〔原著論文〕

黒毛和種の集団構造を考慮に入れた枝肉形質に関するゲノミック予測

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Genomic prediction for carcass traits in Japanese Black cattle considering mixed structure of subpopulations

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ABSTRACT

We performed Bayesian clustering analysis using STRUCTURE software with genotype data on 33,063 commercial single nucleotide polymorphism (SNP) markers in 4,348 Japanese Black fattened steers slaughtered at carcass markets in Tokyo, Osaka, Hyogo, Tottori, and Hiroshima prefectures. When the number of the assumed clusters in STRUCTURE was 2, the steers from Hyogo prefecture were clearly separated from the others. This indicates the usefulness of the STRUCTURE analysis with commercial SNP markers for the clarifications of the difference of the genetic constitutions of each prefecture. Next, genomic predictions for carcass traits were conducted using a statistical model including the proportions of the clusters as partial linear regressions. Genomic breeding values predicted by the model without the STRUCTURE covariates were likely to be divided into the part of explaining the STRUCTURE analysis and the remaining part. This result shows the possibility that the accuracy of genomic prediction depends on the degree of information of the genomic population structure.

Key words: carcass traits, genomic prediction, Japanese Black cattle, population structure, single nucleotide polymorphism

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INTRODUCTION

Practical use of genomic prediction (GP) in Japanese Black cattle has been supported by several studies (e.g., Onogi et al. 2014; Watanabe et al. 2014; Ogawa et al. 2016; Okada et al. 2018; Takeda et al. 2020). For carcass traits, GP using genomic best linear unbiased prediction (GBLUP; VanRaden et al. 2008) is one operational scheme, in which fattened animals shipped to carcass markets are used as a large-scale training population (Watanabe 2016; Takeda et al. 2021). The size of a training population can affect the accuracy of GP (Goddard and Hayes 2009). As well as Japanese Black cattle, enlarging the size of training populations is also investigated for other beef cattle breeds, local dairy cattle breeds, and so on (e.g., Daetwyler et al. 2012; Johnson et al. 2012; Lund et al. 2014). Studies on GP have been also conducted using larger training populations from multiple breeds or subpopulations of a single breed (e.g., Brøndum et al. 2011; Lund et al. 2011; Heringstad et al. 2012). However, the accuracy of GP even got worse in some cases, possibly due to the lower persistence of linkage disequilibrium (LD) phase among breeds or subpopulations, which lead to the difference in allele substitution effects of single nucleotide polymorphisms (SNPs) used as LD markers (e.g., Karoui et al. 2012; Thomasen et al. 2013; Lund et al. 2014). For Japanese Black population, Zoda et al. (2022) reported a difference concerning the degree of persistence of LD phase among commercial SNP markers between fattened steers shipped to the carcass market in Hyogo prefecture and those in Tokyo, Osaka, Tottori, and Hiroshima prefectures. This difference might lower the accuracy of GP from the expectations under the certain size of training population.

It is a challenging but important task to develop a better, practical statistical model for GP (hereafter denoted as GP model) by using fattened animals from various carcass markets as a training population. By using animals with different breed proportions of original Danish and United States Jersey populations, Thomasen et al. (2013) evaluated the performance of GP models accounting for the population structure inferred from STRUCTURE analysis (Prichard et al. 2000). For Japanese Black population, Yoneda et al. (2010) conducted the STRUCTURE analysis of 39 animals of a rare line in Okayama prefecture and 33 animals of other populations (as controls) using 23 microsatellite markers. Nishimaki et al. (2013) and Yoneda et al. (2016), using 52 microsatellite markers, conducted the STRUCTURE analyses on different samples of commercial fattening animals collected from several prefectures including Hyogo and Hiroshima prefectures. In this study, by using the same data of Japanese Black fattened steers used in Zoda et al. (2022), we conducted the STRUCTURE analysis using commercial SNP markers, and then investigated the performance of GP models considering the information of the genomic population structure from multiple prefectures.

MATERIALS AND METHODS

Ethics statement

Animal care and use were according to the protocol approved by the Shirakawa Institute of Animal Genetics Animal Care and Use Committee, Nishigo, Japan (ACUCH21-1).

SNP genotype data

Genotype information on 33,063 SNPs, with minor allele frequencies of >0.01 in Hardy–Weinberg equilibrium (HWE; P >0.001) of 4,348 Japanese Black fattened steers was available (Zoda et al. 2022). The samples were collected during 2000 to 2014 at the Tokyo Metropolitan Central Wholesale Market, the Osaka Municipal South Port Wholesale Market, and markets in Hyogo, Tottori, and Hiroshima prefectures. It should be noted that the information about pedigree and fattening farms was not available in this study.

STRUCTURE analyses

Bayesian clustering was implemented by using STRUCTURE software version 2.3.4 (Prichard et al. 2000). The number of ancestral subpopulations or clusters, referred to as K-value, was changed from 1 to 15, assuming an admixture model with correlated allele frequencies (Falush et al. 2003; Nishimaki et al. 2013). In the STRUCTURE analysis, it is assumed that the loci are at HWE and in linkage equilibrium or weakly linked within each subpopulation (Prichard et al. 2000; Falush et al. 2003). Thomasen et al. (2013) used 412 autosomal SNPs for their STRUCTURE analysis, selecting them to achieve a marker spacing of around 1 cM. On this basis and in order to reduce computational costs, we chose 100, 300, 1,000, and 3,000 evenly spaced SNPs across all autosomes accounting the genome-wide LD in the Japanese Black population (Zoda et al. 2022). For each K-value with the different SNP marker

subsets, 20 independent runs were performed. For each run, the total number of Markov chain Monte Carlo iteration was 40,000, and the first 20,000 discarded as burn-in. Estimated values of LnP(D), which is the log posterior probability of the data for a given K (Prichard et al. 2000), were averaged over the 20 runs. Values of ad-hoc statistic ⊿K, proposed by Evanno et al. (2005) to detect the true K-value, were calculated from the values of LnP(D) estimated in the 20 runs.

Genomic prediction

GP by a single-trait model for GBLUP considering the information from the STRUCTURE analysis, referred to as Model S, was performed:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{S\beta} + \mathbf{g} + \mathbf{e},$$

where **y** is the vector of trait records; **b** is the vector of overall mean, the main effects of market and year at slaughter, and the partial linear and quadratic covariates (regression) of age at slaughter; **S** is a matrix containing the values for clusters inferred by the STRUCTURE analysis; **β** is the vector of partial linear regression coefficients for the results of STRUCTURE analysis; **g** is the vector of genomic breeding values; **e** is the vector of residuals; and **X** is an incidence matrix for **b**. S was constructed with results of K = 2, 3, 4, 5, 8, and 10 using four SNP subsets, totally 24 conditions, with the highest value of LnP(D) among 20 runs. The traits analyzed were cold carcass weight (CW), ribeye area (RA), rib thickness (RT), subcutaneous fat thickness (SF), estimated yield percent (YP), and marbling score (MS) (Japan Meat Grading Association 1988). We excluded 29 steers slaughtered between 2000 and 2002, because they came only from the Tokyo market. We therefore analyzed the carcass records of 4,319 steers ranging from 22 to 37 months of age, which were collected from 2003 to 2014 at the five markets (Table 1). For comparison, GP with the model not including the term **Sβ** (Ogawa et al. 2016; Watanabe 2016), referred to as Model B, was also performed. Henceforth, **g** in the models S and B were separately denoted as $\mathbf{g}_S$ and $\mathbf{g}_B$, respectively.

Table 1. Means and standard deviations (SDs) of phenotypic records for carcass traits of 4,319 fattened steers

Trait; abbreviation	Unit	Mean	SD
Carcass weight; CW	kg	485.6	61.2
Ribeye area; RA	cm^2	57.1	8.9
Rib thickness; RT	cm	7.8	1.0
Subcutaneous fat thickness; SF	cm	2.5	0.8
Estimated yield percent; YP	%	73.7	1.5
Marbling score; MS	BMS No.	6.0	2.6

All parameters were estimated via the Bayesian framework using the Gibbs sampler in BGLR package version 1.0.4 (Pérez and de los Campos 2014). The default settings were used for the prior distributions of **b** and **β**. Vectors **g** and **e** were assumed to follow multivariate normal distributions with the following mean and variance–covariance structure:

$$E\begin{bmatrix}\mathbf{g}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{0}\\ \mathbf{0}\end{bmatrix} \text{ and } V\begin{bmatrix}\mathbf{g}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{G}\sigma_g^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}\sigma_e^2\end{bmatrix},$$

where **G** is the genomic relationship matrix (VanRaden 2008) constructed using genotype information on the SNPs and those allele frequencies in the steers; σ_g^2 additive genetic variance; **I** is the identity matrix; and σ_e^2 residual variance. The prior distributions for σ_g^2 and σ_e^2 were scaled inverse chi-squared distributions with the default settings for their scale parameters. A single chain of 110,000 samples was run, and the first 10,000 samples discarded as burn-in. Samples after burn-in were used with a thinning rate of 10. Parameter estimates and their standard errors were obtained by calculating the averages and standard deviations (SDs) of the 10,000 posterior samples.

Pearson's correlation coefficient between $\hat{\mathbf{g}}_B$ and $\mathbf{S}\hat{\boldsymbol{\beta}} + \hat{\mathbf{g}}_S$, and the simple regression coefficient (where $\hat{\mathbf{g}}_B$ was independent and $\mathbf{S}\hat{\boldsymbol{\beta}} + \hat{\mathbf{g}}_S$ was dependent variables) were calculated. The rate of sample variance of the components of $\mathbf{S}\hat{\boldsymbol{\beta}}$ to that of $\hat{\mathbf{g}}_B$ was also calculated. The model-based accuracy of predicted genomic breeding value ($\hat{\mathbf{g}}_i$) for steer i was calculated as follows (Clark et al. 2012), and then averaged over the steers:

$$\sqrt{1 - \frac{PEV_i}{\mathbf{G}_{ii}\hat{\sigma}_g^2}},$$

where *PEVi* is prediction error variance of $\hat{\mathbf{g}}_i$, which was substituted to the corresponding posterior SD.

RESULTS AND DISCUSSION

STRUCTURE analyses

Patterns in LnP(D) averaged over 20 runs and ⊿K were shown in Figures 1 and 2, respectively. Within a SNP subset, LnP(D) increased with K, although ⊿K was the greatest when K = 2. Therefore, different values of K were suggested as the best setting, in agreement with Evanno et al. (2005). With 100 SNPs, the SD of LnP(D) tended to

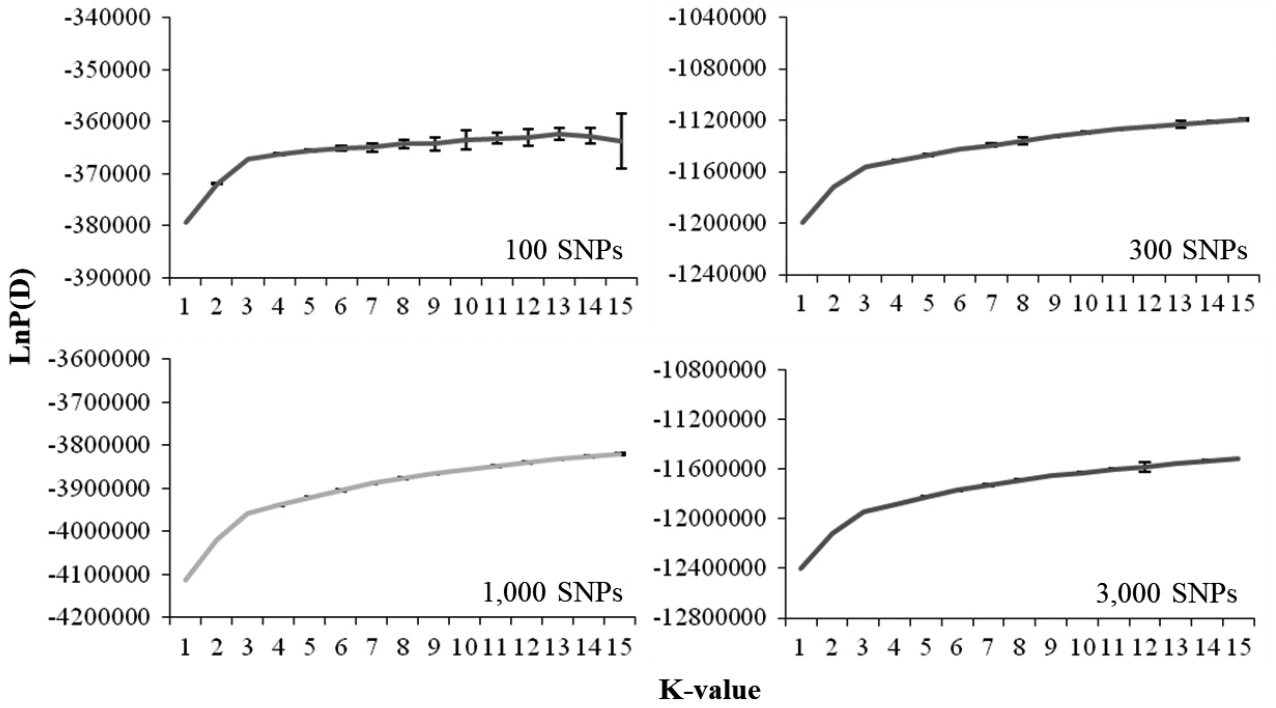

Figure 1. Changes in the average values of LnP(D) obtained from 20 runs with different number of single nucleotide polymorphism markers. Error bars show the standard deviations.

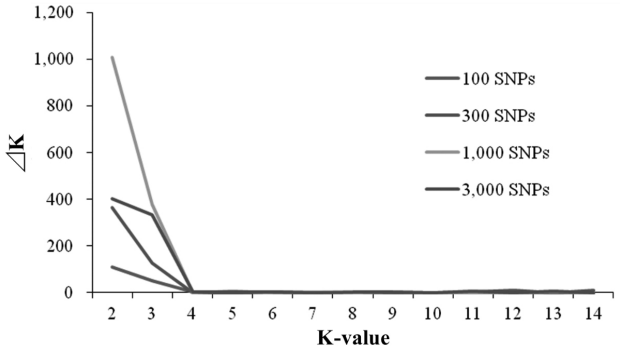

Figure 2. Changes in the values of ⊿ K with different number of single nucleotide polymorphism markers.

increase with K, reflecting certain difficulty in accurate inference in STRUCTURE analysis.

Figure 3 shows the results of Bayesian clustering with the highest LnP(D) in 20 runs by STRUCTURE analysis with K = 2 and 10 using 100 and 3,000 SNPs as examples. In this study, K affected the results of clustering more than that of the number of SNPs. When K = 2, one cluster was dominant in all the steers from Hyogo market, although values ranged from near 0 to near 1 in the other steers. Results were similar when K >2. Nishimaki et al. (2013) conducted a STRUCTURE analysis in the range of K = 2 to 8 under an admixture model with correlated allele frequencies and, as here, the Hyogo samples had one dominant cluster at K = 2, but the Hiroshima samples had no characteristic even at K = 6. The STRUCTURE analyses using commercial SNP markers could clarify the difference of the genomic structures or compositions of the Japanese Black cattle population. Thomasen et al. (2013) calculated the correlation to be 0.81 between the pedigree-based breed origin and the estimated cluster values from the STRUCTURE analysis with K = 2 and 412 autosomal SNPs under linkage model. This is essentially a generalization of the admixture model, even though in the latter method the marker position information is

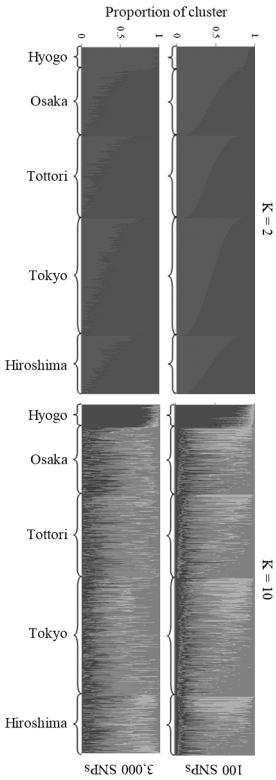

Figure 3. Results of Bayesian clustering obtained. Results with the highest values of LnP(D) over 20 runs are shown. Each steer is represented by a single vertical line divided into K colors, where K is the number of clusters. The colored segment shows the proportion of the individual's genome corresponding to a particular cluster, within steers from the same market.

required and the computational cost would be greater, as denoted by Prichard et al. (2000) and Falush et al. (2003).

Genomic prediction

The estimated value ± standard error of heritability using Model B was 0.52 ± 0.02 for CW, 0.50 ± 0.02 for RA, 0.38 ± 0.02 for RT, 0.37 ± 0.02 for SF, 0.48 ± 0.02 for YP, and 0.51 ± 0.02 for MS, all of which were within the range of values previously estimated through the use of pedigree or genomic information (Oyama 2011; Watanabe et al. 2014; Ogawa et al. 2016). Neither Model B nor Model S could include the effects of fattening farm because of the lack of this information, which might be rather over-estimate of heritability. For example, using pedigree information, Ogawa et al. (2021) estimated heritabilities of the six carcass traits using a statistical model ignoring the effects of fattening farm to be higher than those estimated accounting the farm effects. The heritabilities estimated using Model S ranged from 98.5% to 102.5% of those estimated using Model B. Therefore, the differences between the models seem to be negligible, and estimates of additive genetic and residual variances were similar. Furthermore, the values of deviance information criterion (Spiegelhalter et al. 2002) were similar between the models, Pearson's correlation coefficient between $\hat{\mathbf{g}}_B$ and $\mathbf{S}\hat{\boldsymbol{\beta}}+\hat{\mathbf{g}}_S$ was always >0.99, and the simple regression coefficient was almost 1, where $\hat{\mathbf{g}}_B$ was independent and $\mathbf{S}\hat{\boldsymbol{\beta}}+\hat{\mathbf{g}}_S$ was dependent variables in the regression.

Figure 4 shows the calculated ratio of the sample variance of the components of $\mathbf{S}\hat{\boldsymbol{\beta}}$ that of $\hat{\mathbf{g}}_B$. The ratio for YP tended to increase with K, but the ratio for other traits tended to increase with the number of SNPs used. These results suggest that the addition of $\mathbf{S}\boldsymbol{\beta}$ to the GP model simply led to the division of $\hat{\mathbf{g}}_B$ into $\mathbf{S}\hat{\boldsymbol{\beta}}$ and. As Thomasen et al. (2013) stated, the population structure is already accounted for by using a genomic relationship matrix and the use of SNP markers distributed across the genome in the STRUCTURE analysis were both relevant to these results. On the latter point, Thomasen et al. (2013) also discussed that an analysis might be required considering the different persistency of LD phase among subpopulations through the genomic regions. The differences among traits shown in Figure 4 might be caused by the differences on important genomic regions among traits and by what each cluster reflects, as noted by Daetwyler et al. (2012) and Guo et al. (2014).

Mean accuracy of $\hat{\mathbf{g}}_B$ was 0.83 for CW, 0.83 for RA, 0.78 for RT, 0.77 for SF, 0.82 for YP, and 0.83 for MS. Mean accuracies of $\hat{\mathbf{g}}_S$ were 0.1% to 8.0% lower than those of $\hat{\mathbf{g}}_B$. As shown in Figure 5 for MS, for example, mean accuracy decreased with both the number of SNPs used and the K-value. The decrease of accuracy was due to the increased PEV, which could be caused by the greater model complexity, probably by some confounding between $\mathbf{S}\boldsymbol{\beta}$ and $\mathbf{g}_S$. Note that we calculated the model-based accuracy of predicted genomic breeding value for an individual (Clark et al. 2012), which could be different from the accuracy evaluated using Pearson's correlation as used in previous studies (e.g., Onogi et al. 2014; Ogawa et al. 2016; Takeda et

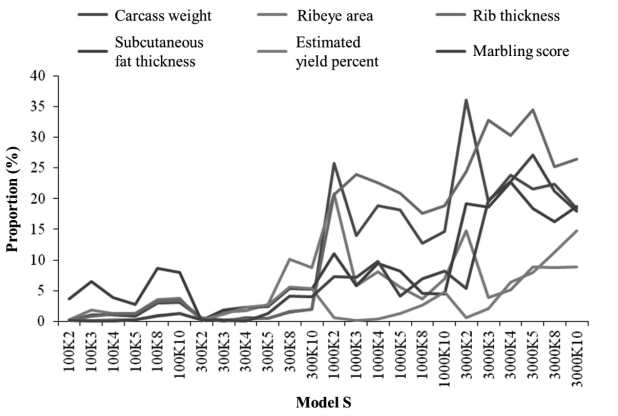

Figure 4. Changes in ratios of the sample variance of $\mathbf{S}\hat{\boldsymbol{\beta}}$ estimated using model S to that of predicted genomic breeding values using model B. Settings for Model S are ordered by K-value within the number of single nucleotide polymorphism markers used. For example, Model S considering the results of STRUCTURE analysis with K = 4 and 100 SNPs is denoted as 100K4.

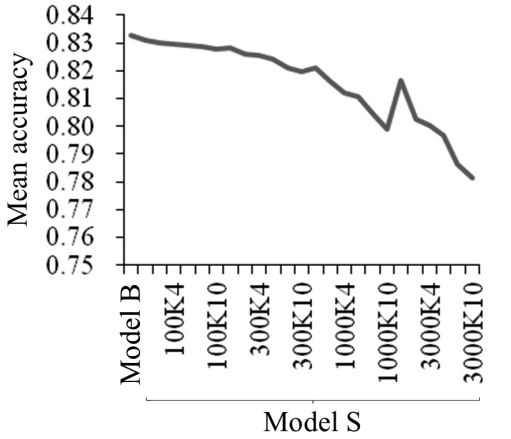

Figure 5. Changes in mean accuracy of genomic prediction for marbling score among models. Settings for Model S are ordered by K-value within the number of single nucleotide polymorphism markers used. For example, Model S considering the results of STRUCTURE analysis with K = 4 and 100 SNPs is denoted as 100K4.

al. 2020) and that estimated as genetic correlation used in Saatchi et al. (2011). On this point of view, previous studies have been performed to develop the methodology for assessing the accuracy of GP (e.g., Dekkers 2007; Goddard 2009; Dekkers et al. 2021), and they seemed to predict the model-based accuracy with their modifications of various theoretical assumptions.

The accuracy of GP depends on not only the size of the training population (Goddard and Hayes 2009), but also LD, additive genetic relatedness, and QTL co-segregation (de Roos et al. 2009; Toosi et al. 2010; Habier et al. 2013). These parameters are in relation to the population structure, which could underlie our results, such that $\hat{\mathbf{g}}_B$ was split into $\mathbf{S}\hat{\boldsymbol{\beta}}$ and $\hat{\mathbf{g}}_S$. In structured populations, genomic variability could be partitioned into components within and between genetic clusters (Janss et al. 2012). Analytical models for large-scale genome-wide association studies often include the results of principal component and STRUCTURE analyses to correct for genomic variability between clusters and therefore decrease the possibility of false positives (Price et al. 2010). The performance of GP models with population structures has been investigated by using multi-breed or structured single-breed training populations (e.g., Daetwyler et al. 2012; Janss et al. 2012; Thomasen et al. 2013). Nontheless, there is no guarantee that the information incorporated into the GP model fully explain only the genomic variability between clusters (Lehermeier et al. 2017), and its effect may vary across traits and clusters (Daetwyler et al. 2012; Guo et al. 2014). Otherwise of our method, various GP models have been proposed, and their performance has been examined (e.g., Karoui et al. 2012; Dadousis et al. 2014; de los Campos and Sorensen 2014). Such efforts should be continued to improve the accuracy of GP in the Japanese Black population.

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