ORIGINAL ARTICLE

Estimation of breeding values from large-sized routine carcass data in Japanese Black cattle using Bayesian analysis

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ABSTRACT

Volumes of official data sets have been increasing rapidly in the genetic evaluation using the Japanese Black routine carcass field data. Therefore, an alternative approach with smaller memory requirement to the current one using the restricted maximum likelihood (REML) and the empirical best linear unbiased prediction (EBLUP) is desired. This study applied a Bayesian analysis using Gibbs sampling (GS) to a large data set of the routine carcass field data and practically verified its validity in the estimation of breeding values. A Bayesian analysis like REML-EBLUP was implemented, and the posterior means were calculated using every 10th sample from 90 000 of samples after 10 000 samples discarded. Moment and rank correlations between breeding values estimated by GS and REML-EBLUP were very close to one, and the linear regression coefficients and the intercepts of the GS on the REML-EBLUP estimates were substantially one and zero, respectively, showing a very good agreement between breeding value estimation by the current GS and the REML-EBLUP. The current GS required only one-sixth of the memory space with REML-EBLUP. It is confirmed that the current GS approach with relatively small memory requirement is valid as a genetic evaluation procedure using large routine carcass data.

Key words: breeding value estimation, carcass field data, computational aspect, Gibbs sampling, Japanese Black cattle.

INTRODUCTION

The genetic evaluation for carcass traits of Japanese Black cattle using routine carcass field data started in 1991. The evaluation has currently been conducted in almost all the producing prefectures. At the beginning stage of this evaluation, sizes of the official data sets to be analyzed were relatively small and then the empirical best linear unbiased prediction (EBLUP) of breeding values had been implemented using variance components (VCs) estimated by the restricted maximum likelihood (REML; Patterson & Thompson 1971) employing the expectation-maximization (EM) algorithm (Dempster *et al.* 1977), and later on, employing the EM algorithm using an Aitken acceleration technique. In recent years, for the step of REML estimation of VCs, a computationally more efficient procedure of the average information (AI) algorithm (Gilmour *et al.* 1995; Johnson & Thompson 1995) has been used (Ashida & Iwaisaki 1998, 1999; Iwaisaki & Ashida 2004). Currently, however, the official data set sizes are increasing very rapidly, especially in some prefectures under active production (Wagyu Registry Association 2008).

Several strategies of the Markov chain Monte Carlo methods such as Gibbs sampling (GS) (Geman & Geman 1984; Gelfand & Smith 1990) for generating marginal distributions have been proposed (Wang *et al.* 1994; García-Cortés & Sorensen 1996; Sorensen & Gianola 2002; Shariati & Sorensen 2008;

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Waagepetersen *et al.* 2008; Waldmann *et al.* 2008). Single-site Gibbs sampler does not need the inverse of the coefficient matrix of mixed model equations and requires only storage of the mixed model equations (Wang *et al.* 1994; Sorensen & Gianola 2002).

Accordingly, a possible alternative approach by Bayesian implementation using single-site Gibbs sampler has been considered and a standard specification of the GS conditions to estimate the relevant VCs has been proposed to analyze the official large data sets of carcass traits in Japanese Black cattle (Arakawa *et al.* 2008). This specification was constructed on a Bayesian approach like REML using non-informative priors on the relevant VCs. However, whether the GS scheme with the proposed specification has essentially the similar ability to estimate breeding values with that of the REML-EBLUP approach is unclear, when applied to an actual large-sized data. Also, only a very limited number of papers have been published on the comparison of Bayesian analyses and EBLUP from the viewpoint of breeding value estimation (Wang *et al.* 1994; Schenkel *et al.* 2002; Ben Gara *et al.* 2006).

This study applied the specification of GS conditions proposed by Arakawa *et al.* (2008) to an actual very large set of the routine carcass field data including about 600 thousand animals in pedigree file, and mainly investigates the estimated breeding values compared with the conventional REML-EBLUP estimates. The computational aspects of the current GS analysis were also examined relative to the conventional REML-EBLUP approach.

MATERIALS AND METHODS

Data used in the present analyses, collected from 1987 through 2007 and provided by one branch of the Wagyu Registry Association, consisted of carcass records of 381 491 Japanese Black fattening animals. The data set included records of progenies of 828 sires and 171 945 dams. The number of animals in the pedigree file was 616 743. Carcass traits analyzed were carcass weight (CW), ribeye area (RA), rib thickness (RT), subcutaneous fat thickness (SFT), estimated yield percent (EYP), and marbling score (MS) that were assessed by official graders according to the carcass grading standards (JMGA 1988). An outline of the data is given in Table 1 with the fundamental statistics for the 6 traits.

A single-trait individual animal model was used to describe the records of each trait. The operational linear model included discrete effects of fattening farms, years at slaughter, sexes of animals, animals' breeding values, and residuals. Age at slaughter (m) and degree of inbreeding of animal were also considered as a covariate.

Table 1 Outline and fundamental statistics (mean ± SD) of carcass traits data used

Item	Characteristics
No. of records	381 491
No. of sires	828
No. of dams	171 945
No. of animals in the pedigree file	616 743
No. of fattening farms	1 173
Age at carcass market, m	29.1 ± 1.6
Inbreeding coefficient, %	3.6 ± 3.7
Trait†	
CW, kg	426.4 ± 55.3
RA, cm²	51.2 ± 7.6
RT, cm	7.4 ± 0.9
SFT, cm	2.7 ± 0.9
EYP, %	73.2 ± 1.4
MS, 0–5	1.4 ± 0.7

†CW, carcass weight; RA, ribeye area; RT, rib thickness; SFT, subcutaneous fat thickness; EYP, estimated yield percent; MS, marbling score.

In the current Bayesian analysis via GS, multivariate normal distributions were used as the priors for fattening farm effects and breeding values of animals, and a flat improper prior distribution was used for the nuisance parameters except for farm effect. For additive genetic and residual VCs, independent scaled inverted chi-square distributions were used. In order to implement a REML-like Bayesian analysis, the prior distributions for the VCs were assumed to be non-informative, so that the values of degree of belief and scale parameters were set to −2 and 0, respectively, according to Wang *et al.* (1994) and Sorensen and Gianola (2002).

Single-site Gibbs sampler (Wang *et al.* 1994; Sorensen & Gianola 2002) was used to generate marginal posterior distributions for all the effects in the model, and a total chain length of 100 000 iterations was run. The first 10 000 iterations were discarded as burn-in, and the samples of the parameters of our concern were saved for each of 10 iterations. Then the samples obtained were used to estimate features of the marginal posterior distribution such as mean and standard deviation. Marginal posterior distributions were estimated using non-parametric kernel estimators (Silverman 1986) by the KernSmooth package in the R software (Wand & Jones 1995). Monte Carlo errors and effective sample sizes of the estimates were computed according to Geyer (1992) and Sorensen and Gianola (2002). For more details on the current Bayesian framework using GS, see Arakawa *et al.* (2008).

The EBLUP of breeding values were also conducted using the estimates of the VCs by the AI-REML procedure (Ashida & Iwaisaki 1998, 1999) in which fattening farm effects, animals' breeding values and residuals were regarded as random effects. Convergence of the REML estimates was reached when changes in the variance ratios between two consecutive rounds were all less than 10^{-8}. Standard errors of the REML estimates were obtained from the information on the inverse of the AI matrix, and those of heritability estimates were computed approximately with the delta method

based on the Taylor expansion (Lynch & Walsh 1998; Waldmann & Ericsson 2006).

The required memory was assessed by considering 8 bytes for *double* and 4 bytes for *integer* variables. Computations were carried out on a workstation with dual Xeon 2.8 GHz processors and 2.0 GB RAM under Windows XP.

RESULTS AND DISCUSSION

Effective sample sizes of farm, additive genetic, and residual variances and heritability ranged from 4304 for RA to 4500 for SFT, from 290 for RT to 503 for SFT, from 314 for MS to 525 for SFT, and from 342 for RT to 590 for CW, respectively. For all the carcass traits, the magnitude of effective sample size obtained here was slightly larger than that reported by Arakawa *et al.* (2008). Monte Carlo errors of posterior means in all cases were found to be smaller than 1% of the means (data not shown). These results indicated that the Gibbs chain lengths of the VCs and heritabilities were sufficiently long and that the estimates of features of marginal posterior distributions could be considered accurate enough.

Posterior means and posterior standard deviations obtained with GS and the corresponding estimates and their standard errors with REML are shown in Table 2 for the VCs and heritabilities for 6 carcass traits. Posterior means and posterior standard deviations were all very close to the REML estimates and their standard errors, respectively. Heritability estimates for carcass traits were generally high, and the fraction of the variance due to fattening farm to phenotypic variance

was in the range of 7% for RA and EYP to 21% for CW. These results, except for the standard errors for the VCs, were generally similar to the previous findings of Oyama *et al.* (2004) and Shojo *et al.* (2006).

In simulation studies, the posterior means from GS and the REML estimates were observed to be quite similar, and VCs estimated with the Gibbs sampler had consistently smaller mean squared errors than those obtained with REML (van Tassell *et al.* 1995; Schenkel & Schaeffer 2000). In the case of field data, GS estimates tended to be slightly different from the REML estimates in smaller datasets (Magnabosco *et al.* 2000; Arakawa *et al.* 2008). The current study using a large data set of field carcass records, in which the specification of the GS conditions proposed by Arakawa *et al.* (2008) was applied, resulted in a very close agreement between the results of the Bayesian and the REML analyses for both the point estimate and the standard error. Marginal posterior distributions of the VCs and heritabilities for CW and MS of the 6 carcass traits are depicted as an example in Figures 1 and 2, respectively, in comparison with the normal distributions with means and standard deviations equal to the corresponding REML estimates and their standard errors, respectively. The estimated marginal distributions for CW and MS and also for the remaining traits were found to be all almost symmetrical and to be similar to the normal distributions derived using the results of the REML analyses. Sorensen *et al.* (1994) and Wang *et al.* (1994) suggested that the marginal posterior distributions of variances and their functions can be not

Table 2 Posterior means and standard deviations of variance components and heritabilities for carcass traits with GS, and the corresponding estimates and the approximate standard errors with REML

Trait	Variance component			Heritability
	Farm	Genetic	Residual	
GS				
CW, kg	501.4 ± 22.5	1050.9 ± 16.7	866.5 ± 10.4	0.43 ± 0.01
RA, cm^2	4.4 ± 0.2	30.9 ± 0.5	24.1 ± 0.3	0.52 ± 0.01
RT, cm	0.13 ± 0.01	0.31 ± 0.01	0.37 ± 0.00	0.38 ± 0.01
SFT, cm	0.08 ± 0.00	0.41 ± 0.01	0.28 ± 0.00	0.53 ± 0.01
EYP, %	0.13 ± 0.01	1.18 ± 0.02	0.68 ± 0.01	0.59 ± 0.01
MS, 0 to 5	0.05 ± 0.00	0.30 ± 0.00	0.13 ± 0.00	0.63 ± 0.01
REML				
CW, kg	499.7 ± 22.2	1051.3 ± 16.8	866.2 ± 10.5	0.44 ± 0.01
RA, cm^2	4.4 ± 0.2	31.0 ± 0.5	24.0 ± 0.3	0.52 ± 0.01
RT, cm	0.13 ± 0.01	0.31 ± 0.01	0.37 ± 0.00	0.38 ± 0.01
SFT, cm	0.08 ± 0.00	0.41 ± 0.01	0.28 ± 0.00	0.53 ± 0.01
EYP, %	0.13 ± 0.01	1.18 ± 0.02	0.68 ± 0.01	0.59 ± 0.01
MS, 0 to 5	0.05 ± 0.00	0.30 ± 0.00	0.13 ± 0.00	0.63 ± 0.01

CW, carcass weight; RA, ribeye area; RT, rib thickness; SFT, subcutaneous fat thickness; EYP, estimated yield percent; MS, marbling score.
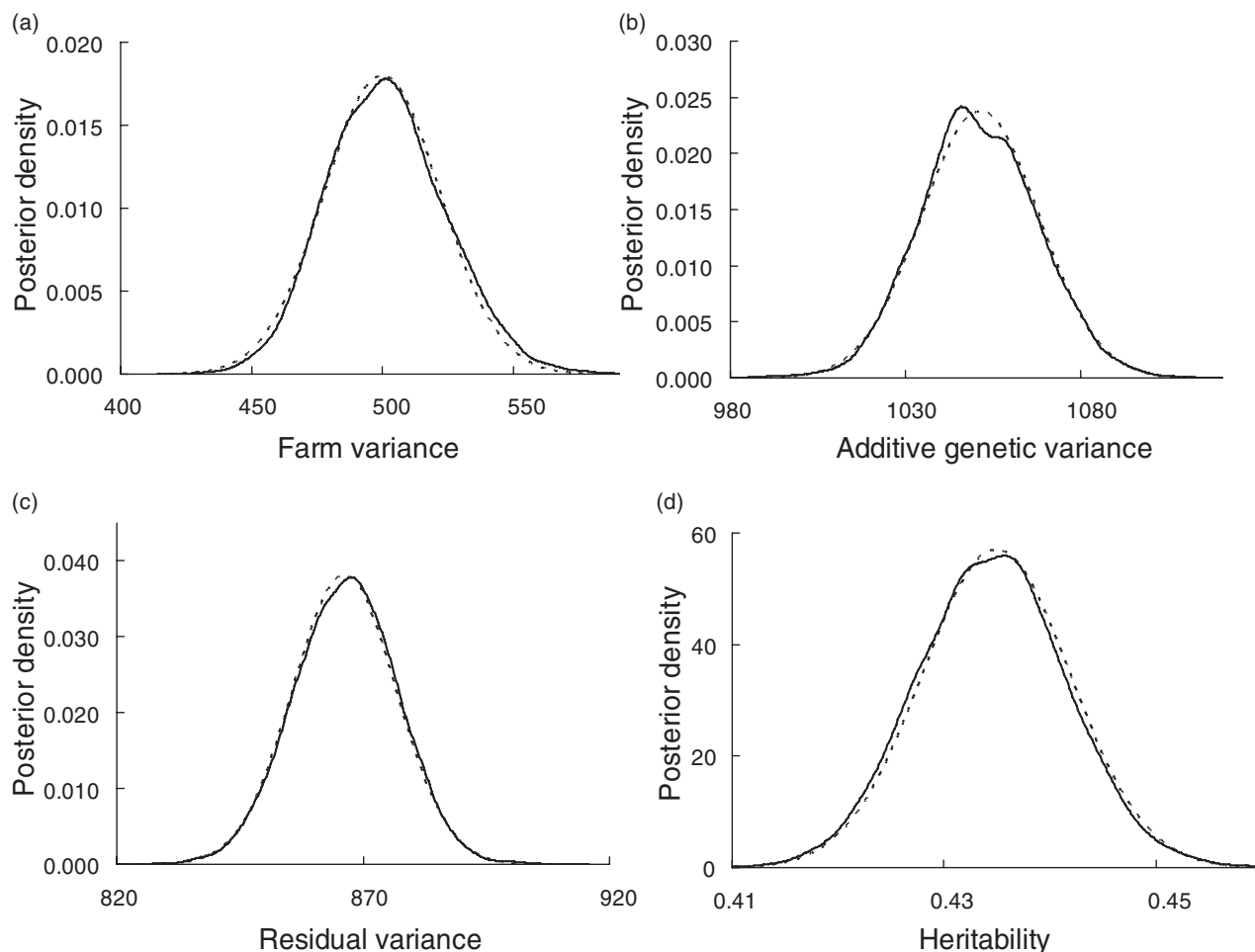
Figure 1 Estimated marginal posterior distribution with GS (solid curve) and normal distribution with mean and standard deviation equal to REML estimate and its approximate standard error, respectively (dotted curve) of farm variance (a), additive genetic variance (b), residual variance (c), and heritability (d) for carcass weight.

symmetrical. In their studies, sizes of data were about one thousand and 1.2 million iterations were implemented. When the heritability estimate is low, it is likely that the marginal posterior distribution has a longer tail in the positive direction.

Table 3 gives moment and rank correlations for breeding values of all animals estimated by the current GS and the REML-EBLUP and the linear regressions of the Bayesian on the REML-EBLUP estimates for 6 carcass traits. Both the moment and rank correlations were obviously very close to 1, and the linear regression coefficients and the intercepts were all substantially 1 and 0, respectively, showing a very good agreement between breeding values estimated by the GS and the REML-EBLUP. These correlations and

regressions for the sires and the dams of animals with record were found to be quite similar to those listed in Table 3 (data not shown).

In a simulation study, Schenkel *et al.* (2002) used 430 records, conducted 10 000 iterations with a burn-in period of 1000 and observed that rank correlations between GS and REML-EBLUP predictions of breeding values were higher than 0.998. Using approximately 110 thousand records of milk yield of Holstein-Friesian cows, with 3000 samples used to estimate marginal distributions of parameters, rankings of bulls and cows on the BLUP breeding values and the Bayesian estimates were found to be very comparable (Ben Gara *et al.* 2006). With these numerical results including the current results, it appears that the Bayesian and REML-
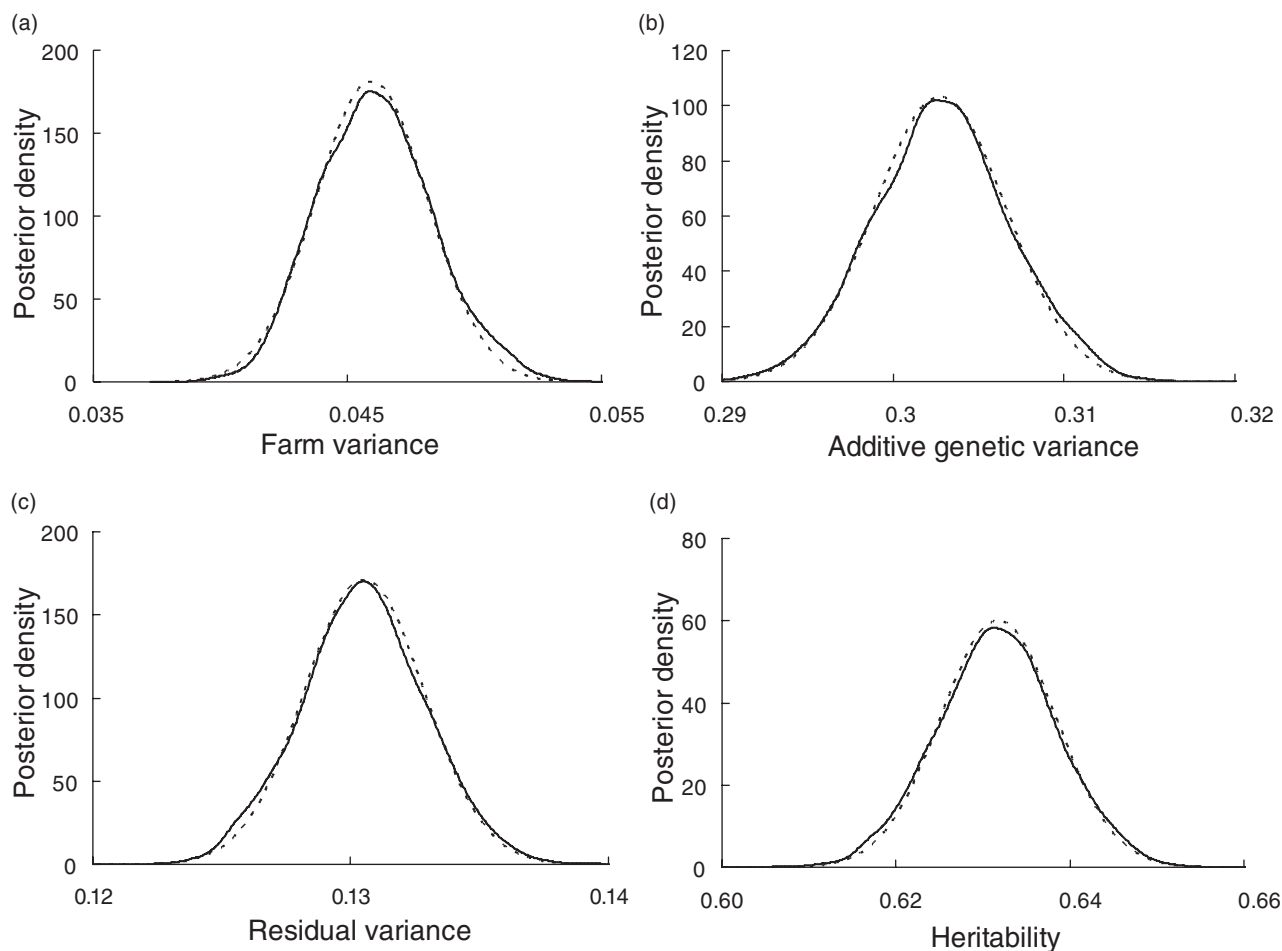
Figure 2 Estimated marginal posterior distribution with GS (solid curve) and normal distribution with mean and standard deviation equal to REML estimate and its approximate standard error, respectively (dotted curve) of farm variance (a), additive genetic variance (b), residual variance (c), and heritability (d) for marbling score.

Table 3 Comparison between posterior means obtained with GS and estimates with REML-EBLUP for breeding values of carcass traits

Trait†	Correlation‡		Regression§	
	Pearson	Spearman	Slope	Intercept
CW, kg	0.9999	0.9999	1.0002	0.1236
RA, cm²	0.9999	0.9999	0.9999	0.0214
RT, cm	0.9999	0.9999	1.0005	0.0021
SFT, cm	0.9999	0.9999	0.9997	0.0027
EYP, %	0.9999	0.9999	0.9999	0.0041
MS, 0 to 5	0.9999	0.9999	1.0004	0.0014

†CW, carcass weight; RA, ribeye area; RT, rib thickness; SFT, subcutaneous fat thickness; EYP, estimated yield percent; MS, marbling score. ‡Pearson: Pearson's moment correlation, Spearman: Spearman's rank correlation. §Slope and intercept for the linear regression of posterior means with GS on estimates with REML-EBLUP.

EBLUP implementations have essentially the same ability to rank animals. From theoretical consideration, one deficiency of EBLUP is that uncertainty of estimation of dispersion parameters are not taken into account when predicting breeding values (Gianola & Fernando 1986; Sorensen *et al.* 1994; Wang *et al.* 1994). Contrary to this, Gibbs sampler can fully take into account those by considering the marginal posterior distributions of breeding values. Wang *et al.* (1994) suggested that the uncertainty of estimation of dispersion parameters are accounted for in the Bayesian probability intervals of predicted breeding values. Following our current results, therefore, further investigation might be necessary from the viewpoints of sampling variances of the estimated breeding values and the details of ranking of animals.

Table 4 Computing time and memory requirements with GS and REML-EBLUP for carcass weight and marbling score

Trait†	Computing time (h)		Required memory (Mb)	
	GS	REML-EBLUP	GS	REML-EBLUP
CW	25.71	4.34	66.64	368.97
MS	25.11	4.29		

†CW, carcass weight; MS, marbling score.

For CW and MS, computing properties of the current GS scheme are, compared with those of the REML-EBLUP procedure, shown in Table 4. As would be expected, implementation of the current GS required about six times more computing time relative to that of REML-EBLUP. Computing time per iteration for the GS method increases approximately linearly for the number of animals in the pedigree file, but this approach necessitates many rounds. On the other hand, computing time of the REML method is known to increase approximately quadratically with respect to the number of the animals, but the REML method using the AI algorithm usually needs only a limited number of iterations. It was observed that GS required only one-sixth of the memory space required with REML-EBLUP. Computationally, the current GS scheme needed only storage of mixed model equations and consequently has memory requirements proportional to the number of animals. However, implementation of the current REML using FSPAK (Pérez-Enciso *et al.* 1994) additionally required the memory space used to obtain the inverse of the coefficient matrix of, and the solutions to, mixed model equations.

In this study, we applied a Bayesian framework via GS using non-informative priors and the GS conditions which were proposed by Arakawa *et al.* (2008) to an actual large set of the routine carcass field data in Japanese Black cattle. Our primary concern was the ability of the current GS scheme in the estimation of breeding values for carcass traits relative to the REML-EBLUP scheme. Memory space requirement in computation, as well as computing time, was also of concern. From the results obtained, it is confirmed that with relatively small memory requirement, the current GS scheme has a very similar ability to the conventional REML-EBLUP scheme and is valid as a genetic evaluation procedure for the large routine carcass data. We have an interest in verifying the details of ranking of sires and dams considering the Bayesian probability intervals of predicted breeding values in the future.

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