

## Population Structure of Sable in the Baikal Mountain Land: Analysis of Genetic and Phenotypic Traits

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**Abstract**—The genetic and phenotypic structure (according to the fur color) of 14 sable samples from the Baikal mountain land (BML) has been studied by analyzing 257 animals for 11 microsatellite loci and evaluating over 12000 pelts with respect to seven standard color categories. It has been found that the population structure of sable in the region is heterogeneous both phenotypically and genetically. An isolated population group of sable with dark fur inhabits Zabaikalsky krai (Uletovsky, Petrovsk-Zabaikalsky, and Krasnochikoysky districts). The Khamar-Daban Ridge in the south of Lake Baikal is inhabited by a sable population with a high genetic diversity and the lightest fur color in the study region, which is most likely due to its contacts with the East Sayan population. The other BML samples have a relatively high genetic diversity and intermediate parameters of fur color, which may result from their large-scale intraregional translocations and migrations. The results of comparative tests suggest an indirect correlation between the phenotypic and genetic structures in samples from at least seven sable populations inhabiting the study region.

**Keywords:** *Martes*, sable, nuclear markers, fur coloration, genetics, population structure

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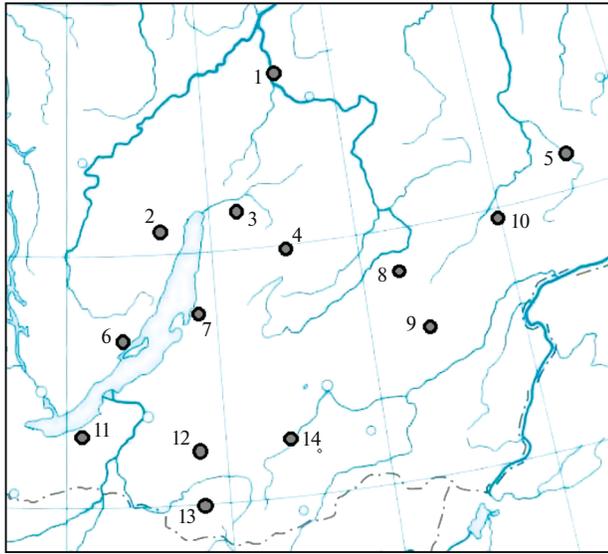
The sable is an essential natural resource of taiga forests in the Baikal region and the main fur-bearing animal not only in this region but also in Russia as a whole. Sable pelts are in sustainable demand in foreign markets. About half a million pelts are exported annually, and a major proportion of them are of the Barguzinsky type, one of the most valuable lines of pelts in the fur trade. Special attention in evaluating the quality of pelt is given to the quality of the fur, particularly its color. Fur coloration in mammals is also an important feature of the species phenotype, which has an adaptive pattern. The identification of color polymorphism and the patterns of its dynamics in populations is important not only for science, but also for practice. The rational use of species resources, their monitoring, planning of protection measures, classification and standardization of fur products, etc. cannot be carried out without knowing the patterns of intraspecific variability, in particular, fur color variation.

About a century ago, overhunting resulted in a catastrophic decrease in the abundance of sable and endangered this highly valuable species. The government of Russia paid close attention to this problem in those years. It was in the Baikal region where the first nature reserve in Russia was established in 1916; the main purpose of this reserve was to organize measures to protect the sable [1]. This reserve also laid foundation for creating a broad network of protected areas (seven reserves, four national parks, numerous wildlife

local protected areas, and natural landmarks). In addition, it was decided to undertake introduction measures to accelerate recolonization of vacant sites within the sable range. The main breeding material (61.4% [2]) was taken from the Baikal region (Irkutsk oblast and Buryatia) and included about 12000 sable pelts.

The results of reintroduction proved to be successful. The current sable range was restored almost to its historical boundaries, which was largely facilitated by the newly formed reacclimatized populations of the descendants of sables introduced from the Baikal region [2]. Presumably, the diversity of the sable population in the Baikal mountain land (BML) and, hence, the genetic diversity of the released animals became a factor of successful reintroduction of Baikal sable to Western and Eastern Siberia. Although no genetic tests were performed with the animals used for reintroduction, close attention was paid to their morphological characteristics, namely, the quality of fur, which is the most economically important trait [2].

Sable fur coloration has been taken into account in systematic reviews of the species since the 17th–18th centuries. Its variability has been studied mainly in geographical aspect, during substantiation of the standard for fur, in taxonomic terms, and for assessing the results of reintroduction [3–10]. Different authors have described the following subspecies for Baikal



**Fig. 1.** Locations of sable samples included in the study (for sample numbers, see Table 1).

sable: *Mustela zibellina* var. *baicalensis* Dybowski, 1922; *Martes z. princeps* Birula, 1922; *M. z. vitimensis* Timofeev and Nadeev, 1955; and *M. z. obscura* Timofeev and Nadeev, 1955 [11]; some of them are considered synonymous [12]. The last of these authors only confirms *M. z. princeps*, Barguzin sable (for the Barguzin Range and Transbaikalia) and *M. z. obscura*, Chikoy sable (for Krasnochikovsky, Uletovsky, Khiloksky, and Kyrensky districts and part of Petrovsk-Zabaikalsky district in Chita oblast [1, p. 247], now Zabaikalsky krai).

Studies on the genetic basis of sable variability began relatively recently [13–16]; however, they are as yet few in number, and no special studies of this kind have been performed in the Baikal region. It has become possible now to combine classical zoological studies with genetic tests. We decided to use this approach in the study of fur color variation in several populations of Baikal sable whose genetic characteristics were evaluated for the first time using nuclear DNA markers. It was hypothesized that there may be disparity between the structural classifications based on the two methods (null hypothesis).

Accordingly, the main purpose of this study was to analyze the structure of the sable population in the BML. The following tasks were set: (1) to evaluate the population genetic structure of sable based on variation in nDNA microsatellite loci and (2) to reveal the population phenotypic structure based on variation in the fur color of sable from the BML, which is usually considered one of the most valuable in terms of fur quality [1–4, 9].

## MATERIAL AND METHODS

### *Study Area*

As defined in [17], the Baikal mountain land (BML) borders on the Eastern Sayan in the west and on Mongolian steppes in the south; in the east, its boundary passes along the interfluvium of the Olekma and Zeya rivers; it adjoins the Central Siberian Plateau and Prilensky Plateau from the north.

Analysis of the population structure of the BML sable included individuals that were collected in 14 areas (districts) of Irkutsk and Amur oblasts, the Republic of Buryatia, and Zabaikalsky krai (Fig. 1): Kabansky district (Khamar-Daban Ridge), Severo-Baikalsky, Bauntovsky, and Barguzinsky districts (the Republic of Buryatia), Krasnochikovsky, Petrovsk-Zabaikalsky, Chernyshevsky, Uletovsky, Tungokhensky, and Tungiro-Olekminsky districts (Zabaikalsky krai), and Olkhonsky and Kazachinsko-Lensky districts and the lower basin of the Vitim River within Bodaibinsky and Mamsko-Chuisky districts (Irkutsk oblast); on the eastern edge of the BML, samples were taken from the basin of the Nyukzha River (a tributary of the Olekma River).

### *Genetic Analysis*

Analysis of the genetic structure of the sable population from the BML included data on 257 animals from 14 geographic samples (Table 1, Fig. 1). The tissue samples were provided by legal sable hunters. DNA was extracted from skin and muscle samples using special DNA-extran-2 KIT kits (Syntol, Russia). All the individuals were genotyped by 11 microsatellite loci that were previously developed for sable (Mzf51 and Mzf56; [18]), American marten *Martes americana*, wolverine *Gulo gulo*, American badger *Taxidea taxus* (Ma1, Ma3, Ma8, Ma15, and Ma19; [19]), stone marten *Martes foina* (Mf8.7 and Mf8.8; [20]), American mink *Neovison vison*, and ermine *Mustela erminea* (Mvis72 and Mvi2243; [21, 22]).

Amplification was performed in a 10  $\mu$ L volume containing the following: 10 $\times$  TaqBuffer with (NH<sub>4</sub>)SO<sub>4</sub> (Thermo Scientific), Taq DNA polymerase (SibEnzyme, Russia), 5 mM MgCl<sub>2</sub>, 0.2 mM dNTP, 8.6 mM (1%) DMSO, and 20–200 ng of genomic DNA. The primer concentration varied from 0.4 to 11  $\mu$ L; PCR was performed using a T100 Thermal Cycler (BioRad).

Amplification was performed at 94°C for 3 min, followed by four denaturation cycles at 98°C for 30 s, annealing at 59°C for 120 s and 72°C for 90 s; the next 20 denaturation cycles were performed at 90°C for 30 s, followed by annealing at 59°C for 120 s, 72°C for 75 s, and 68°C for 30 min. The rate of heating from 59 to 72°C was no more than 0.3°C/s.

At the next stage, PCR products were mixed with formamide and the S-550 Lyz size standard (Gordiz,

**Table 1.** Results of analyzing 14 BML sable samples for the allelic composition of 11 nDNA microsatellite loci

Sample (area)	Abbreviation	Region	$n$	$N_a$	$N_e$	$H_o$	$H_e$
(1) Vitim River (lower reaches)	VIT	Irkutsk oblast	16	6.18	4.29	0.61	0.72
(2) Kazachinsko-Lensky district	KZL	Irkutsk oblast	17	5.91	3.70	0.68	0.69
(3) Severo-Baikalsky district	SBA	Buryatia	25	6.91	4.09	0.69	0.70
(4) Bauntovsky district	BAU	Buryatia	5	4.55	3.71	0.73	0.63
(5) Nyukzha River	NYUK	Amur oblast	21	6.64	3.68	0.65	0.70
(6) Olkhonsky district	OLKH	Irkutsk oblast	7	5.09	3.30	0.61	0.67
(7) Barguzinsky district	BAR	Buryatia	14	6.09	3.73	0.62	0.69
(8) Tungokochensky district	TKCH	Zabaikalsky krai	14	6.18	3.88	0.64	0.69
(9) Chernyshevsky district	CHER	Zabaikalsky krai	7	5.18	3.71	0.62	0.69
(10) Tungiro-Olekminsky district	TOL	Zabaikalsky krai	11	6.55	4.46	0.70	0.70
(11) Khamar-Daban ridge	KHMN	Buryatia	54	7.45	4.42	0.67	0.71
(12) Petrovsk-Zabaikalsky district	PZA	Zabaikalsky krai	25	5.09	3.15	0.58	0.60
(13) Krasnochikoysky district	CHIK	Zabaikalsky krai	18	4.82	2.74	0.54	0.58
(14) Uletovsky district	ULE	Zabaikalsky krai	23	4.36	2.58	0.46	0.54

**Note:**  $n$ , sample size;  $N_a$ , average number of alleles per locus,  $N_e$ , effective number of alleles per locus,  $H_o$ , observed heterozygosity,  $H_e$ , expected heterozygosity.

Russia) according to the manufacturer's protocol. After 5-min denaturation, followed by rapid cooling, we determined PCR products using an ABI 3130 genetic analyzer (Applied Biosystems) and estimated the fragment length using GeneMapper v. 3.7.

The indices of allelic diversity and heterozygosity of  $F_{st}$  distances were calculated using GenAlEx 6.5; we also used this software to analyze the matrix of genetic distances by principal component analysis (PCA) [23, 24]. The genetic structure was estimated by Bayesian clustering in STRUCTURE 2.3.4 [25]; the most probable number of clusters was estimated using the Structure Harvester [26].

### Phenotypic Analysis

Data on the color of sable fur for our samples were obtained from two sources. The monograph by Petrenko [27] presents the results of sorting sable skins by color categories for 1996–2003, including data on 1122 pelts related to our research (samples nos. 1–3, 5–7, 9, and 13; see Table 2). Data for 2016–2019 (11529 skins) were taken from the certificates for sorting pelt export consignments at the *Russkii Sobol'* (Russian Sable) auction company (Irkutsk). The total size of samples for studying fur color was 12651 ind. (see Table 2).

Color classification of the pelts was performed by fur experts. The All-Union Standard for Raw Sable Skins OST NKZag-414 used in the classification divides all sable skins into seven color categories, similarly to the separation for American marten *Martes americana* [28]. We combined the initial color categories into three groups: the “dark-colored” group

included skins of the “golovka” (very dark) categories (two categories) and “vysokaya podgolovka” (dark-brown) category; the “medium-colored” group included the “normalnaya podgolovka” (dark-chestnut) and “temnyi vorotovyi” (medium-dark) categories; and the “light-colored” group included the “normalnyi vorotovy” (brownish) and “mekhovoy” (light) skin categories.

It was previously proposed [3] to evaluate the colorographic structure of sable populations using an integral indicator, the coloration index (score), which is calculated using the weighted average formula, according to which the lightest “mekhovoy” category is assigned score 1, while the darkest “golovka vysokaya” category is assigned score 7. We used this indicator to compare our data with the published data. Group mean values, standard deviations, and standard errors were calculated for each sample group. All calculations were performed using the Statistica 6 (Statsoft) package.

## RESULTS

### Genetic Variability

We developed a multiplex of 11 microsatellite loci to estimate genetic differences between the 14 samples [29]. During the comparison of genotypes frequencies, the ratio of genotypes generally did not differ from the expected number according to Hardy–Weinberg; the revealed deviations were not unidirectional.

The average number of alleles per locus ( $N_a$ ) in the studied sable samples (see Table 1) varied from 4.36 (Uletovsky district) to 7.45 (Khamar-Daban); the lowest values were observed for sables from Uletovsky

**Table 2.** Color composition of sable samples studied between 1996 and 2019 (proportions of groups of dark, medium-colored, and light-colored skins, %  $\pm$  SE)

Sample (area)	<i>n</i>	Dark skins	Medium-colored skins	Light-colored skins	Coloration index
(1) Vitim River (lower reaches)	3267	31.0 $\pm$ 0.81	53.3 $\pm$ 0.87	15.7 $\pm$ 0.64	3.77 $\pm$ 0.020
(2) Kazachinsko-Lensky district	269	7.8 $\pm$ 1.64	51.3 $\pm$ 3.05	40.9 $\pm$ 3.00	2.87 $\pm$ 0.063
(3) Severo-Baikalsky district	971	17.2 $\pm$ 1.21	63.2 $\pm$ 1.55	19.6 $\pm$ 1.27	3.44 $\pm$ 0.033
(4) Bauntovsky district	640	30.9 $\pm$ 1.83	52.2 $\pm$ 1.97	16.9 $\pm$ 1.48	3.67 $\pm$ 0.044
(5) Nyukzha River	889	23.2 $\pm$ 1.42	51.4 $\pm$ 1.68	25.4 $\pm$ 1.46	3.45 $\pm$ 0.040
(6) Olkhonsky district	525	12.0 $\pm$ 1.42	49.9 $\pm$ 2.18	38.1 $\pm$ 2.12	2.99 $\pm$ 0.049
(7) Barguzinsky district	82	11.0 $\pm$ 3.45	47.6 $\pm$ 5.52	41.5 $\pm$ 5.44	2.91 $\pm$ 0.113
(8) Tungokochensky district	2917	30.5 $\pm$ 0.85	57.5 $\pm$ 0.92	12.0 $\pm$ 0.60	3.81 $\pm$ 0.019
(9) Chernyshevsky district	549	25.0 $\pm$ 1.85	63.9 $\pm$ 2.05	11.1 $\pm$ 1.34	3.69 $\pm$ 0.043
(10) Tungiro-Olekminsky district	121	28.9 $\pm$ 4.12	58.7 $\pm$ 4.48	12.4 $\pm$ 3.00	3.76 $\pm$ 0.098
(11) Khamar-Daban ridge	2155	7.7 $\pm$ 0.57	38.7 $\pm$ 1.05	53.6 $\pm$ 1.07	2.64 $\pm$ 0.023
(12) Petrovsk-Zabaikalsky district	68	32.4 $\pm$ 5.67	52.9 $\pm$ 6.05	14.7 $\pm$ 4.29	3.74 $\pm$ 0.139
(13) Krasnochikoysky district	135	38.5 $\pm$ 4.19	56.3 $\pm$ 4.27	5.2 $\pm$ 1.91	4.13 $\pm$ 0.076
(14) Uletovsky district	63	23.8 $\pm$ 5.37	69.8 $\pm$ 5.78	6.3 $\pm$ 3.07	3.83 $\pm$ 0.109
Total	12651	23.7 $\pm$ 0.38	52.8 $\pm$ 0.44	23.6 $\pm$ 0.38	3.48 $\pm$ 0.019

**Table 3.** Sable introductions to the BML areas in the mid-20th century

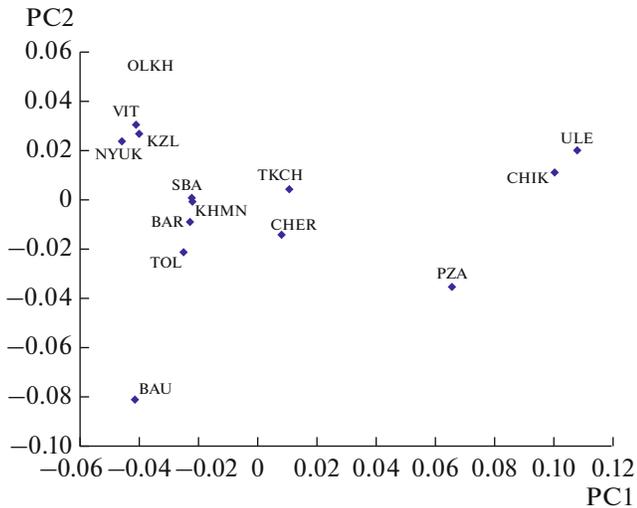
Sample localities	Region	<i>n</i> (2630)	Release years	Origin of the breeding material (areas)
Khamar-Daban	Irkutsk oblast (Slyudyansky district)	86	1939–1952	Bodaibinsky, Barguzinsky, and Kirensky districts
Olkhonsky district	Irkutsk oblast	87	1941–1949	Bodaibinsky and Kirensky districts
Khamar-Daban	Buryatia (Kabansky and Selenginsky districts)	141	1940–1950	Pribaikalsky raion
Bauntovsky district	Buryatia	223	1950–1954	Severo-Baikalsky and Barguzinsky districts
Tungokochensky district	Zabaikalsky krai	584	1950–1958	Kabansky, Bodaibinsky, and Severo-Baikalsky districts
Tungiro-Olekminsky district	Zabaikalsky krai	905	1953–1958	Verkhnebureinsky district (Khabarovsk krai)
Nyukzha (Dzheltulasky district, now Tyndinsky district)	Amur oblast	604	1953–1958	Verkhnebureinsky and Zeisko-Uchursky districts (Khabarovsk krai)

and Krasnochikoysky districts. The indices of allelic diversity were slightly higher for other studied areas of the BML, with the highest values recorded for samples from Khamar-Daban and Severobaikalsky and Tungiro-Olekminsky districts.

The values of genetic distances  $F_{st}$  varied from 0.016 to 0.124 for all intergroup comparisons (mean 0.051, see the Appendix, Table S1). The highest genetic similarity was revealed for samples from Uletovsky and Krasnochikoysky districts ( $F_{st} = 0.016$ ), while the largest difference ( $F_{st} > 0.09$ ) was recorded for the populations from Olkhonsky, Kazachinsko-Lensky, and Bauntovsky districts and the Nyukzha

and Vitim river basins. The results of PCA ordination of the  $F_{st}$  matrix (Table S1) along PC1, which accounts for 40% of the explained variance, show differences between samples from Uletovsky, Krasnochikoysky, and Petrovsk-Zabaikalsky districts (Fig. 2). A sample from Bauntovsky district is differentiated along PC2; however, since the analysis included only five individuals from this district, most of the  $F_{st}$  values are unreliable for this sample (see the Appendix, Table S1).

According to the results of the analysis of the genetic structure of the sable population from the BML using the Bayesian clustering method, the 14 studied samples form three main clusters (Fig. 3). Sables living



**Fig. 2.** Results of PCA analysis of genetic distances ( $F_{St}$ ) for the 14 sable samples. The proportion of the explained variance is 40% for PC1 and 15% for PC2 (here and in Figs. 3–5, sample abbreviations are as in Table 1).

in the southern part of Lake Baikal, on the Khamar-Daban ridge, differ from all other groupings by their genetic characteristics (they are marked in red in the figure). Samples from Krasnochikoysky, Uletovsky, and Petrovsk-Zabaikalsky districts also form a separate cluster (they are marked in green in the figure). The other samples form the third, more heterogeneous cluster (they are marked in main blue).

#### *Fur Color Structure*

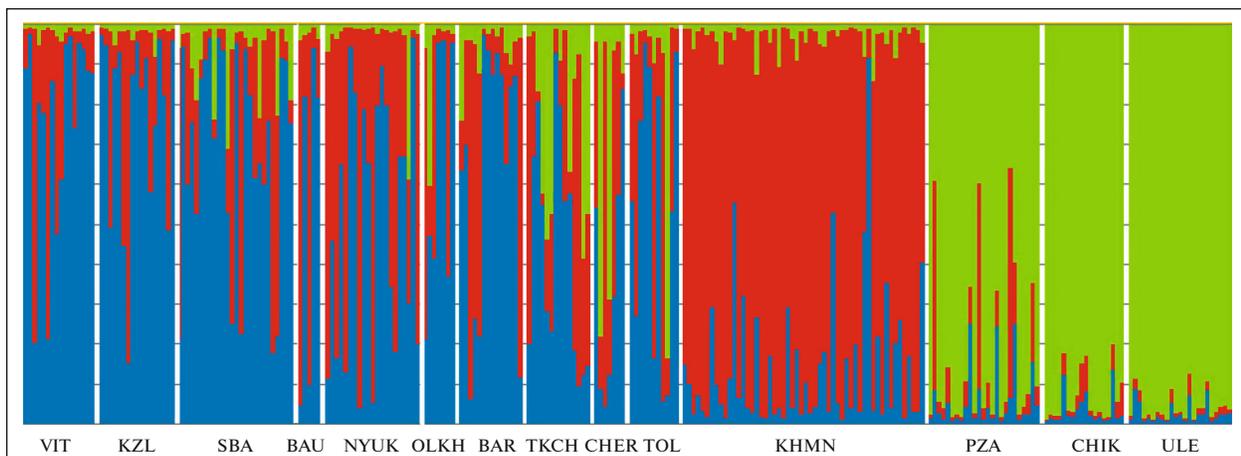
Analysis of the colorographic structure of sable samples also showed their heterogeneity. The fur color structure for each population is given in Table 2. The lowest (less than 5%) proportion of light skins (and,

accordingly, the highest proportions of medium and dark color categories) were observed among sables from Krasnochikoysky, Uletovsky, Chernyshevsky, Tungokochensky, Tungiro-Olekminsky, and Petrovsk-Zabaikalsky districts. These groups form the core of the BML sable populations with the most valuable fur. The lightest fur color was recorded in sables from Olkhonsky, Kazachinsko-Lensky, and Barguzinsky districts and Khamar-Daban. The distribution of the studied samples by fur coloration is shown in Fig. 4. The calculated coloration indices varied from 2.64 (Khamar-Daban) to 4.13 (Krasnochikoysky district).

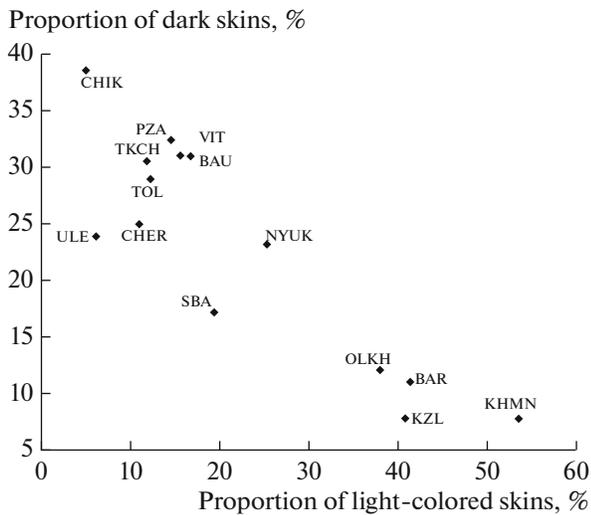
Pairwise comparison of the samples by the color index using Student's *t*-test (see the Appendix, Table S2) showed that the samples from Khamar-Daban and Krasnochikoysky district differed with high statistical significance ( $p < 0.001$ ) from all the others in the region. Two samples (from Nyukzha and Severo-Baikalsk) are similar ( $p > 0.05$ ) and form a separate group with medium color indices. The group with the light fur color is formed by three samples from Olkhonsky, Barguzinsky, and Kazachinsko-Lensky districts. They are similar to each other ( $p > 0.05$ ) and, at the same time, statistically differ from the other samples, which, in turn, form the fifth group with dark fur. On the whole, the distribution by the proportions of dark and light skins and integral parameter of fur color proved to be quite similar.

#### DISCUSSION

We know only a few studies on the **genetic structure** of sable based on microsatellite loci [18, 19, 30, 31]. However, none of them was devoted to the sable population from the BML. The authors of only one study [32] attempted to compare two samples from the Baikal region (11 specimens) and one sample from Sikhote-Alin (ten specimens) based on mtDNA analysis. The studied individuals were divided into two clades



**Fig. 3.** Results of clustering of sable samples from the BML using the STRUCTURE software ( $K = 3$ ). One vertical stripe = one individual.



**Fig. 4.** Classification of sable samples from the BML based on fur coloration traits.

with approximately equal proportions of Far Eastern and Baikal specimens. The authors revealed no significant differences either between samples from different regions or between the two Baikal samples from the neighboring areas on the Upper Lena.

The genetic analysis of the sable population structure (see Figs. 2, 3) showed that the BML is inhabited by a fairly isolated population localized in Krasnochikoy, Uletovsky, and Petrovsk-Zabaikalsky districts (“Chikoy” population according to Timofeev and Nadeev [1]). Samples from these areas are characterized by the lowest indices of genetic diversity: the genetic distances ( $F_{st}$ ) were the greatest between these samples and samples from the other areas of the BML (see Table S1, Fig. 2).

Another isolated sable population lives in the southwestern part of the BML, on the Khamar-Daban ridge. The animals from this area have a genetic peculiarity (see Fig. 3); however, unlike the “Chikoy” population, they have a high genetic variability (see Table 1) and medium  $F_{st}$  values when paired with other samples (see Table S1, Fig. 2). Most likely, this population is not so much isolated from the neighboring Baikal sable populations as genetically related to migrants from the neighboring Sayan Mountains (from the west), which distinguishes it from the other BML populations and, at the same time, increases the genetic diversity within the population itself. It is no coincidence that Monakhov and Timofeev [33] combined the Khamar-Daban groupings with the East Sayan sable population.

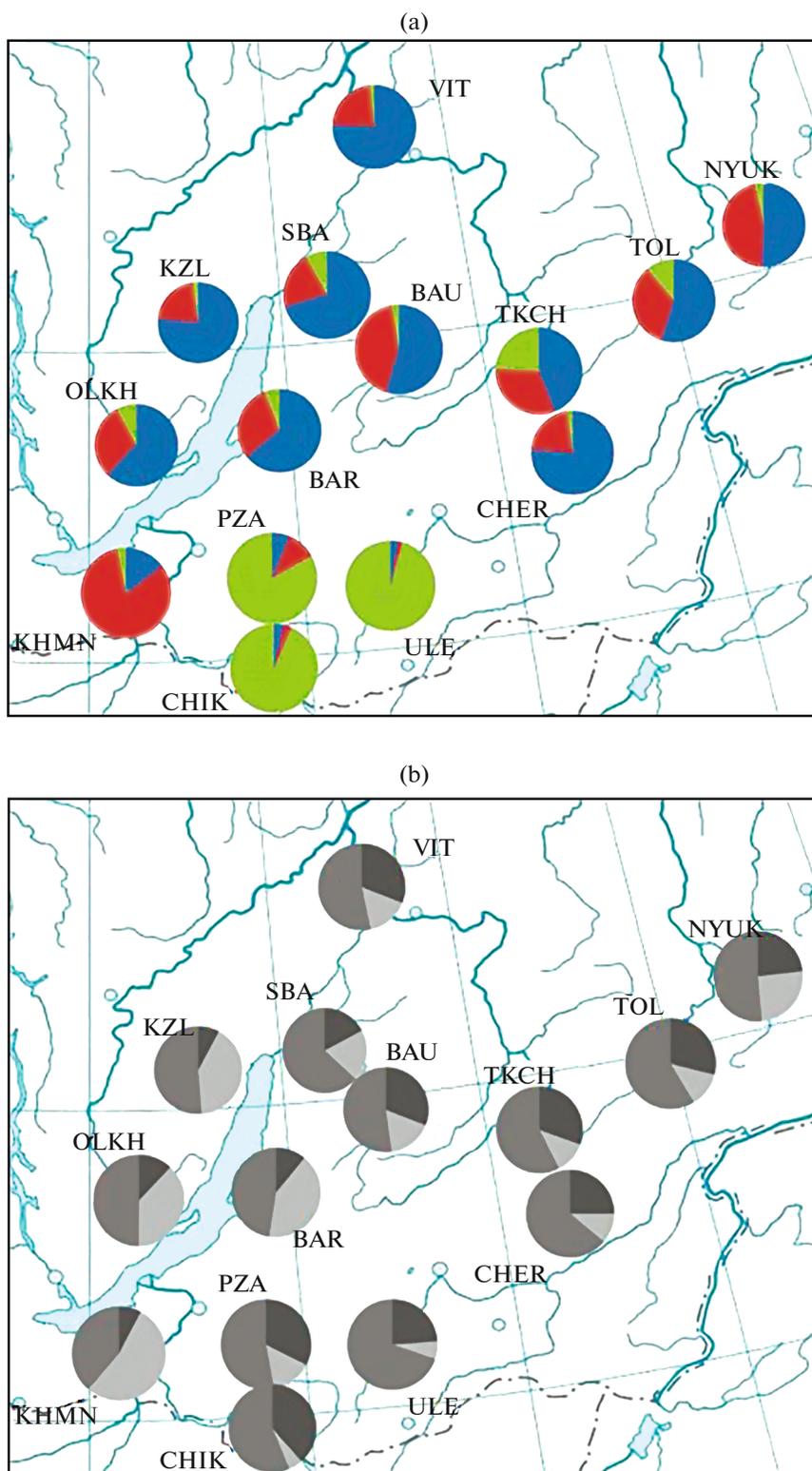
Samples from the other BML areas had similar values both with respect to their genetic diversity (see Fig. 3) and with respect to the genetic distances during their pairwise comparison (see Table S1, Fig. 2). In addition to the migration activity of sable, this can be

explained by the influence of numerous interregional sable translocations within the BML [2]. This concerns six of the 14 studied localities (Table 3). There were no introduction works in other studied regions except Barguzinsky raion, where two sable individuals were released to from the Barguzin Reserve in 1930 [2].

According to [2], a total of 2630 sables were translocated between 1939 and 1958. Most of them were introduced to two areas of the Zabaikalsky krai (1489 ind., or 56.6%), followed by the Nyukzha basin (23%), where the animals were introduced exclusively from the Bureya River; the proportion of sables introduced to the other four areas (Table 3) was 20.4%. Therefore, the regional introductions in 1939–1958 combine half of the samples that we studied (Vitim, Khamar-Daban, and Olkhonsky, Bauntovsky, Severo-Baikalsky, Barguzinsky, and Tungokochensky districts). Undoubtedly, translocations within the BML contributed to the mixing of the gene pool in the region, which is reflected in the results of our tests (see Figs. 2 and 3).

Therefore, based on the results of analysis of variation in the allelic composition of the 11 nDNA microsatellite loci, we identified three population groups: (1) samples from Uletovsky, Petrovsk-Zabaikalsky, and Krasnochikoy districts in Zabaikalsky krai, which form a single population that is somewhat isolated from the neighboring ones; (2) the Khamar-Daban sample, which also has genetic differences from the other sable samples from the Baikal region and a high genetic diversity; and (3) all the other studied samples, which do not differ significantly from each other; this may result from the translocations and migratory activity of sable even under the conditions of a rather complex mountain landscape (Fig. 5a).

A number of studies were devoted to analyzing the structure of Baikal populations **by fur color**; each of these studies differed from the previous one in a larger amount of material and a greater number of samples. The first representative data on the fur color of Baikal sable were published by Eremeeva [3], who provided data on the colorographic structure of sable in the northern part of the Baikal region in 1946–1948 and calculated its mean score (3.9). Bakeev [5] provided the color characteristics for three populations from the BML (the Vitim, Severo-Baikalsk, and Khamar-Daban populations) for 1951–1966 and recorded a gradual decrease in the mean color score for all of them (3.46–3.07; 3.57–3.07; and 3.4–2.89, respectively). Monakhov [6] performed a more detailed analysis, which included data on more than 120.5 thousand skins and provided an integral characteristics for the Khamar-Daban population (3.08) and Barguzin population (3.29), as well as for the Vitim and Mamsko-Chuisky populations as one (2.96). Monakhov [10] described the colorographic structure of sable in the Baikal region in most detail using data on 238 000 skins for 1950–1985. The mean color score according to his



**Fig. 5.** Distribution of genetic traits (a) and fur color groups (b) in 14 *M. zibellina* samples from the BML: (a) proportion of genetic clusters according to the results of Bayesian classification by 11 microsatellite loci; (b) proportion of individuals with dark (black), medium (dark-gray), and light (light-gray) fur coloration.

calculation was 3.08 for the Khamar-Daban population, 3.17 for the Barguzin population, and 3.18 for the Vitim population.

In this study, we used the material that allowed us to give a colorographic description of the studied sable groups over the past 20 years, i.e., over the period during which the genetic material was collected (see Table 2 and Fig. 4) and compare the revealed features with our previous data and literature data and with our data on the genetic structure based on the 11 microsatellite loci.

Comparison of the data on the colorographic structure of populations from the Baikal region after 2000 and over the period from 1950 to 1985 [10] revealed noticeable changes in the proportions of color groups in some of the populations. For instance, the fur became lighter in sables from the Barguzin ridge: the proportion of light-colored skins increased by 13.5% ( $p = 0.05$ ) and the coloration index decreased by 0.26 ( $p = 0.05$ ; see Table 2). The sample from the Khamar-Daban ridge was also characterized by a noticeable decrease (by 0.44 scores,  $p < 0.001$ ) of the coloration index and a significant increase (by 25.5%,  $p < 0.001$ ) in the proportion of light-colored skins. This might be determined by their contacts with the light-colored sample population from the Eastern Sayan (to the west of the Barguzin ridge).

However, the fur of sables from the Lower Vitim basin darkened during this period: the proportion of light-colored skins decreased by 11% ( $p < 0.001$ ) and the coloration index increased by 0.6 scores ( $p < 0.001$ ) ([34], Table 2). An increase of the coloration index was also recorded for the sable population from Krasnochikovsky raion (0.8 scores ( $p < 0.001$ )), in which the proportion of dark skins increased by 30% ( $p < 0.001$ ). Fur darkening was also recorded for sable from the Nyukzha River basin and Tungiro-Olekminsky, Uletovsky, Petrovsk-Zabaikalsky, Tungokochensky, and Chernyshevsky districts.

Sables with dark fur (the total coloration index 3.93 points) concentrate mainly along the Yablonovy, Malkhansky, Daur, Khentei, and Chersky ridges. This group (the “Chikoy focus”) is characterized by the darkest fur color throughout the species range. According to our data [10], the closest color index to this group (3.37) is observed only for sable population of the Bureya River basin. Timofeev and Nadeev [1] noted a high fur quality in sable from the South Baikal region and distinguished it as a separate subspecies, *M. z. obscura*, Chikoy sable, [1, p. 47]. They revealed that this population was isolated by steppe and forest-steppe areas from all sides [1, p. 246], which prevents the sable population from contacting with the neighboring populations.

The fur of sables from the Lower Vitim, Bauntovsky, Chernyshevsky, Tungokochensky, and Tungiro-Olekminsky populations is somewhat lighter (the total coloration index is 3.77). The coloration index

for sables from Severo-Baikalsk and the Nyukzha basin is 3.44–3.45; in other populations, the proportion of light-colored animals is 38–53% (the average coloration index is less than 3.0) (see Table 2).

Therefore, the results of analysis of variation in the fur coloration of sables from the BML suggest that the proportion of individuals with medium-colored fur prevailed in all studied samples of the species (52.8%, Table 2). These samples differ in the proportions of light- and dark-colored individuals. Thus, Khamar-Daban, Kazachinsko-Lensky, Barguzin, and Olkhon samples with the lowest coloration index and highest proportion of light-colored individuals among the studied samples (41–53%) can be distinguished as a separate group. Other samples are characterized by a significantly lower proportion of light individuals and a greater proportion of dark individuals, among which the sample from Krasnochikovsky district differs by the highest proportion of individuals with dark fur coloration (39%, Table 2, Fig. 5b).

The morphological structure of populations according to our data does not fully reflect their genetic structure. Nevertheless, samples with the greatest morphological differences (the Khamar-Daban sample and the other three samples with light fur (Olkhonsky, Barguzinsky, and Kazachinsko-Lensky samples)), as well as the Krasnochikovsky, Uletovsky, and Petrovsk-Zabaikalsky samples, belong to different genetic clusters (see Fig. 2–5). In addition, a significant correlation was revealed between the coloration index and the eigenvalue of PC1 in PCA analysis of genetic distances  $F_{st}$  ( $r = 0.558$ ,  $F_{1,12} = 5.5$ ,  $p = 0.038$ ,  $\beta = 0.066$ ).

Bakeev [35] described the Vitim and Barguzin geographic populations in this region. According to our data, samples from these areas really differ significantly in their coloration; however, the genetic data do not confirm isolation of these populations. Monakhov and Timofeev [33] divided the study area into four natural regions: the Patom and North Baikal highlands, the northwestern and northeastern Baikal regions, the East Sayan and Khamar-Daban ridges, and southern Transbaikalia. Geographically, this conclusion is based on the fact that these areas are separated from each other by steppe zones, river valleys, and intermountain troughs [33; p. 85, Fig. 20]; this implies differentiation between at least three geographically isolated natural areas. The results of this research confirm the existence of separate populations only on the Khamar-Daban ridge and in southern Transbaikalia (samples from Krasnochikovsky, Uletovsky, and Petrovsk-Zabaikalsky districts). According to our data, samples from the northwestern and northeastern Cisbaikalia differ in fur coloration (the proportion of light-colored individuals is higher and, accordingly, the proportion of dark-colored individuals is lower in the northwest); however, there are

genetic differences between the samples from these areas (see Fig. 5).

The results of the comparative tests showed indirect links between the phenotypic and genetic structures of the sable population in the study region (at least for 7 out of 14 samples studied), which confirms the structural similarity between the BML sable populations in their microsatellite markers and group composition based on the proportions of color morphs, which rejects the proposed null hypothesis.

As a result, the population structure of sable from the BML is heterogeneous in both phenetic and genetic aspects. In Zabaikalsky krai, a fairly isolated population groupings of sable with dark fur lives in Uletovsky, Petrovsk-Zabaikalsky, and Krasnochi-kovskiy districts. The sable population inhabiting the Khamar-Daban ridge in the south of Lake Baikal differs from its populations in the other regions in a high genetic diversity and the lightest color, which is most likely determined by its contacts with the East Sayan population to the west of this area. Other samples from the Baikal mountainous area have a relatively high genetic diversity and the intermediate (compared to the previous groupings) indices of fur coloration, which may result from their large-scale intraregional translocations and migrations.

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#### COMPLIANCE WITH ETHICAL STANDARDS

None of the animals was procured specially for this research. The animals were legally caught using humane methods.

#### CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

#### SUPPLEMENTARY INFORMATION

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#### REFERENCES

1. Timofeev, V.V. and Nadeev, V.N., *Sobol'* (The Sable), Moscow: Zagotizdat, 1955.
2. Timofeev, V.V. and Pavlov, M.P., The sable, in *Akklimatizatsiya okhotnich'e-promyslovykh zverei i ptits v SSSR* (Acclimation of Commercial Game Animals and Birds in the Soviet Union), Kirov: Volgo-Vyatskoe Knizhn. Izd., 1973, pp. 51–105.
3. Ereemeva, K.M., Geographic variation of sable fur color, *Tr. Mosk. Pushn.-Mekh. Inst.*, 1952, vol. 3, pp. 81–89.
4. Gerasimova, M.A., Fur quality in Barguzin sables acclimated in Tomsk oblast, *Tr. VNI Zhivot. Syr'ya Pushniny*, 1958, no. 7, pp. 139–160.
5. Bakeev, N.N., Geographic variation and dynamics of sable fur color, *Tr. VNIIOZ* (Kirov), 1976, no. 26, pp. 26–54.
6. Monakhov, G.I., Geographic variation and taxonomic structure of the sable in the Fauna of the Soviet Union, *Tr. VNIIOZ* (Kirov), 1976, no. 26, pp. 54–86.
7. Monakhov, G.I., and Bakeev, N.N., *Sobol'* (The Sable), Moscow: Lesnaya Promyshlennost', 1981.
8. Monakhov, V.G., *Sobol' Urala, Priob'ya i Eniseiskoi Sibiri: rezul'taty reakklimatizatsii* (The Sable in the Urals, Ob Region, and Yenisei Region of Siberia: Results of Reacclimation), Yekaterinburg: Bank Kul'turnoi Informatsii, 1995.
9. Bakeev, N.N., Monakhov, G.I., and Sinitsyn, A.A., *Sobol'* (The Sable), Vyatka: VNIIOZ, 2003.
10. Monakhov, V.G., *Dinamika razmernoi i feneticheskoi struktury sobolya v areale* (Dynamics of the Size and Phenetic Structure of the Sable within Its Range), Yekaterinburg: Bank Kul'turnoi Informatsii, 2006.
11. Monakhov, V.G., *Martes zibellina* (Carnivora: Mustelidae), *Mammalian Species*, 2011, vol. 43, no. 1, pp. 75–86.
12. Wozencraft, W.C., Order Carnivora, in *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd ed., Wilson, D.E. and Reeder, D.M., Eds., Baltimore, MD: Johns Hopkins Univ. Press, 2005, pp. 532–628.
13. Balmysheva, N.P. and Solovenchuk, L.L., Genetic variation of the mitochondrial DNA gene encoding cytochrome *b* in the Magadan population of sable *Martes zibellina* L., *Russ. J. Genet.*, 1999, vol. 35, no. 9, pp. 1077–1081.
14. Rozhnov, V.V., Pishchulina, S.L., Meshchersky, I.G., et al., Genetic structure of sable (*Martes zibellina* L.) in Eurasia: Analysis of the mitochondrial lineages distribution, *Russ. J. Genet.*, 2013, vol. 49, no. 2, pp. 220–227.
15. Kashtanov, S.N., Svishcheva, G.R., Pishchulina, S.L., et al., Geographical structure of the sable (*Martes zibellina* L.) gene pool on the basis of microsatellite loci analysis, *Russ. J. Genet.*, 2015, vol. 51, no. 1, pp. 69–79.
16. Shishatskaya, D.I. and Frisman, L.V., Preliminary data on the genetic variation of sable (*Martes zibellina* L.) in the Middle Amur region: Analysis of two microsatellite loci, *Region. Probl.*, 2014, vol. 17, no. 2, pp. 60–64.
17. Rakovskaya, E.M. and Davydova, M.I., *Fizicheskaya geografiya Rossii* (Physical Geography of Russia), Moscow: VLADOS, 2001.

18. Zhu, W., Wei, Q., Xue, S., et al., Isolation and characterization of microsatellite markers for the sable, *Martes zibellina* (Mammalia: Mustelidae), *Pakistan J. Zool.*, 2017, vol. 49, pp. 1909–1912.
19. Davis, C.S. and Strobeck, C., Isolation, variability, and cross-species amplification of polymorphic micro-satellite loci in the family Mustelidae, *Mol. Ecol.*, 1998, vol. 7, pp. 1771–1788.
20. Basto, M.P., Rodrigues, M., Santos-Reis, M., et al., Isolation and characterization of 13 tetranucleotide microsatellite loci in the stone marten (*Martes foina*), *Conserv. Genet. Res.*, 2010, vol. 2, pp. 317–319. <https://doi.org/10.1007/s12686-010-9217-2>
21. Fleming, M.A., Ostrander, E.A., and Cook, J.A., Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*), *Mol. Ecol.*, 1999, vol. 8, pp. 1351–1362. <https://doi.org/10.1182/blood-2006-08-044172>
22. Vincent, I.R., Farid, A., and Otieno, C.J., Variability of thirteen microsatellite markers in American mink (*Mustela vison*), *Can. J. Anim. Sci.*, 2003, vol. 83, pp. 597–599.
23. Peakall, R. and Smouse, P.E., GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research, *Mol. Ecol. Notes*, 2006, vol. 6, pp. 288–295.
24. Peakall, R. and Smouse, P.E., GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research: An update, *Bioinformatics*, 2012, vol. 28, pp. 2537–2539.
25. Pritchard, J.K., Stephens, M., and Donnelly, P., Inference of population structure using multilocus genotype data, *Genetics*, 2000, vol. 155, pp. 945–959.
26. Earl, D.A. and von Holdt, B.M., STRUCTURE HARVEST: A website and program for visualizing STRUCTURE output and implementing the Evanno method, *Conserv. Genet. Resour.*, 2012, vol. 4, no. 2, pp. 359–361.
27. Petrenko, V.D., *Produktivnost' taezhnykh okhotnich'ikh ugodii na severe Krasnoyarskogo kraya* (Productivity of Taiga Hunting Grounds in the North of Krasnoyarsk Krai), Krasnoyarsk: Krasnoyarsk. Gos. Agr. Univ., 2009.
28. Obbard, M.E., Fur grading and pelt identification, in *Wild Furbearer Management and Conservation in North America*, Ontario: Ministry of Natural Resources, 1987, pp. 717–824.
29. Modorov, M., Monakhov, V., Mikryukov, V., et al., Microsatellite multiplex assay for sable (*Martes zibellina*) and pine marten (*Martes martes*), *Mammal Res.*, 2020, vol. 65, no. 4, pp. 855–862. <https://doi.org/10.1007/s13364-020-00529-4>
30. Kashtanov, S.N., Rubtsova, G.A., and Lazebnyi, O.E., Analysis of the genetic structure of commercial sable population (*Martes zibellina* Linnaeus, 1758) based on microsatellite markers, *Vestn. VOGiS*, 2010, vol. 14, pp. 426–431.
31. Frisman, L.V., Shlyufman, K.V., and Brykova, A.L., Genetic structure of sable population (*Martes zibellina*) in the Bureya mountain range based on the catch of one season, *Region. Probl.*, 2019, vol. 22, no. 4, pp. 46–55. <https://doi.org/10.31433/2618-9593-2019-22-4-46-55>
32. Fedorova, L.I. and Kaigorodova, I.A., Microevolution of the Baikal sable, *Izv. Irkutsk. Gos. Univ., Ser. Biol. Ekol.*, 2014, vol. 7, pp. 32–36.
33. Monakhov, G.I. and Timofeev, V.V., Cisbaikalia and Transbaikalia, in *Sobol', kunitsy, kharza* (The Sable, Pine Marten, and Yellow-throated Marten), Moscow: Nauka, 1973, pp. 84–95.
34. Monakhov, V.G., Stability and variability of fur color in Cisbaikalian sables, in *Sovreennye problemy okhotovedeniya: Mater. Nats. nauchno-prakt. konf.* (Current Problems in Game Management: Proc. Natl. Sci.-Pract. Conf.), Irkutsk: OOO Megaprint, 2019, pp. 129–135.
35. Bakeev, N.N., Sable geographic variation and population structure, in *Sobol', kunitsy, kharza* (The Sable, Pine Marten, and Yellow-throated Marten), Moscow: Nauka, 1973, pp. 39–49.

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