
SHORT
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Genetic Effects of Sable (*Martes zibellina* L.) Reintroduction in Western Siberia

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Abstract—In the middle of the 20th century, massive introductions of sables were performed to recover the area of this valuable fur species. In this work, genetic variation of a naturalized sable population from the Vakh River basin (Nizhnevartovskiy district, Khanty-Mansi Autonomous Okrug) was investigated. This population developed as a result of sable introduction from Cisbaikalia in 1952–1957. The naturalized sable population of the Vakh basin occupies an intermediate position between two autochthonous sable populations from the Ob River area and Cisbaikalia, as assessed by variation of five microsatellite loci. Apparently, the genetic structure of the modern sable population from the Vakh basin was formed by mixing the gene pools of the original Cisbaikalian population and the neighboring autochthonous populations from the Ob River area which recovered their numbers in a natural way. Data on genetic variation in the naturalized sable population agree with the results of previous morphological studies and can be employed for long-term monitoring of the outcome of sable introduction.

Keywords: sable, introduction, population, genetic structure, microsatellite loci

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The sable (*Martes zibellina*) is a valuable fur species; the greater part of its natural area is located in Russia. By the beginning of the 20th century, the sable had nearly completely disappeared in a large part of its area because of overhunting. A number of measures were undertaken to restore the species abundance; in particular, sables were reintroduced into territories that they used to inhabit (mainly from Cisbaikalia). According to [1], altogether 19187 sables were transferred to new habitats in the period from 1901 to 1970.

In Western Siberia, the area of the sable was reduced to isolated inaccessible locations in the areas between the river courses of the Ob and the Irtysh and the Konda and the Sosva [2, 3]. On the right shore of the Ob River, hardly any sables could be found in middle of the 20th century [4–7], even though in the 17th century it used to be a major “sable site” yielding up to 120 animals per hunter per season [8, 9].

From 1940 to 1959, to restore the sable population in the Ob basin, 42 transfers were undertaken to release 3045 animals, mainly from Irkutsk oblast and Buryatia, in the basins of the Kazym, Agan, Vakh, Vasyugan, Parabel, Tym, and Ket rivers [1, 10]. In the basin of the Vakh, three releases were performed in 1952–1957, which involved 224 sables from Buryatia and 107 sables from the Bodaibinskii district of Irkutsk oblast (lower stream of the Vitim River). It was usually animals with the darkest, most appreciated fur that

were selected to be released into novel habitats. It should be mentioned that autochthonous sables of the Ob basin represent the subspecies *Martes zibellina zibellina*, while the introduced animals originated from the Lake Baikal area inhabited by another subspecies, *M. z. princeps* [11]. Thus, the efforts to naturalize Cisbaikalian sables in Western Siberia represented a sort of large-scale ecological experiment, where one sable subspecies was introduced into an area inhabited by another subspecies with a significantly different phenotype [1, 10, 12–15].

Morphological studies of naturalized sable populations showed that, in 40 years after introduction, these animals developed specific morphological traits that distinguished them both from Cisbaikalian sables and from autochthonous sables of the Ob basin, making the initial features of introduced sables more similar to the phenotype of autochthonous animals [10, 14–16]. Morphological traits of the naturalized population may have changed as a consequence of natural selection. Apart from that, the fact that they have become more similar to the autochthonous phenotype may be due to crossbreeding between introduced sables and sables from neighboring autochthonous populations whose numbers have been restored in a natural way.

The goal of the present study was to characterize the genetic structure of the naturalized sable popula-

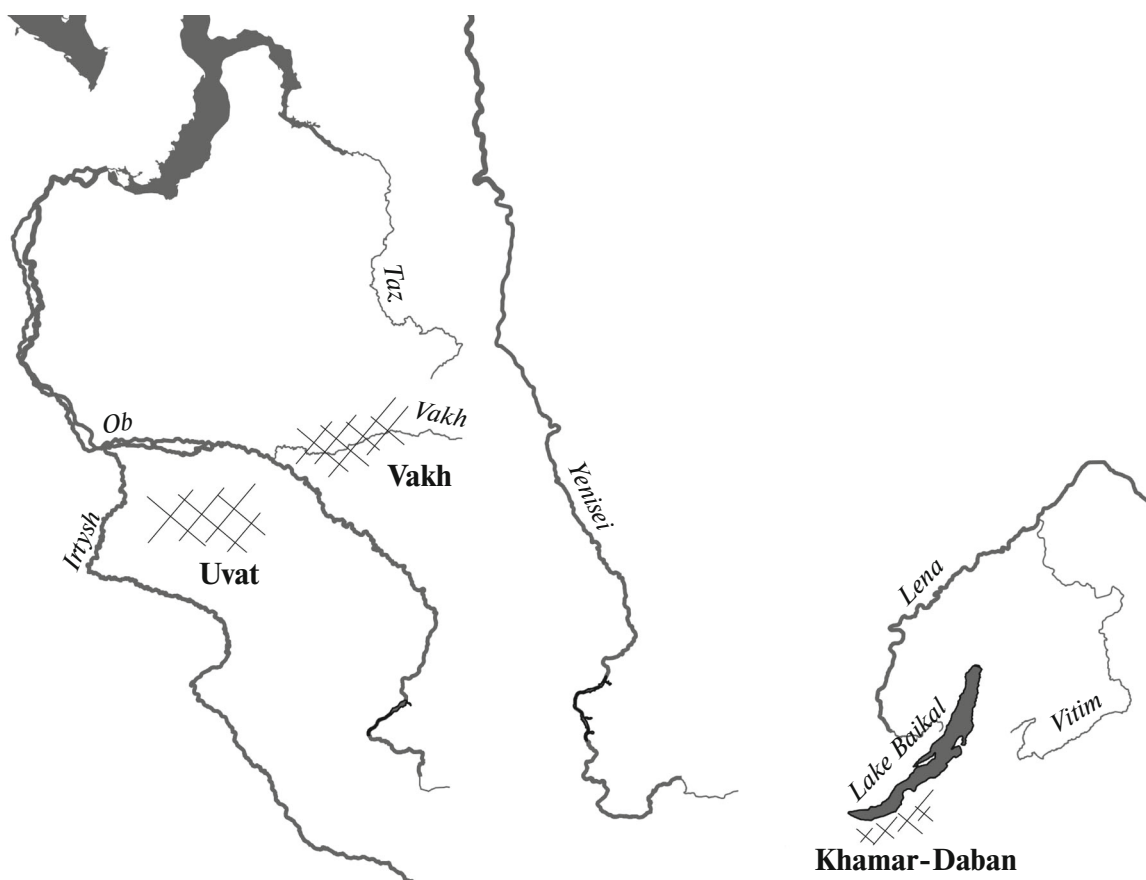


Fig. 1. Scheme of geographic location of the studied samples of sable.

tion on the basis of variation of microsatellite loci in nuclear DNA.

The study was performed using data on 139 sables from three population samples: Vakh ($n = 59$; collected in 2011–2014 in the basin of the River Vakh, Nizhnevartoskii district, Khanty-Mansi Autonomous Okrug), Uvat ($n = 39$; Uvatskii district of Tyumen oblast, 2010–2011), and Khamar-Daban ($n = 41$; Khamar-Daban Mountain Range, Kabanskii district, Buryatia, 2004–2005) (Fig. 1). Specimens of muscle tissue were collected by licensed hunters in the corresponding regions. Each specimen was genotyped by five microsatellite loci: *Ma2*, *Ma8*, *Ma15* [17], *Mer41*, and *Mvis72* [18]. These loci were previously successfully applied in molecular genetic studies of the sable [19, 20]. PCR was performed as described in [20]. The length of the resulting fragments was determined using a Genetic Analyzer 3130 (Applied Biosystems, United States) in the presence of molecular weight marker S-450 (Syntol, Russia). Chromatograms were analyzed using GeneMapper v. 4.0 software.

Genetic differentiation (F_{ST}) was considered significant at $p < 0.01$. The agreement of the observed genotype distribution to the Hardy–Weinberg equilibrium

was assessed using the χ^2 test. Data were analyzed using the GenAlex 6.501 software program [21, 22].

In all three populations, each of the five loci was represented by six to ten alleles (Table 1). In the naturalized Vakh population, the effective number of alleles per locus was the highest ($N_e = 4.8 \pm 0.7$); in the autochthonous populations of Uvat and Khamar-Daban, this value was lower ($N_e = 3.7–3.8$). The number of unique alleles (i.e., those not represented in the other populations) was the highest in the population of Vakh (eight alleles); in the Khamar-Daban population, there was one unique allele, and no unique alleles were found in the Uvat population (Table 1). In 11 of 15 cases, the observed genotype frequency distributions did not deviate from the Hardy–Weinberg equilibrium; in the remaining cases, the observed deviations were not systemic.

Genetic differentiation among the three populations was significant in all pairwise comparisons ($P < 0.01$). F_{ST} values were 0.041 between the populations of Vakh and Khamar-Daban and 0.036 between the populations of Vakh and Uvat. The highest level of differentiation was observed between the autochthonous populations of Cisbaikalia (Khamar-Daban) and the Ob basin (Uvat): $F_{ST} = 0.067$.

Table 1. Genetic diversity of autochthonous and naturalized sable populations as assessed by microsatellite variation

Population	Parameter	Locus					
		<i>Ma15</i>	<i>Ma2</i>	<i>Ma8</i>	<i>Mer41</i>	<i>Mvis72</i>	all loci
Vakh	<i>N</i>	57	57	58	59	58	57–59
	<i>N_a</i>	6	7	10	7	10	8.0 ± 0.84
	<i>N_e</i>	2.8	4.4	6.5	4.5	6.1	4.8 ± 0.67
	<i>G</i>	1	2	1	1	3	8
Uvat	<i>N</i>	39	39	39	39	38	38–39
	<i>N_a</i>	6	6	8	6	8	6.8 ± 0.49
	<i>N_e</i>	2.41	5.1	3.8	3.0	4.9	3.8 ± 0.52
	<i>G</i>	0	0	0	0	0	0
Khamar-Daban	<i>N</i>	41	41	41	40	41	40–41
	<i>N_a</i>	6	6	7	8	8	7 ± 0.45
	<i>N_e</i>	2.8	3.8	4.5	4.5	3.0	3.7 ± 0.36
	<i>G</i>	0	0	0	1	0	1
All populations	<i>N</i>	137	137	138	138	137	45.8
	<i>N_a</i>	7	8	10	9	11	7.27 ± 0.36
	<i>N_e</i>	2.7	4.4	4.9	4.0	4.7	4.1 ± 0.31
	<i>G</i>	1	2	1	2	3	9

N, sample size; *N_a*, average number of alleles per locus; *N_e*, effective number of alleles per locus; *G*, number of unique alleles in the sample.

Genetic structure of a population is determined by a combined effect of mutations, migrations, genetic drift, and natural selection [23, 24]. Sable introduction in the Vakh basin took place about 60 years ago (which corresponds to 8–30 generations of animals). We believe that this period is too short for mutations to have any significant effect on the genetic structure of the naturalized population.

The two autochthonous sable populations of the Lake Baikal region and the Ob basin (Khamar-Daban and Uvat) represent two sable subspecies [11] characterized by significantly different morphological features (condylobasal skull length was 80.1 in the Khamar-Daban sample and 84.9 in the Uvat sample; fur color index was 3.08 and 1.68, respectively [10]) and considerable genetic differentiation. Previously, Kashtanov et al. used microsatellite markers to evaluate genetic distances among six mainland sable populations [20]. The highest level of genetic differentiation was observed between the populations of the northern Ural and the Sikhote-Alin mountain range ($F_{ST} =$

0.058) [20]. Thus, Cisbaikalian sables that were introduced in the Vakh basin must have been genetically different from the autochthonous population of the Ob basin.

The Vakh population of introduced sables occupies an intermediate position between the autochthonous populations of the Ob basin and Cisbaikalia, as suggested both by genetic markers and by morphological traits (condylobasal skull length, 82.4; fur color index, 2.6; the difference from the autochthonous population of the Ob basin was significant: $P < 0.0001$) [10]). At the same time, the naturalized population had a significantly higher number of unique alleles (eight) than autochthonous populations (zero or one).

The most likely explanation of the obtained results is that the introduction of Cisbaikalian sables into the Vakh basin led to mixing of the gene pools of the two initial populations. Therefore, the development of the modern sable population of the Vakh basin was affected both by the introduced animals from Cisbaikalia (331 individual released in 1952–1957) and by

autochthons of the Ob basin. Moreover, the latter group could have comprised not only those animals that remained in the basin of Vakh at the moment when the introduction was undertaken but also those that migrated from neighboring autochthonous populations. It should be noted that animals introduced into the Vakh basin could have contacted indigenous sables only in the west (basins of the Dem'yanka and Yugan rivers, via the vast floodplain of the Ob River) and the north (upper course of the Taz River), since the neighboring populations in the south and the east (basins of the Tym, Sym, and Elogui rivers) also originate from introduced Cisbaikalian sables [10].

The high level of genetic diversity observed in the naturalized Vakh population in comparison to the autochthonous populations studied may be due to genetic heterogeneity of sable populations of the Ob basin and Cisbaikalia. In this work, on the basis of morphological similarity of sables inhabiting territories on the left and the right bank of the Ob River [10], we assumed that these animals represent a single population and have similar frequencies of microsatellite alleles. It is, however, possible that the genetic structure of the sable population from the right bank of the Ob (basin of the river Taz) is different from the one of the left-bank population. Moreover, animals introduced into the Vakh basin originated from two Cisbaikalian regions: Buryatia (which is represented by the Khamar-Daban sample) and Bodaibinskii region of Irkutsk oblast. Perhaps, the unique alleles found in the naturalized Vakh population may also be detected in a study involving a broader range of the Ob and the Baikal area autochthons. However, a previous work that analyzed microsatellite variation in the sable showed that the genetic differentiation between neighboring geographic populations in Central Siberia was low [20], probably owing to the high migratory activity of this species.

Thus, it is currently possible to observe the results of introducing 331 sable individuals in the basin of the Vakh River, which was performed in 1952–1957. The sable population that has developed in this region exhibits morphological and genetic distinctness. Judging both by morphological and by genetic markers, the modern sable population of the Vakh basin occupies an intermediate position between autochthonous populations of Cisbaikalia and the Ob basin. These data may be used for monitoring and predicting the outcome of sable introduction.

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