2.63 | 1.82 |
| Data2 | 168 | 42,025 | 93,805 | 25,633 | 1,042,383 | 29.8 | 9.0 | 1,037,861 | 2.62 | 1.82 |
| Data3 | 162 | 40,888 | 83,389 | 24,386 | 1,044,649 | 29.5 | 9.0 | 1,038,200 | 2.67 | 1.86 |
| Data4 | 164 | 40,361 | 85,252 | 24,517 | 1,007,869 | 28.8 | 8.9 | 1,006,702 | 2.65 | 1.84 |
| Data5 | 165 | 42,894 | 95,854 | 26,301 | 1,071,692 | 29.7 | 9.0 | 1,071,689 | 2.62 | 1.78 |

Table 2. Residual variance (RV) for various models and each residual variance type (H0 = one residual variance for the whole lactation stage; H5 = separate residual variances for 5 lactation stages; HD = one residual variance for the whole lactation stage + separate residual variances for 5 lactation stages) for each dataset (Data1–5)

| Dataset | Milk | | | SCS | | | PSR ¹ | | |
|---------|------|------|------|-------|-------|-------|------------------|--------|--------|
| | H0 | H5 | HD | H0 | H5 | HD | H0 | H5 | HD |
| Data1 | 7.55 | 7.67 | 7.67 | 0.873 | 0.883 | 0.884 | 0.0112 | 0.0114 | 0.0114 |
| Data2 | 7.44 | 7.56 | 7.56 | 0.843 | 0.853 | 0.853 | 0.0115 | 0.0117 | 0.0117 |
| Data3 | 7.42 | 7.54 | 7.54 | 0.860 | 0.871 | 0.871 | 0.0115 | 0.0110 | 0.0110 |
| Data4 | 7.36 | 7.47 | 7.47 | 0.840 | 0.850 | 0.850 | 0.0116 | 0.0118 | 0.0118 |
| Data5 | 7.98 | 8.11 | 8.11 | 0.826 | 0.836 | 0.836 | 0.0116 | 0.0117 | 0.0117 |
| Average | 7.55 | 7.67 | 7.67 | 0.848 | 0.858 | 0.859 | 0.0115 | 0.0115 | 0.0115 |

¹Pseudo-survival rate

Table 3. Spearman's correlation coefficients for comparisons among EBVs of the pseudo-survival rate for each residual variance type (H0 = one residual variance for the whole lactation stage; H5 = separate residual variances for 5 lactation stages; HD = one residual variance for the whole lactation stage + separate residual variances for 5 lactation stages) at 305 DIM, and EBV of relative risk (RR) of sires with over 30 recorded daughters (Sire30) for each dataset (Data1–5)

| Trait 1 | No. of | H0 | | | H5 | | HD |
|---------|--------|--------|-------|--------|-------|--------|--------|
| | | Sire30 | H5 | HD | RR | HD | RR |
| Data1 | 178 | 0.912 | 0.908 | -0.634 | 0.996 | -0.686 | -0.693 |
| Data2 | 192 | 0.950 | 0.957 | -0.601 | 0.987 | -0.646 | -0.650 |
| Data3 | 181 | 0.940 | 0.952 | -0.721 | 0.990 | -0.685 | -0.716 |
| Data4 | 184 | 0.865 | 0.859 | -0.637 | 0.966 | -0.675 | -0.688 |
| Data5 | 196 | 0.921 | 0.928 | -0.687 | 0.993 | -0.791 | -0.798 |
| Average | 186 | 0.918 | 0.915 | -0.656 | 0.986 | -0.697 | -0.709 |

FIGURE LEGENDS

Figure 1. Genetic parameter estimates of the milk yield for each residual variance type (H0 = one residual variance for the whole lactation stage; H5 = separate residual variances for 5 lactation stages; HD = one residual variance for whole lactation stage + separate residual variances for 5 lactation stages). (a) Estimated additive genetic variance. (b) Estimated permanent environmental variance between lactation. (c) Estimated permanent environmental variance within lactation. (d) Estimated residual variance. (e) Estimated heritability

Figure 2. Genetic parameter estimates of the somatic cell score (SCS) for each residual variance type (H0 = one residual variance for the whole lactation stage; H5 = separate residual variances for 5 lactation stages; HD = one residual variance for the whole lactation stage + separate residual variances for the 5 lactation stages). (a) Estimated additive genetic variance. (b) Estimated permanent environmental variance between lactation. (c) Estimated permanent environmental variance within lactation. (d) Estimated residual variance. (e) Estimated heritability.

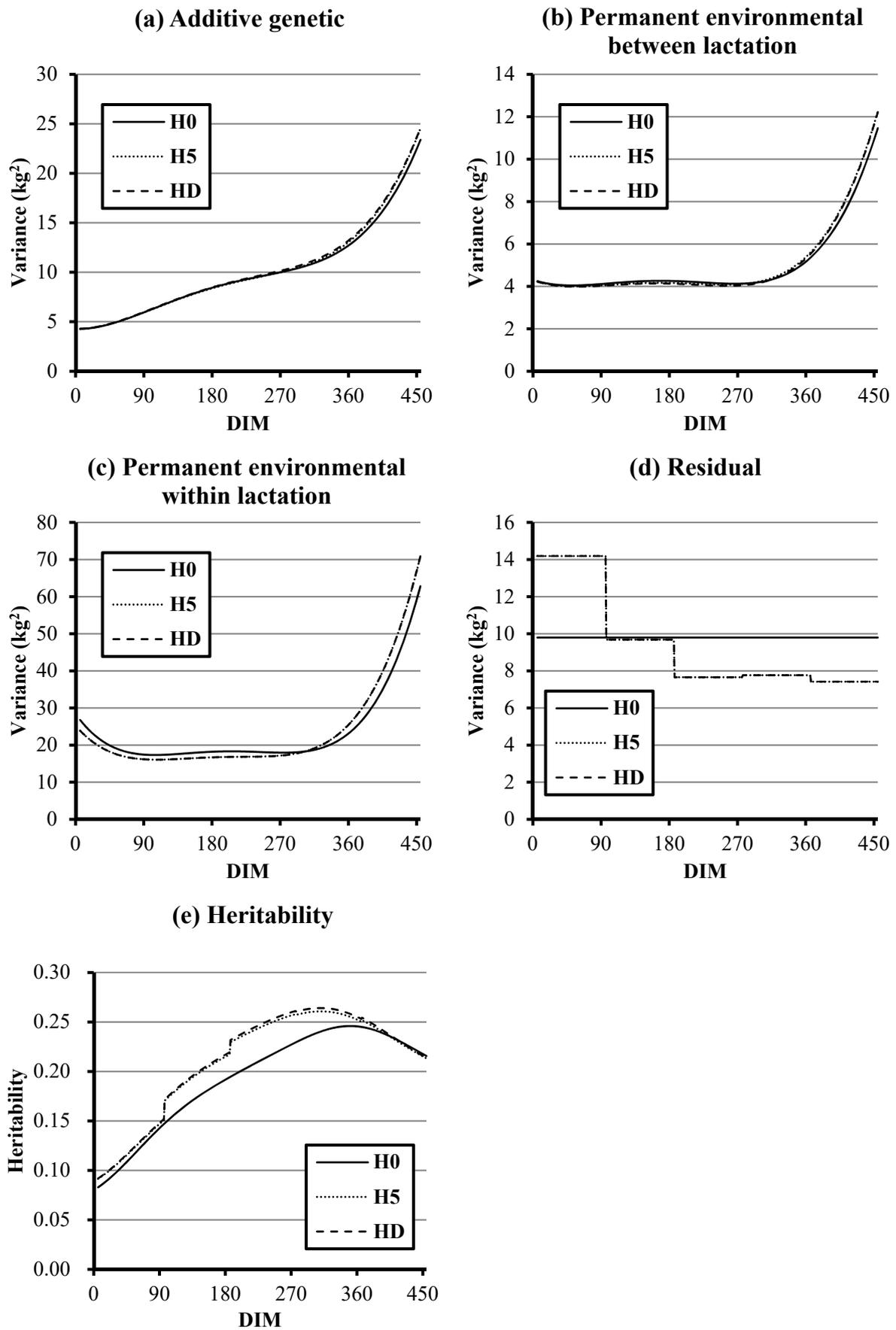
Figure 3. Genetic parameter estimates of the cumulative pseudo-survival rate for each residual variance type (H0 = one residual variance for the whole lactation stage; H5 = separate residual variances for the 5 lactation stages; HD = one residual variance for the whole lactation stage + separate residual variances for the 5 lactation stages). (a) Estimated additive genetic variance. (b) Estimated permanent environmental variance within lactation. (c) Estimated residual variance. (d) Estimated heritability.

Figure 4. Genetic correlation between (a) milk yield and somatic cell score (SCS), (b) milk

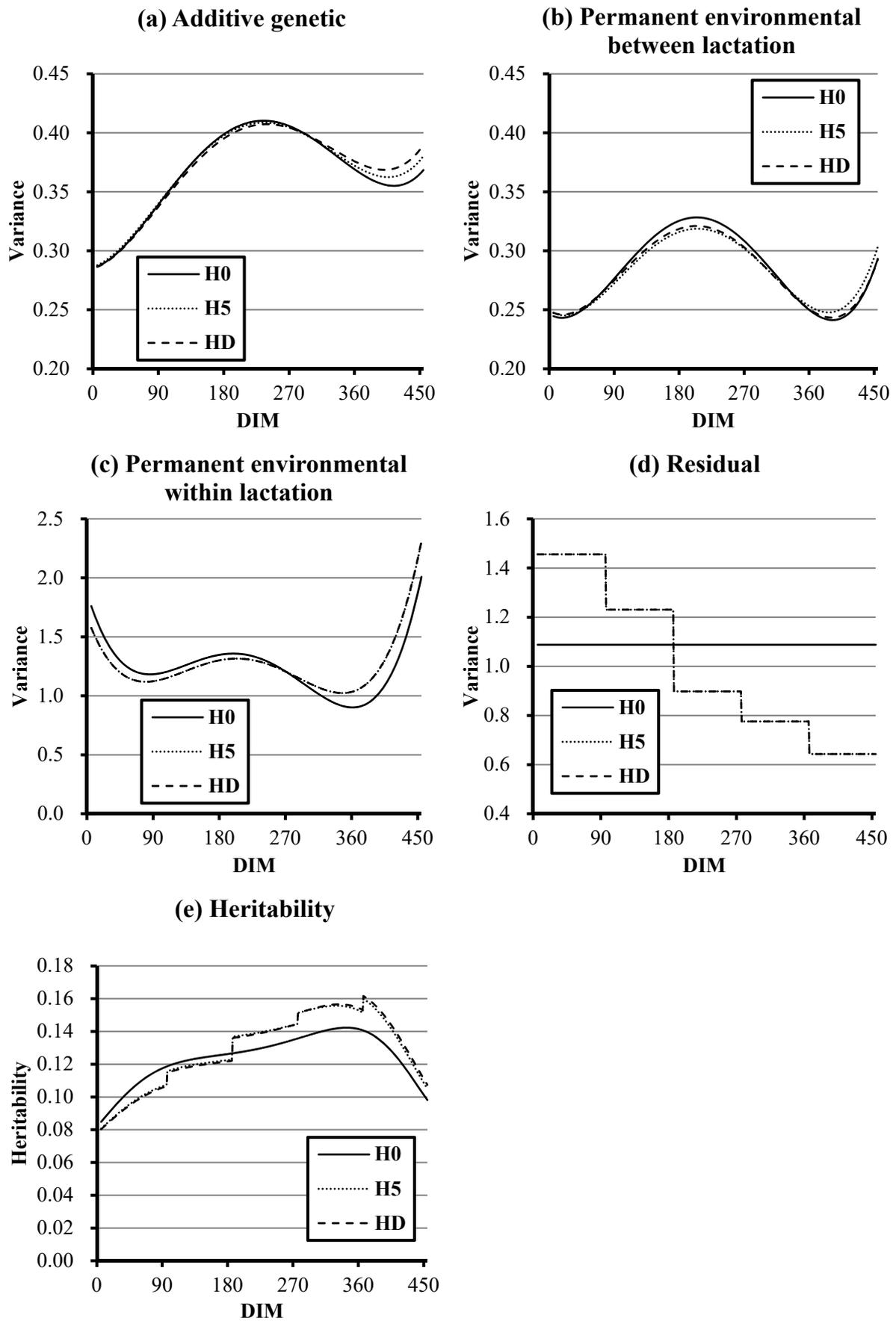
yield and pseudo survival rate (PSR), and (c) SCS and PSR (H_0 = one residual variance for the whole lactation stage; H_5 = separate residual variances for the 5 lactation stages; H_D = one residual variance for the whole lactation stage + separate residual variance for the 5 lactation stages).

Figure 5. Average reliabilities of the cumulative pseudo-survival rate (PSR) of sires with over 30 recorded daughters, calculated using the multiple-trait random regression animal model. The reliabilities of the EBV of daily PSR were estimated for the following four cases: using PSR information (PSR), PSR and milk yield (PSR + milk), PSR and SCS used (PSR + SCS), and PSR, milk yield, and SCS (PSR + milk + SCS).

Sasaki Figure 1

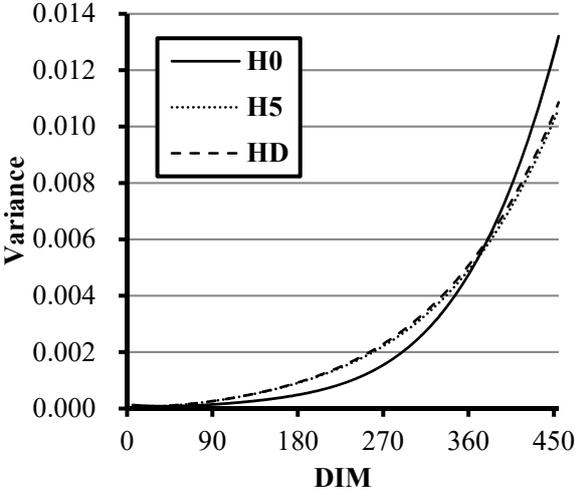


Sasaki Figure 2

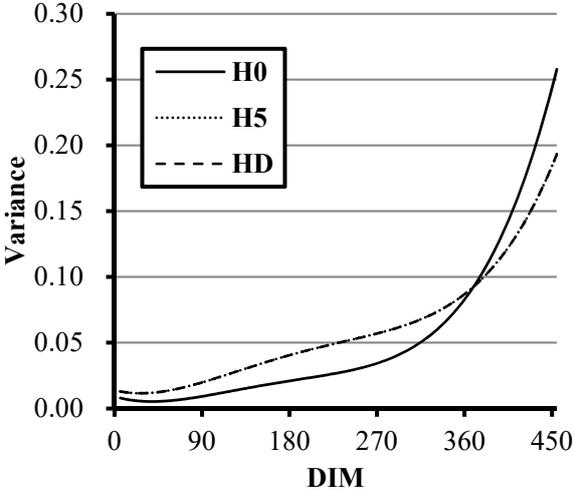


Sasaki Figure 3

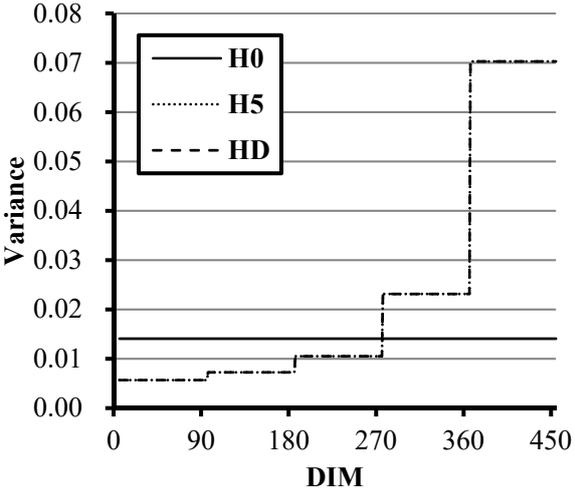
(a) Additive genetic



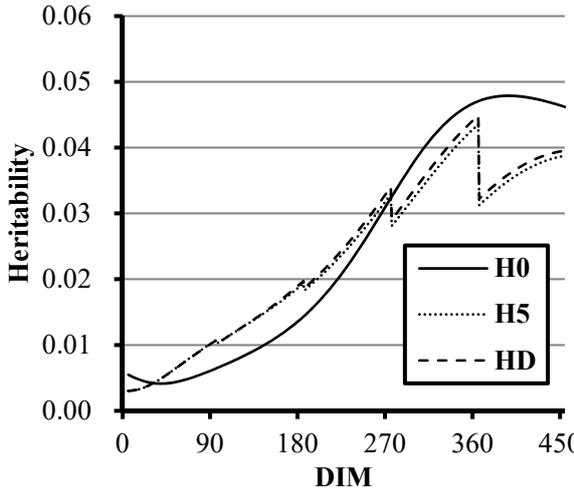
(b) Permanent environmental within lactation



(c) Residual

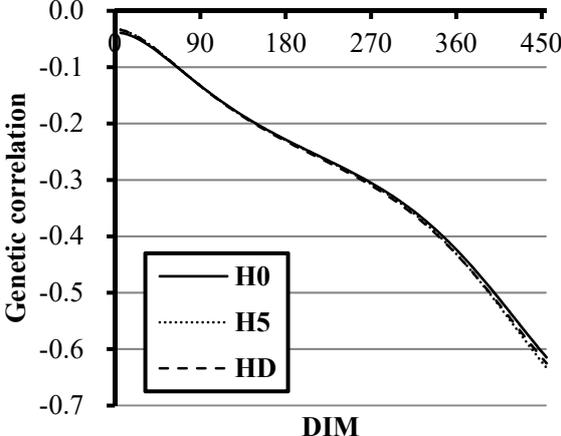


(d) Heritability

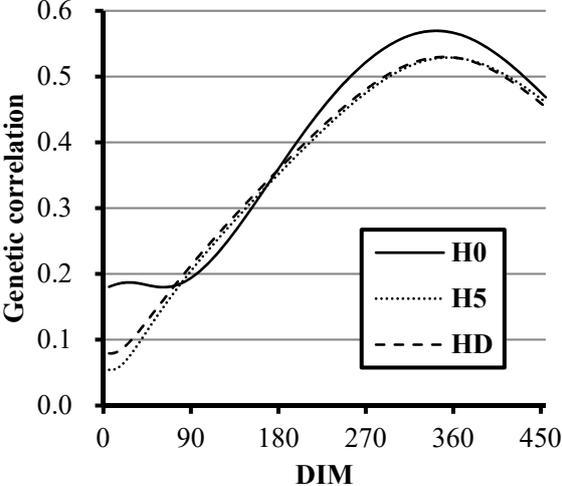


Sasaki Figure 4

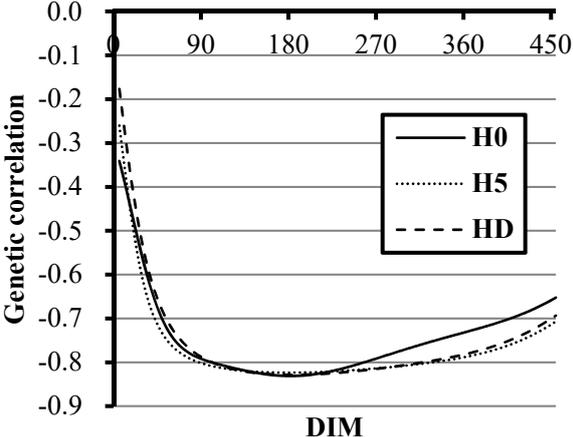
(a) Milk and SCS



(b) Milk and PSR



(c) SCS and PSR



Sasaki Figure 5

