

〔原著論文〕

ゲノムワイドな一塩基多型マーカーを用いた 黒毛和種集団における遺伝的特性把握の試み

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Inferring genetic characteristics of Japanese Black cattle populations using genome-wide single nucleotide polymorphism markers

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ABSTRACT

This study attempted to infer the population structure of Japanese Black cattle by using genotype data on 33,063 genome-wide single nucleotide polymorphism (SNP) markers of totally 4,348 fattened steers slaughtered at carcass markets in Tokyo, Osaka, Hyogo, Tottori, and Hiroshima prefectures. We evaluated allele frequency, heterozygosity, linkage disequilibrium, correlation of linkage phase, and genotype concordance among the steers. The distribution of allele frequencies in the steers sampled in Hyogo differed from the others, showing >10% of the SNPs as monomorphic. Observed heterozygosity was lowest and degree of linkage disequilibrium was highest in Hyogo. Genotypes were more similar among Hyogo steers than between other steer pairs. These results show the genetic characteristics of the Japanese Black cattle populations inferred from genotype data on genome-wide SNPs obtained using a commercial chip.

Key words: allele frequency, Japanese Black cattle, linkage disequilibrium, population structure, single nucleotide polymorphism

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INTRODUCTION

The historical closed breeding system in Japanese Black cattle, with breeding plans varying from prefecture to prefecture, has brought a subpopulation structure (Nomura *et al.* 1987; Namikawa 1992). In Japanese Black production, prefectures may be roughly divided into those as suppliers of seedstocks including ones such as Hyogo, Tottori, and Hiroshima prefectures, and those as their multipliers (Nomura and Sasaki 1986). In Hyogo prefecture, there has been continuing closed breeding (Takayanagi *et al.* 1996; Honda *et al.* 2001, 2004). In 1991, genetic evaluation of carcass traits based on pedigree information using mixed model methodology was begun (Ashida and Iwaisaki 1998; Sasaki *et al.* 2006; Wagyu Registry Association 2007). This led to intensive use of frozen semen from fewer elite sires beyond prefectural borders, resulting in an increase of the genetic relationship among subpopulations and a sharp decline in effective population size, revealed by using wide pedigree information (Nomura *et al.* 2001).

DNA markers can be used to investigate population structure in livestock. Nishimaki *et al.* (2013) evaluated the structure of eight subpopulations of Japanese Black cattle, including those of Hyogo and Hiroshima prefectures, using 52 microsatellite markers. Other studies elucidated the population structure of foreign cattle by using genome-wide high-density single nucleotide polymorphism (SNP) markers (e.g., de Roos *et al.* 2008; Engelsma *et al.* 2012; Thomasen *et al.* 2013). The SNP-based approach might be powerful enough to study the population structure in Japanese Black cattle. Here we attempted to extract information on the population structure of Japanese Black cattle using genotype data on genome-wide SNP markers of fattened steers transported to carcass markets including major seed stock prefectures in Japan.

MATERIALS AND METHODS

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).

We used genotype information on 33,063 SNPs with minor allele frequencies (MAFs) of >0.01, in Hardy-Weinberg equilibrium (HWE; $P > 0.001$), of 4,348 fattened steers in total. The steers were originally sampled for studies of genomic prediction of carcass traits (Ogawa *et al.* 2016;

Watanabe 2016), and their pedigree information was not available. The samples were collected during 2000 to 2014 at the Tokyo Metropolitan Central Wholesale Market, the Osaka Municipal South Port Wholesale Market, and the markets in Hyogo, Tottori, and Hiroshima prefectures. Genomic DNA extraction, SNP genotyping, and missing genotype imputation were conducted following Ogawa *et al.* (2016) and Watanabe (2016). Steers marketed within a prefecture are denoted as, for example, “Hyogo” steers, and 2,300 steers transported to the Tokyo and Osaka markets are denoted as “TO” steers. The number of steers in each prefecture are shown in Table 1. The steers were assumed to be samples from the commercial population in each prefecture. The TO steers were sampled at the two large-scale carcass markets in Tokyo and Osaka where Japanese Black fattened steers from all over Japan are marketed, and therefore they may be considered to reflect the parameters of the overall population structure of Japanese Black cattle (Ogawa *et al.* 2014).

The allele frequencies of SNPs, which were initially determined by using all (4,348) steers, were again calculated separately within each of the Hyogo, Tottori, Hiroshima, and TO steers. Observed heterozygosity (H_o) for each steer was based on the proportion of heterozygous SNPs. Expected heterozygosity (H_e) in HWE was calculated as $\sum_{i=1}^t 2p_i(1-p_i)/t$ (Engelsma *et al.* 2012), where p_i is the MAF of SNP i in all (4,348) steers and t is the number of SNPs.

Haplotypes were phased by Beagle 4.1 software (Browning & Browning 2007) with the default settings but an effective population size of 50 (Nomura *et al.* 2001). Linkage disequilibrium (LD) coefficients between two SNPs, namely r and r^2 (Hill & Robertson 1968), were calculated for each SNP pair ≤ 2 Mb apart. Pearson’s correlation coefficients of r between subgroups were obtained according to de Roos *et al.* (2008) and Thomasen *et al.* (2013).

Genomic relationship matrices (G matrices) \mathbf{G}_V (VanRaden 2008) and \mathbf{G}_V (Yang *et al.* 2010) were respectively calculated as:

$$\mathbf{G}_V = \frac{\mathbf{M}\mathbf{M}'}{\sum_{i=1}^t 2p_i(1-p_i)} \quad \text{and} \quad \mathbf{G}_V = \frac{\mathbf{M}\mathbf{D}\mathbf{M}'}{t},$$

where \mathbf{M} is the matrix with element m_{ji} equal to $2-2p_i$, $1-2p_i$, and $0-2p_i$ when the number of counted allele at SNP i in individual j is 2, 1, and 0, respectively; and \mathbf{D} is the diagonal matrix whose i th diagonal element is $1/2p_i(1-p_i)$.

Genetic diversity inferred using SNPs

The allele frequency p_i was determined by using all (4,348) steers.

To assess the degree of genotype concordance between steers, we obtained the proportions of SNPs where the genotypes were the same (namely 2 to 2, 1 to 1, 0 to 0; denoted as P_2), either of the two alleles corresponded (2 to 1, 1 to 0, and vice versa; P_1), or no allele was shared (2 to 0, and vice versa; P_0) between two steers. Expected P_2 , P_1 , and P_0 values for SNP i in HWE were calculated from the allele frequencies in all (4,348) steers as:

$$E(P_2) = \sum_{i=1}^t \left\{ p_i^4 + 4p_i^2(1-p_i)^2 + (1-p_i)^4 \right\} / t,$$

$$E(P_1) = \sum_{i=1}^t 4p_i(1-p_i) \left\{ p_i^2 + (1-p_i)^2 \right\} / t,$$

$$E(P_0) = \sum_{i=1}^t 2p_i^2(1-p_i)^2 / t.$$

RESULTS AND DISCUSSION

The distribution of allele frequencies of 33,063 SNPs in Hyogo steers was different from the other prefectures (Figure 1). Because the allele frequencies were determined by all (4,348) steers, several alleles showed the larger frequency than 0.5 within each prefecture as shown in Figure 1. For instance, the number of SNPs with allele frequency of >0.5 within each prefecture was 3,782 SNPs in Hyogo steers versus 408 SNPs in TO steers, 830 SNPs in Tottori steers, and 852 SNPs in Hiroshima steers. There were 0 monomorphic SNPs in TO and Tottori, 1 SNP in Hiroshima, and 4,237 SNPs in Hyogo, which amounts to $>10\%$ of the total SNPs. Average HO was similar to HE in TO, Tottori, and Hiroshima steers, but was significantly lower in Hyogo steers (Table 1). The standard deviation and maximum value were lowest in Hyogo steers, although the minimum value was similar to the others. These results indicate that Japanese Black cattle in Hyogo prefecture have more homozygous genotypes owing to a higher degree of inbreeding (Honda et al. 2001). Nishimaki et al. (2013) assessed the genetic diversity of Japanese Black cattle using information on 52 microsatellite markers in 1,006 fattened animals from eight prefectures including Hyogo and Hiroshima, revealing that the heterozygosity, average allele number, and allelic richness were significantly lower in animals from Hyogo.

Patterns of LD decay in Tottori, Hiroshima, and TO steers were similar to each other (Figure 2). On the other hand, r^2 values in Hyogo steers were obviously higher than those of others, reflecting the effects of the ongoing closed

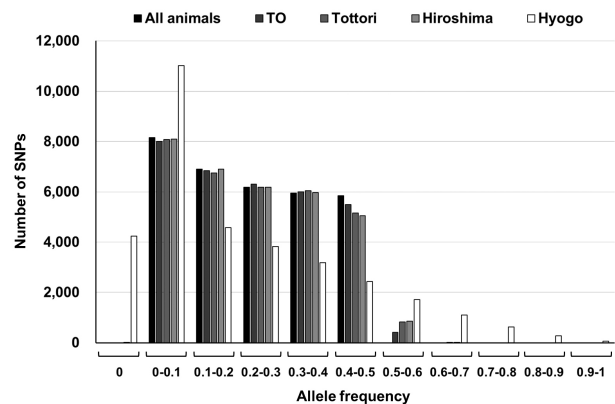


Figure 1 Histograms of the number of single nucleotide polymorphism (SNP) on the different allele frequencies of the SNPs. Class 0 includes only monomorphic SNPs, and class 0-0.1 includes SNPs with an allele frequency of just 0.1 but not those with allele frequencies of just 0. Allele frequencies within subgroup were calculated based on the only inner steers of each subgroup.

Table 1. Expected (HE) and observed heterozygosity (HO) of fattened steers

Group	No. of steers	HE	HO				nSNP of $p > 0.5$
			Ave	SD	Min	Max	
All	4,348	0.31	0.32	0.03	0.20	0.39	0
Tottori	1,036		0.32	0.02	0.21	0.39	830
Hiroshima	733		0.32	0.02	0.21	0.36	852
Hyogo	279		0.23**	0.01	0.20	0.27	3,782
TO	2,300		0.32	0.02	0.23	0.39	408

Ave, average; SD, Standard deviation; Min, Minimum value; Max, Maximum value; nSNP of $p > 0.5$, number of SNPs with allele frequency $p > 0.5$ in each prefecture; TO, steers from Tokyo Metropolitan Central Wholesale Market and Osaka Municipal South Port Wholesale Market; **, P -value < 0.01

breeding in the prefecture (Honda et al. 2001; Nishimaki et al. 2013). Correlations for r values between Hyogo steers and others were lower (Figure 3), reflecting the isolation of the population in Hyogo from the other subpopulations for a long time, owing to closed breeding begun before establishment of the Japanese Black breed in 1944 (Mukai et al. 1989; Honda et al. 2001).

The ranges in values of diagonal elements were larger by G_V (Table 2), probably because G_V adds more weight than G_Y to the SNPs with higher allele frequencies used for the matrix calculation (Meuwissen et al. 2011; Ogawa et al. 2016). The results from a genomic relationship-based approach may be affected by the SNP markers used, the values of the allele frequencies, and the calculation method of the relationship matrix (e.g., VanRaden 2008; Chen et al. 2011; Moore et al. 2019). Here, we calculated the two G matrices by using SNPs in HWE and the allele frequencies based on all (4,348) steers, and the elements of

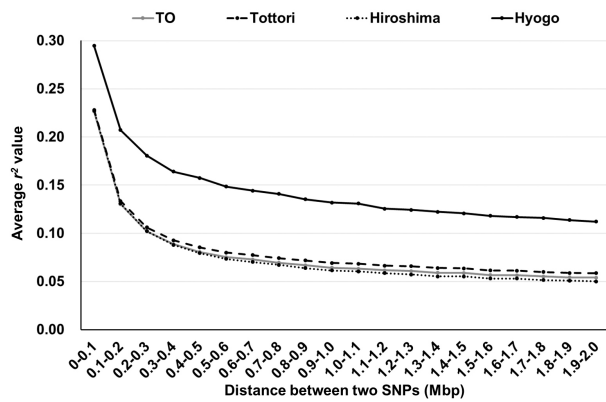


Figure 2. Changes in average squared linkage disequilibrium coefficient (r^2) on distance between two single nucleotide polymorphism (SNP) markers. Class of 0-0.1 includes SNP pairs with a distance of just 0.1 Mbp but not those with a distance of just 0 Mbp.

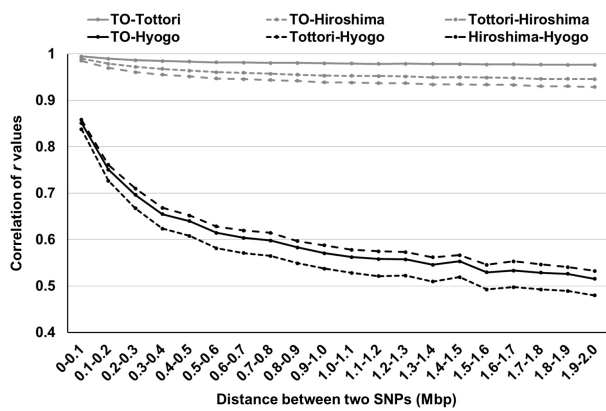


Figure 3. Changes in correlations of linkage disequilibrium coefficient (r) between subgroups on distance between two single nucleotide polymorphism (SNP) markers. Class 0-0.1 includes SNP pairs with a distance of just 0.1 Mbp but not those with a distance of just 0 Mbp.

G matrices were extracted for each prefecture separately. The average diagonal elements of the two G matrices were theoretically expected as 1. Considering the results of H_o (Table 1), Hyogo steers have more homozygous genotypes, which lead to an expectation of the average diagonal elements for Hyogo steers as >1 . However, the average diagonal element in Hyogo steers was 1.00 by G_V and 0.87 by G_Y (Table 2), probably because of the values of allele frequencies used in calculating the G matrices. When the G matrices were composed from the mixture populations, the diagonal elements of the matrix of inner subpopulation might be biased due to the discrepancy of allele frequencies on the subpopulation steers from the allele frequencies on all (4,348) steers. VanRaden (2008) stated that the genomic inbreeding coefficient, defined as $G_{jj}-1$ for individual j , is

Table 2. Summary of diagonal elements of the two genomic relationship matrices

Group	G_V				G_Y			
	Ave	SD	Min	Max	Ave	SD	Min	Max
Tottori	1.00	0.09	0.78	1.36	1.01	0.14	0.70	1.68
Hiroshima	1.00	0.09	0.80	1.40	1.01	0.13	0.72	1.62
Hyogo	1.00	0.04	0.92	1.15	0.87	0.04	0.80	1.03
TO	1.00	0.09	0.80	1.42	1.01	0.14	0.70	1.80

G_V and G_Y , Genomic relationship matrices based on VanRaden (2008) and Yang et al. (2010), respectively. For other abbreviations, see Table 1.

greater if the individual is homozygous for rare alleles than if it is homozygous for common alleles. The standard deviations of diagonal elements were lower for Hyogo steers.

Some of the Hyogo-other steer pairs showed relatively high values of the corresponding upper triangular elements of the G matrices (Table 3), likely reflecting gene flow from the Hyogo subpopulation to others. We theoretically expected the averages of the upper triangular elements of the two G matrices to be 0, although those among Hyogo steers were 0.31 by G_V and 0.26 by G_Y (Table 3). To resolve the discrepancy between the expected and realized values, we calculated P_2 , P_1 , and P_0 values. The average P_2 was highest but the average P_1 and P_0 were lowest within Hyogo-Hyogo steer pairs (Table 4), indicating that Hyogo steers had more same homozygous genotypes with each other than other pairs, possibly owing to the lower genetic diversity in the Japanese Black population in Hyogo (Honda et al. 2001; Nomura et al. 2001).

As far as we know, this is the first study to report the results of compared allele frequencies, heterozygosity for individuals, r^2 values, correlations of r values, elements of G matrices, and genotype concordances calculated by using genome-wide SNP markers among certain subgroups of

Table 3. Summary of upper triangular elements of the two genomic relationship matrices

Group pair		G_V				G_Y			
1	2	Ave	SD	Min	Max	Ave	SD	Min	Max
Tottori	Tottori	0.01	0.07	-0.23	0.63	0.01	0.06	-0.19	0.63
	Hiroshima	0.00	0.06	-0.27	0.69	0.00	0.05	-0.21	0.84
	Hyogo	-0.03	0.08	-0.23	0.55	-0.03	0.07	-0.19	0.46
Hiroshima	TO	0.00	0.06	-0.25	0.63	0.00	0.06	-0.20	0.69
	Hiroshima	0.01	0.07	-0.24	0.56	0.01	0.06	-0.19	0.57
	Hyogo	-0.01	0.09	-0.27	0.46	-0.01	0.08	-0.21	0.39
Hyogo	TO	0.00	0.06	-0.26	0.59	0.00	0.05	-0.21	0.60
	Hyogo	0.31	0.07	0.12	0.59	0.26	0.06	0.11	0.51
	TO	-0.02	0.08	-0.26	0.40	-0.02	0.07	-0.20	0.35
TO	TO	0.00	0.06	-0.24	0.62	0.00	0.05	-0.19	0.64

For abbreviations, see Tables 1 and 2.

Table 4. Average proportions of single nucleotide polymorphisms at which both, either, or neither of the two alleles were shared between two animals (P_2 , P_1 , and P_0 , respectively)

Group pair		Proportion		
1	2	P_2	P_1	P_0
Expected value		0.56	0.38	0.06
Tottori	Tottori	0.56	0.39	0.06
	Hiroshima	0.55	0.39	0.06
	Hyogo	0.57	0.36	0.07
	TO	0.55	0.39	0.06
Hiroshima	Hiroshima	0.56	0.39	0.06
	Hyogo	0.57	0.36	0.07
	TO	0.55	0.39	0.06
Hyogo	Hyogo	0.68	0.28	0.04
	TO	0.57	0.36	0.07
	TO	0.55	0.39	0.06

For abbreviations, see Table 1.

Japanese Black fattened steers. The results for Tottori and Hiroshima steers seem to be only slightly different from those for TO steers, which might reflect the fact that the genetic composition of these prefectures has been penetrated by gene flow due to intensive use of fewer common elite sires across prefectures (Nomura et al. 2001; Nishimaki et al. 2013). On the other hand, the results for Hyogo steers were obviously different from those for the others, mainly reflecting the lowered genetic diversity in the Hyogo population due to continuous closed breeding from the 1900s (Mukai et al. 1989; Honda et al. 2001).

Note that we used only a limited number of animals, DNA markers, and simple approaches and could not use pedigree information; that some fattened animals transported to carcass market in a prefecture might have been born in different prefectures; and that, as Nishimaki et al. (2013) also stated, the genetic diversity of commercial populations could change in relatively short time frames, since sires mated for fattened animals may vary year by year. More informative results might be obtained by using more samples with more DNA markers, including copy number variation and indel information obtained by next generation DNA sequencing techniques (Hirano et al. 2013; Pérez-Enciso 2014; Sasaki et al. 2021), as well as pedigree information (Komiya et al. 2021).

Our results also provide information on implementing genomic prediction in Japanese Black cattle. The size of a training population heavily affects the accuracy of genomic prediction (Daetwyler et al. 2008; Goddard 2009). Ongoing schemes of genomic prediction for carcass

traits in this breed construct its training population by collecting records of carcass performance and SNP genotypes for fattened animals from multiple carcass markets (Watanabe 2016). Information on genetic characteristics for subpopulations obtained by using genome-wide SNP markers could be useful for constructing better training population(s). In addition, our approach can probably content a need for systematic studies on controlling inbreeding in the long-term and genetic diversity by using genome-wide marker information (e.g., de Cara et al. 2011; Sonesson et al. 2012; Eynard et al. 2016), because genomic selection would lower the effective population size in this breed, as already observed in dairy cattle populations (e.g., Doekes et al. 2018; Forutan et al. 2018; Doublet et al. 2019).

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