

Genetic Contribution of Indigenous Yakutian Cattle to Two Hybrid Populations, Revealed by Microsatellite Variation

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ABSTRACT : Indigenous Yakutian cattle's adaptation to the hardest subarctic conditions makes them a valuable genetic resource for cattle breeding in the Siberian area. Since early last century, crossbreeding between native Yakutian cattle and imported Simmental and Kholmogory breeds has been widely adopted. In this study, variations at 22 polymorphic microsatellite loci in 5 populations of Yakutian, Kholmogory, Simmental, Yakutian-Kholmogory and Yakutian-Simmental cattle were analysed to estimate the genetic contribution of Yakutian cattle to the two hybrid populations. Three statistical approaches were used: the weighted least-squares (WLS) method which considers all allele frequencies; a recently developed implementation of a Markov chain Monte Carlo (MCMC) method called likelihood-based estimation of admixture (LEA); and a model-based Bayesian admixture analysis method (STRUCTURE). At population-level admixture analyses, the estimate based on the LEA was consistent with that obtained by the WLS method. Both methods showed that the genetic contribution of the indigenous Yakutian cattle in Yakutian-Kholmogory was small (9.6% by the LEA and 14.2% by the WLS method). In the Yakutian-Simmental population, the genetic contribution of the indigenous Yakutian cattle was considerably higher (62.8% by the LEA and 56.9% by the WLS method). Individual-level admixture analyses using STRUCTURE proved to be more informative than the multidimensional scaling analysis (MDSA) based on individual-based genetic distances. Of the 9 Yakutian-Simmental animals studied, 8 showed admixed origin, whereas of the 14 studied Yakutian-Kholmogory animals only 2 showed Yakutian ancestry (>5%). The mean posterior distributions of individual admixture coefficient (\hat{q}) varied greatly among the samples in both hybrid populations. This study revealed a minor existing contribution of the Yakutian cattle in the Yakutian-Kholmogory hybrid population, but in the Yakutian-Simmental hybrid population, a major genetic contribution of the Yakutian cattle was seen. The results reflect the different crossbreeding patterns used in the development of the two hybrid populations. Additionally, molecular evidence for differences among individual admixture proportions was seen in both hybrid populations, resulting from the stochastic process in crossing over generations. (*Asian-Aust. J. Anim. Sci.* 2005, Vol 18, No. 5 : 613-619)

Key Words : Yakutian Cattle, Hybrid, Admixture Analysis, Microsatellite DNA

INTRODUCTION

The Yakutian cattle, an endangered native cattle breed in the Sakha Republic (formerly the Yakutia Republic), northeast of Siberia in Russia, exhibit strong resistance to the extreme cold northern climate down to -60°C and to poor feeding. The special characteristics of the Yakutian cattle make them a valuable genetic resource for agriculture in the subarctic regions. To combine their adaptability with productivity, they have been crossed with the Simmental

and Kholmogory cattle breeds on a large scale from the year 1929 onwards (Dmitriev and Ernst, 1989). In this study, two hybrid populations of the Yakutian-Simmental and Yakutian-Kholmogory cattle breeds, established by continuous crossbreeding between native Yakutian cattle and East Siberian populations of Simmental and Kholmogory cattle, were analysed for their genetic admixture. In the Megino-Kangalasskyi region (61°N 130°E), the Yakutian-Simmental hybrid population had been formed by crossing commercial Simmental cows with local Yakutian bulls followed by inter se breeding of the first crossbred generations since 1995. In the Namsky region (62°N 129°E), Kholmogory cows had been crossed with Yakutian bulls, continued by backcrossing with Kholmogory bulls as the recurrent parent over generations since 1979 (Felius, 1995; Ivanova, 1997). However, the not well-registered pedigree information and the stochastic processes in carrying out the breeding schedules made the proportional contributions of the parental cattle populations in the two hybrid populations unclear. Knowledge of the parental contributions in the hybrid populations is of great commercial, conservational, ethnographic and historical

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interest (McAllister et al., 2002; Li et al., 2004; Selvi et al., 2004).

The estimation of the genetic contributions of the ancestral populations to the admixed populations has been the focus of several studies (Parra et al., 1998; Hansen et al., 2001; Kumar et al., 2003). Previous admixture analyses have indicated that compared with traditional genetic markers such as allozymes, highly variable microsatellite DNA loci can provide critical information about the current status of hybrid populations when coupled with admixture analysis at the population and individual levels (Chakraborty et al., 1992; Pritchard et al., 2000; Chikhi et al., 2001).

In this study, the main purpose was to estimate the admixture proportions of the indigenous Yakutian cattle in two contemporary hybrid cattle populations in the Sakha Republic by using population and individual level admixture analyses. Multidimensional scaling analysis (MDSA) based on Nei's (1978) standard genetic distances among all samples was performed for assessing the genetic structure in the cattle populations independent of any prior classification.

MATERIALS AND METHODS

Populations studied and microsatellite analysis

Data for 22 microsatellite DNA loci were collected from 169 cattle individuals representing 5 populations. Two hybrid cattle populations, the Yakutian-Simmental (YS; n=9) and the Yakutian-Kholmogory (YK; n=14), were collected on the collective farm "Krasnaya Zvezda" in the Megino-Kangalasskiy region and on the farm "Edei" of the "Edeisky" collective agricultural enterprise in the Namskiy region of the Sakha Republic, northeast of Russia, respectively. The sampling process ensured that the animals selected were unrelated. Purebred Yakutian cattle (YA; n=54) and Kholmogory cattle (KH; n=42) were sampled in the villages of Batagay-Alyta, Kustur and Uluu-Sysyy in the Sakha Republic and in Kholmogory village in the Arkhangelsk district of northwest Russia, respectively. The Simmental cattle (SIM; n=50) were sampled and genotyped in Germany.

A total of 22 microsatellite loci were included in this investigation: *BoLA-DRBP1*, *HEL10*, *BM1818*, *BM1824*, *BM2113*, *ETH3*, *ETH10*, *ETH152*, *ETH225*, *HEL1*, *HEL5*, *HEL9*, *HEL13*, *ILSTS005*, *ILSTS006*, *INRA005*, *INRA023*, *INRA032*, *INRA035*, *INRA037*, *INRA063* and *CSSM66*. The latter 20 loci have been selected from a list of 30 recommended for collaborative genetic diversity studies (<http://www.ri.bbsrc.ac.uk/cdiv/www/homepage.htm>). Standard polymerase chain reactions (PCR) were performed and the microsatellites were subsequently run on a MegaBACE™500 DNA sequencer (Amersham Biosciences)

according to the manufacturer's recommendations. In order to ensure the compatibility of the results obtained by using different equipment and from different laboratories, two international reference samples used in the Simmental cattle genotyping were also typed in conjunction with the genotyping of the Yakutian, the Kholmogory and the hybrid cattle populations.

Statistical analysis

Departures from Hardy-Weinberg equilibrium (H-WE) were calculated based on exact tests (Guo and Thompson, 1992), including additional tests for heterozygote deficiency and heterozygote excess (Raymond and Rousset, 1995). Fisher's exact tests were further applied to genetic linkage equilibrium (LE) determinations between all locus pairs. These analyses were performed using the program GENEPOP 3.1c (Raymond and Rousset, 1995).

Genetic relationships among individuals of the whole sample set (n=169) were described by a multidimensional scaling analysis (MDSA), which was carried out based on a matrix of Nei's (1978) standard genetic distances among all individuals, using the program VISTA 5.6.3 (Young, 1996). In this analysis, population clusters are identified graphically and it is not possible to assign the individuals to the clusters quantitatively (probabilistically) (Pierpaoli et al., 2003).

We then proceeded to perform the population-level admixture analysis by means of the weighted least-squares method (WLS) (Long, 1991). The term 'population admixture proportion' was used to describe the relative genetic contributions of the parental populations (in this case the indigenous Yakutian cattle population and the Kholmogory or the Simmental cattle population) to each of the hybrid populations (Yakutian-Simmental and Yakutian-Kholmogory cattle populations), regardless of whether the samples consisted of admixed individuals or not (Nielsen et al., 2003). Long's method incorporates the effect of the evolutionary and sampling variance in the admixture estimates. Based on all allele frequencies, it yields simple estimates of the proportions of Yakutian cattle genes in the two hybrid populations and the error variance can be computed easily (Blott et al., 1998; Parra et al., 1998). Chakraborty et al. (1992) have presented closed form expressions for the estimations of admixture proportion and its standard error, which were utilised here.

In addition, a recently developed implementation of a Markov chain Monte Carlo (MCMC) method, likelihood-based estimation of admixture (LEA) (Chikhi et al., 2001), was employed in estimating the relative contributions of the indigenous Yakutian cattle in the two hybrid cattle populations. This method estimates admixture proportions at the population level taking into account drift since the admixture event, variation due to sampling, and uncertainty

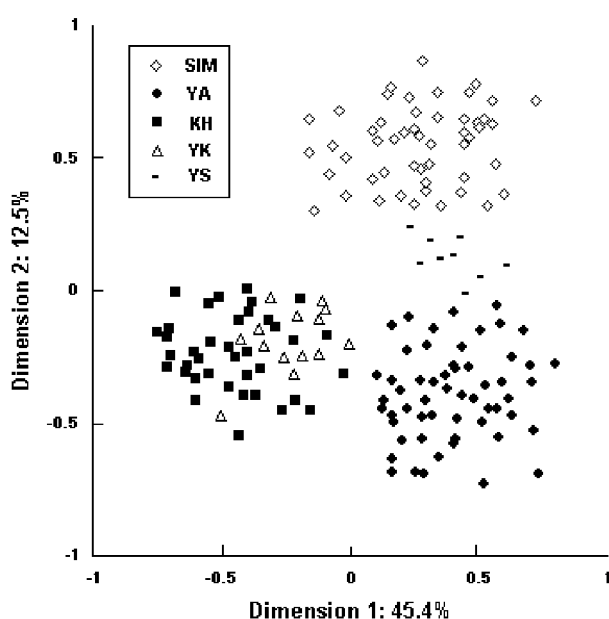


Figure 1. Multidimensional scaling analysis (MDS) of Nei's (1978) genetic distance data of the Yakutian cattle (YA), Simmental cattle (SIM), Kholmogory cattle (KH), Yakutian-Kholmogory hybrid population (YK) and Yakutian-Simmental hybrid population (YS) animals. Dimensions 1 and 2 explain 45.4% and 12.5% of the total variance, respectively.

in the estimation of the ancestral allele frequencies (Chikili et al., 2001; Hansen 2002; Choisy et al., 2004). Each analysis was based on 100,000 MCMC steps and the results were reported as likelihood curves estimated by using the program Locifit (Loader, 1996) as implemented in the Locifit package for R v. 1.0. We chose the point having the highest density as an estimate of the genetic contribution by the indigenous Yakutian cattle, in parallel with 90% probability intervals of the posterior distribution of admixture proportions.

In individual-level admixture analyses the individual admixture coefficient (q) was assessed by using a model-based Bayesian procedure, implemented in the program STRUCTURE (Pritchard et al., 2000). The program STRUCTURE is a Markov chain Monte Carlo approach that clusters individuals to minimize Hardy-Weinberg disequilibrium and gametic phase disequilibrium between loci within groups (Pritchard et al., 2000). Several kinds of analyses, including characterizing parental populations, assigning individuals to these populations, estimating individual admixture coefficient (q) and detecting admixed individuals are allowed in the STRUCTURE based on allele frequency data (Kumar et al., 2003). For this analysis we used the last two options. The posterior distribution of individual admixture coefficient (q) and their 90% probability intervals were estimated by assuming an admixture model with two parental populations, namely, the indigenous Yakutian cattle population and the Kholmogory

or the Simmental cattle population. The mean posterior distribution of the individual admixture coefficient had been denoted \hat{q} and represented an estimate of the amount of an individual's genome that was derived from one of the parental populations. In each run, we used the STRUCTURE with $K=2$ (K is the number of the populations assumed to have contributed to the gene pool of the hybrid population) to compute the ancestry. A burn-in period of 50,000 steps, which was followed by 100,000 MCMC replicates, was used here. A threshold value of $\hat{q} \geq 0.95$ was chosen to provide a statistical cut-off within the range of suggested values (Manel et al., 2002). It indicates that individuals with $\geq 95\%$ of the ancestry can be attributed to one of the parental populations. Individuals were inferred as admixed ones, if the proportion of the membership to either of the parental population was $\hat{q} < 0.95$, though it is also possible that some of them just exhibited noninformative genotypes (Hansen et al., 2001).

RESULTS

Hardy-Weinberg expectation and linkage equilibrium tests

Eleven of a total of 110 (10%) tests for Hardy-Weinberg equilibrium were rejected at $\alpha=5\%$ level. Two significant outcomes observed in the Yakutian-Kholmogory hybrid population resulted from heterozygote deficiency. A further round of tests, given an alternative hypothesis of heterozygote excess, resulted in one significant outcome in the Yakutian-Simmental hybrid population. 19 locus combinations within populations were not in linkage equilibrium ($p < 5\%$): two cases in the indigenous Yakutian cattle, one case in the Simmental cattle, two cases in the Kholmogory cattle, eight cases in the Yakutian-Simmental cattle, and six cases in the Yakutian-Kholmogory cattle. However, we detected no systematic deviations of the locus pairs with respect to linkage equilibrium across all populations.

Multidimensional scaling analysis

The coordinate positions of individuals, derived from their allele sharing distances, are shown in Figure 1. The two principal axes cumulatively explained 57.9% of the total genetic diversity. Dimension 1 accounted for 45.4% of the underlying variation and dimension 2 condensed 12.5% of the variation. The MDSA plotting including all samples showed four distinct groupings and the first two dimensions separated the Simmental cattle (mainly in 1st quadrant), the Yakutian cattle (mainly in 4th quadrant), the Yakutian-Simmental cattle, and the group of the Kholmogory cattle and the Yakutian-Kholmogory cattle (mainly in 3rd quadrant) clearly. Kholmogory cattle and Yakutian-Kholmogory cattle samples were almost totally overlapping on these two

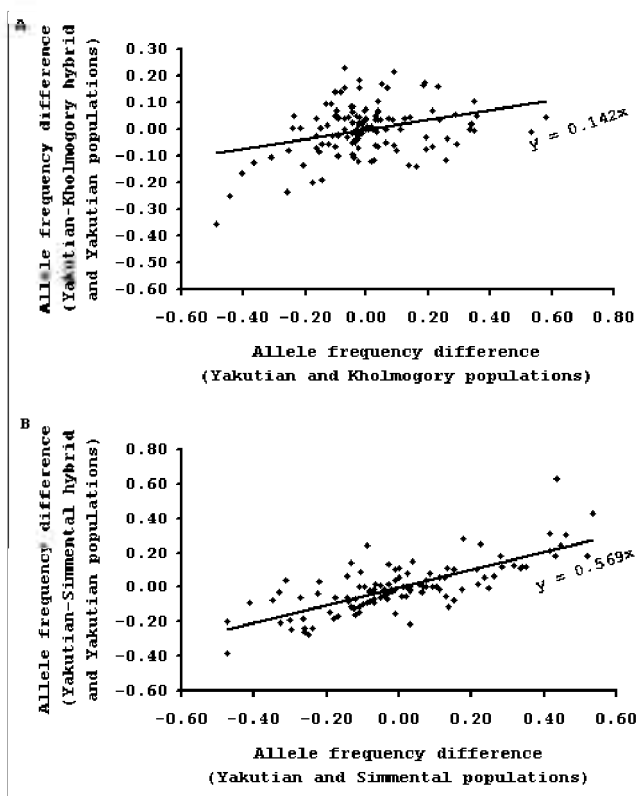


Figure 2. (a) Relationship between the difference in allele frequencies in the Yakutian and Kholmogory cattle populations and the differences in allele frequencies between the Yakutian-Kholmogory hybrid and the Yakutian cattle populations for all their alleles at 22 microsatellite loci; (b) Relationship between the difference in allele frequencies in the Yakutian and Simmental cattle populations and the differences in allele frequencies between the Yakutian-Simmental hybrid and the Yakutian cattle population for all their alleles at 22 microsatellite loci. The slopes of the regression lines show the estimates of admixture proportions (14.2% and 56.9%).

dimensions and the absence of genetic distance between these two populations was clearly shown. The Yakutian-Simmental hybrid animals were located in a roughly intermediate area between the indigenous Yakutian cattle population and the Simmental cattle population. However, score distributions were widespread and it was impossible to use the MDSA to measure the admixture proportions and identify admixed ones.

Population-level admixture analysis

The difference in allele frequencies between the indigenous Yakutian cattle population and each hybrid population, plotted against the difference in allele frequencies between the parental populations for all the alleles encountered at the 22 loci surveyed, are shown in Figure 2. The slopes of the regression lines (0.142 and 0.569), which were in good agreement with the data points, gave estimates of the proportions of genes from the

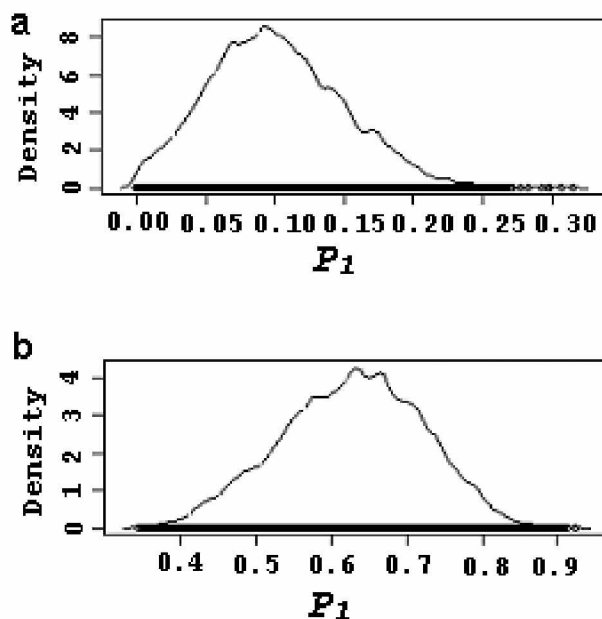


Figure 3. (a) Probability density function (pdf) of P_1 (Indigenous Yakutian Cattle's contribution to the Yakutian-Kholmogory hybrid population); (b) Probability density function (pdf) of P_1 (Indigenous Yakutian cattle's contribution to the Yakutian-Simmental hybrid population).

indigenous Yakutian cattle in the Yakutian-Kholmogory (14.2%) and the Yakutian-Simmental (56.9%) hybrid populations, respectively. The goodness of fit of the linear admixture model for the present data was also revealed by the graphical displays (Figure 2). By Long's method, the standard errors were 2.2% (Yakutian-Kholmogory) and 8.9% (Yakutian-Simmental).

The second approach for estimating the population admixture proportions of the indigenous Yakutian cattle in the two contemporary cattle hybrid populations was carried out by using the program LEA (Chukhi et al., 2001). The results showed a small genetic contribution of the indigenous Yakutian cattle in the Yakutian-Kholmogory cattle population, pointing to a value of $P_1=9.6\%$ (90% probability interval: 1.0%-19.4%) (Figure 3a). However, a look at the genetic contribution of the indigenous Yakutian cattle in the Yakutian-Simmental hybrid population showed a much higher admixture proportion of $P_1=62.8\%$ (90% probability interval: 44.4%-80.5%) (Figure 3b). The standard errors of the estimates obtained with this method were 5.4% (Yakutian-Kholmogory) and 1.7% (Yakutian-Simmental).

Individual-level admixture analysis

A detailed analysis of the posterior distributions of individual admixture proportions (q) was performed by using the STRUCTURE program (Pritchard et al., 2000). For presenting the results of individual admixture

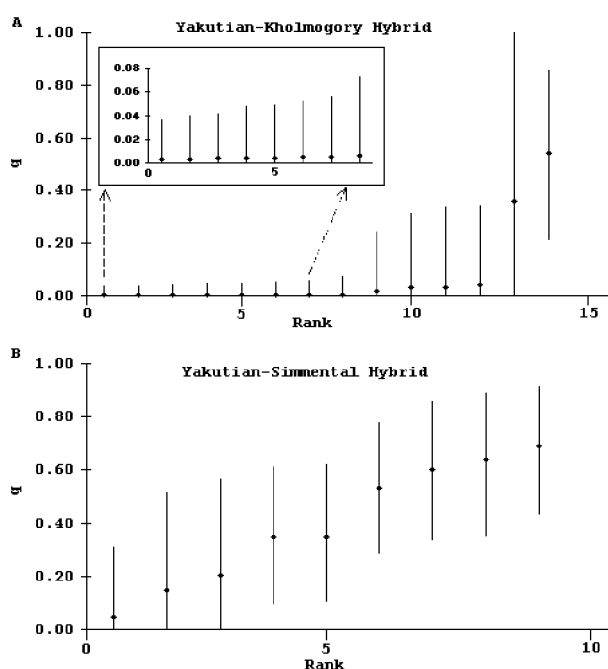


Figure 4. Distribution of mean individual admixture proportion (\hat{q}) among individuals, including their 90% posterior probability intervals. The \hat{q} values have been ranked starting from (a) 'pure' Kholmogory Cattle and (b) 'pure' Simmental Cattle ($\hat{q}=0$) to 'pure' indigenous Yakutian Cattle ($\hat{q}=1.00$). The ranks are plotted against \hat{q} .

proportions (q), individuals in each hybrid population were ranked from the lowest to the highest \hat{q} -values (the mean of q) and rank was plotted against \hat{q} -value including their 90% probability intervals as in Beaumont et al. (2001) (Figure 4). A \hat{q} value between 0.95 and 1.00 would denote a pure indigenous Yakutian cattle, whereas a \hat{q} value between 0 and 0.05 would denote a pure Kholmogory cattle or a pure Simmental cattle. Individuals with intermediate \hat{q} values between 0.05 and 0.95 were taken to be admixed ones.

The results from the Yakutian-Simmental hybrid population (Figure 4b) showed that 8 of 9 individuals exhibited \hat{q} values ranging from 0.05 to 0.95. Six of these admixed animals exhibited 90% probability intervals not spanning either 0 or 1. Two intermediate samples showed probability limits that encompassed 0. It was possible that these two intermediate individuals were actually either admixed or pure Simmental cattle, but had little information on q . The single individual, whose \hat{q} value was less than 0.05 and its 90% probability interval spanned 0, was more likely full of Simmental cattle origin. The eight individuals with \hat{q} between 0.05 and 0.95 showed evidence of genetic contribution from the Yakutian cattle. Nevertheless, the

mean distribution of individual admixture proportions (\hat{q}) in the 8 samples inferred as admixed Yakutian-Simmental varied a lot: one had a \hat{q} value in the range of 0.10-0.20, three of 0.20-0.40 and four of 0.40-0.70.

The distribution of the q values in the Yakutian-Kholmogory hybrid population showed a different pattern with a tendency towards much lower \hat{q} values (Figure 4a). Only 2 out of 14 individuals exhibited relatively higher \hat{q} values (0.361 and 0.544) and were more likely of admixed than of parental origin, whereas 12 individuals with a high impact of the Kholmogory cattle, exhibited \hat{q} values ≤ 0.05 and very narrow 90% probability intervals (range 0.00-0.10) that spanned 0. Furthermore, 8 of the 12 animals showing around 0.4% Yakutian cattle ancestry were completely identical to the pure Kholmogory cattle. In conclusion, the analysis showed the presence of two individuals with admixed origin and a very small genetic contribution of the indigenous Yakutian cattle in most animals of the contemporary Yakutian-Kholmogory cattle population.

DISCUSSION

In the case of population-level admixture analysis, we are interested in the fraction of genes in the admixed population that comes from one or other of the parental population. The results of both the WLS and LEA methods showed that the contribution of the indigenous Yakutian cattle in the Yakutian-Kholmogory hybrid population (9.6% by the LEA and 14.2% by the WLS method) was smaller than that in the Yakutian-Simmental hybrid population (62.8% by LEA and 56.9% by WLS). This is concordant with the known history of backcrossing with Kholmogory bulls as the recurrent parent in the Yakutian-Kholmogory hybrid population. On the other hand, because after the initial crosses of Yakutian bulls with commercial Simmental cows, inter se breeding of the first crossbred generations was adopted in forming the Yakutian-Simmental cattle, it was no surprise to find a large genetic contribution of the indigenous Yakutian cattle in the Yakutian-Simmental hybrid population.

The method based on the LEA (Chikhi et al., 2001) gave similar estimates of admixture proportions of the indigenous Yakutian cattle in the two hybrid populations as those obtained by the weighted least-squares (WLS) method. Both values of the admixture proportion, suggested by the WLS method, were within the 90% credible intervals (1.0%-19.4% in the Yakutian-Kholmogory hybrid population; 44.4%-80.5% in the Yakutian-Simmental hybrid population) suggested by the LEA (Chikhi et al., 2001). Furthermore, the results of population-level admixture analysis provided a confirmation for those obtained by the individual-level admixture analysis.

However, a look at the standard errors obtained with the two population-level analysis methods showed conflicting results: 2.2% by the LEA and 8.9% by the WSL method in the Yakutian-Kholmogory hybrid population, 5.4% by the LEA and 1.7% by the WSL method in the Yakutian-Simmental hybrid population. Neither of the two methods seemed to indicate a much greater certainty on the value of q than the other one. Both methods are based on the analysis of frequency data but are different in the way the allele frequencies are used in computations. The different performances of the two methods may be due to the small sample sizes of the hybrid populations, which may result in the small number of alleles encountered. Some similar conclusions were drawn and some guidelines for choosing the methods were given by Choisy et al. (2004).

Multidimensional scaling analysis (MDSA), a graphical representation of similarity, does not allow quantitative assignments of the individuals to the population (Pritchard et al., 2000; Randi et al., 2001; Pierpaoli et al., 2003). Genetic differentiation among samples was recognized by the multivariate clustering procedure, which split the samples into four separate clusters (Figure 1). In general, there was no separation between the Yakutian-Kholmogory cattle and the Kholmogory cattle. Given the considerable overlapping distributions between the Yakutian-Kholmogory cattle samples and the Kholmogory cattle individuals, this gave a first indication that the Kholmogory cattle had contributed significantly to the present Yakutian-Kholmogory hybrid population. On the other hand, the general distribution of the Yakutian-Simmental hybrid population was intermediate between the indigenous Yakutian cattle population and the Simmental cattle population, though some individuals showed more or less closer relationships to one parental population than the other. The most plausible explanation for this outcome was that the genetic contribution of each parental population in the hybrid population was similar. This agreed with the results of the admixture analysis at the population and individual levels. However, admixed individuals of both hybrid populations would be poorly identified by the MDSA procedure, which did not offer objective criteria for assigning individuals to populations.

By contrast, the Bayesian approach of the STRUCTURE (Pritchard et al., 2000) proved to be a more powerful and informative method than the multidimensional scaling analysis (MDSA). It assigns a probability to the membership of each individual in each parental population, allowing extraction of precise quantitative information from the data set (Randi et al., 2001). Here a large proportion (12/14) of individuals with very low \hat{q} values (<5%) and narrow probability intervals (range 0.00-0.10) were observed in the Yakutian-Kholmogory hybrid population. These results documented the small contribution of the indigenous Yakutian cattle and

the presence of many Kholmogory-like animals in the population. Backcrossing of the Kholmogory cattle into the Yakutian-Kholmogory hybrid generations had led to a dilution of the proportion of the Yakutian cattle gene pool. Mean posterior distributions of individual admixture coefficient (\hat{q}) varied a lot among the samples from the Yakutian-Kholmogory population: 8 animals contained a similar small contribution (0.4%) of the indigenous Yakutian cattle in the Yakutian-Kholmogory hybrid population; 4 samples had relatively higher proportions (around 3%) of the indigenous Yakutian cattle, and two individuals were inferred as admixed ones ($5\% < \hat{q} < 95\%$). Contrary to only two individuals inferred to be admixed in the Yakutian-Kholmogory cattle, most animals (8/9) of the Yakutian-Simmental cattle were observed to have intermediate mean admixture coefficients ($5\% < \hat{q} < 95\%$) and probability intervals that did not span either 0 or 1. This suggested that the indigenous Yakutian cattle had contributed substantially to the Yakutian-Simmental population and this could be explained by the fact that this hybrid population had been developed by inter se breeding of the first Yakutian-Simmental crossbred generations. On the other hand, the Yakutian-Simmental animals showed very different contributions of the Yakutian cattle among them. Some animals contained strong Yakutian cattle genetic contributions, while others showed very little influence, especially one sample that was inferred as being of pure Simmental cattle. The different individual admixture proportions (q) observed within both hybrid populations were most probably due to stochastic processes in crossbreeding over generations.

The algorithm in the STRUCTURE program presumes that the original ancestral parental populations were in H-WE, with the markers used in complete linkage equilibrium, and that the two parental populations contributed alleles to the hybrid populations as independent draws (Kumar et al., 2003). Despite meeting most of these recommended conditions in this study, some discordance was evident. However, it is still not known how departures from H-WE and LE might affect the efficiency of individual assignments and the identification of admixed ancestry (Pierpaoli et al., 2003). More hypervariable microsatellite loci and larger sample sizes of the hybrid populations would be needed for improving the accuracy of individual level admixture analysis. This would substantially improve our understanding of the production performance, health and fertility traits among the animals with different Yakutian cattle ancestry and the usefulness of the Yakutian cattle for the development of cattle populations in subarctic regions.

CONCLUSION

This study demonstrates the utility of these approaches for estimating admixture proportions in crossbred domestic

animal populations. The results of the population-level admixture analysis showed that the Yakutian-Kholmogory cattle population contained a low proportion of genetic contribution from the indigenous Yakutian cattle, while a strong contribution of the Yakutian cattle was detected in the Yakutian-Simmental hybrid population. Further, as illustrated by the individual-level admixture analysis, the contributions of the Yakutian cattle in animals of both hybrid populations differed greatly. In order to shed more light on the differences, additional detailed studies of the interactions between the respective parental populations are still needed and specific measures aimed to limit the stochastic process should be considered to be of high priority in cattle crossbreeding projects.

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