APPLICATION ESSAY

Mitochondrial DNA markers for the study of introgression between the sable and the pine marten

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Abstract

We clarify the contribution of gene introgression in the recovery of the sable *Martes zibellina*, which has undergone significant population declines by the end of the nineteenth century. To verify the contribution of interspecific gene introgression, variation among the sable and the pine marten *Martes martes* was investigated utilizing restriction fragment analysis of the mitochondrial cytochrome b gene as a genetic markers. Evidence of symmetric introgression of mitochondrial genes between the species was detected. Frequency of marten haplotypes in the sable was 8.3%, while sable haplotype was found in 10% of the martens. The low frequency of mitochondrial DNA haplotype A indicates a comparatively low portion of the Eastern lines in the current sable populations in Western Siberia, despite the introduction of a large number of Eastern sable subspecies. These findings are of great importance for the conservation genetics of the sable. Overhunting of the sable as a more fur valuable species than the pine marten may lead to violation of the dynamic equilibrium between genetic systems of these related species. Mitochondrial markers can be used to identify genetic lines of other species or subspecies in hybrid zones.

Keywords *Martes zibellina* · *Martes martes* · mtDNA · Reintroduction · Introgression · Hybrid zone

Introduction

In recent years, due to the use of molecular methods, interspecific hybridization and gene introgression for many animal species have been evidenced. Gene introgression is the incorporation of genetic material from one species into the genome of the other. Recently diverged species can have incomplete reproductive barriers, allowing gene introgression. The effects of gene introgression on the genetic structure of wild populations have been investigated by many researchers. Staubach et al. (2012) investigated gene transmission between subspecies of the house mouse *Mus musculus domesticus* and *M. m. musculus*. Authors argue that at least 10% of the genome was affected by partial or full introgression. In other species the share of incorporated genes from "sister" species varied from 2–4 to 27% (Fedorov et al. 2009; Harris and Nielsen 2016). In some cases, complete replacement of the mitochondrial genome took place (Zieliński et al. 2013). Interspecific gene introgression has been shown to be a widespread phenomenon in many animal groups from helminthes (Detwiler and Criscione 2010) and insects (Llopart et al. 2014) to amphibians (Liu et al. 2010; Zieliński et al. 2013), birds (Fedorov et al. 2009) and mammals (Tegelström 1987; Beaumont et al. 2001; Murtskhvaladze et al. 2012), including humans (Wills 2011; Harris and Nielsen 2016). Due to the prevalence of introgression in natural populations, the hypothesis of adaptive significance of this phenomenon has been verified (Hawks and Cochran 2006; Llopart et al. 2014). Introgression can have different evolutionary consequences, such as rapid evolution of new hybrid forms, or, on the contrary, extinction of native species. Thus, this process has strong implications for genetic diversity conservation.

Mustelidae are one of mammalian groups with frequent interspecific hybridization. Davison et al. (2001) hypothesized that there was interspecific mitochondrial introgression between *M. martes* and the sable *M. zibellina* in Fennoscandia. Stone and Cook (2002) pointed that "americana" and "caurina" subspecies groups of *Martes americana* Turton, 1806 may interbreed in a region of limited geographic

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overlap. Kyle et al. (2003) and Jordan et al. (2012) found evidence of hybridization of *M. americana* with *M. martes* in England. Lode et al. (2005) detected natural hybridization events between two native species, the European mink *Mustela lutreola* L., 1761 and the European polecat *Mustela putorius* L., 1758. Frequent interspecific hybridization in this group of animals may be due to low genetic differentiation and recent divergence in evolution (Davison et al. 2000; Sato et al. 2003) or may be associated with the scarcity of mating partners for rare species (Lode et al. 2005).

In addition to natural processes, human factors can have a major impact on the distribution of animals, creating new hybrid zones, with little-known consequences for the genetic integrity of species. This group tends to have a high economic value because of their valuable fur. Therefore, many species of this group are subject to anthropogenic influence. Some species (*Mustela putorius* L., 1758) have been domesticated, while others (*Neovison vison* Schreber, 1777) have been introduced into new territories. Moreover, many species (*Enhydra lutris* L., 1758, *Mustela lutreola* L., 1761) have undergone significant population declines due to overhunting. The sable *Martes zibellina* L., 1758 is a species in which all these phenomena have taken place. As a result of overhunting, the sable population number significantly declined almost to zero in some areas in the late nineteenth century and was restored in the 1970s following the ban on hunting, establishment of reserves, and reintroduction programs. The sable population structure was poorly understood prior the population crash. Some authors have identified several sable subspecies based on morphology, especially the body size and the fur color that are important for the skin value. These subspecies have been named according to the distribution area: the Western Siberian sable *M. z. zibellina*, the Yenisey sable *M. z. yenisejensis*, the Sayan sable *M. z. sajanensis*, the Barguzin sable *M. z. princeps*, the Sakhalin sable *M. z. sahalinensis*, the Kamchatka sable *M. z. kamtschadalica*. As some sable subspecies had more valuable fur than others ones, they were used to recover the number of the endangered subspecies and to improve the quality of their fur. In Western Siberia, small local populations were preserved during depressed population growth. Nevertheless, several thousands of individuals from different sable subspecies were released to speed up the restoration of the Western Siberian sable population number (Bobrov et al. 2008, 2011). Thus, intensive mixing of the sable gene pool occurred. Although a recent study has shown that the restored sable populations from different regions maintain their specific features, the whole effect of such mixing on the sable subspecies structure is not known (Kashtanov et al. 2015).

In addition, there is a hybrid zone and gene introgression between the sable and the "sister" species pine marten *Martes martes* L., 1758 in the Urals and Siberia (Rozhnov et al. 2010; Kassal and Sidorov 2013; Zhigileva et al. 2014a). The sable and the pine marten differ in color and quality of fur, size and shape of neck spot and head, and tail length. Hybrids differ from parental species having intermediate values of all these parameters. The proportion of such 'atypical' individuals in some areas of Western Siberia varies from 5.6 to 42.9% among sables and from 0 to 66.7% among martens. Hybrids are fertile in backcrossing with their parental species, especially with the sable (Starkov 1947). Effects of interspecific hybridization on the sable population recovering have not been investigated.

The aim of this paper is to clarify the contribution of gene introgression in recovering the sable population number. Specifically, we test two hypotheses. The first hypothesis is that the genetic contribution of the sable subspecies introduced into the territory of Western Siberia is insignificant in the current status of the local sable population gene pool. The second hypothesis is that the proportion of the pine marten genes in the sable gene pool was historically large, and it played a major role in the restoration of the sable number.

Materials and methods

Sampling

To test our hypotheses, we used tissue samples of the sable, the pine marten and hybrids *M. zibellina × M. martes*, obtained from different parts of the range. The samples were collected during the hunting seasons (December to February) in 2008–2017 in eight areas: the North Urals (the Sos'va River basin), the South Urals (Bashkiria, the Belaya River basin), Western Siberia (Tyumen and Omsk region), Eastern Siberia (Yakutia; Sayany mountains), and the Far East (the Amur River basin; Sakhalin Island; the Kamchatka Peninsula) (Fig. 1). The animals were caught by professional hunters during licensed hunting. Legally permitted trapping methods were used. The animals were euthanized and their carcasses were frozen. The tissue samples were collected for laboratory studies. One part of the materials collected from Western Siberia was muscles, while the one from Eastern Siberia and the Far East was pieces of skin. Samples of muscle tissue were fixed in 70% ethanol; pieces of skin were dried and used for DNA extraction. All tissue samples were kept frozen at −20 °C until laboratory analysis.

A total number of 158 samples of the sable, 87 of the pine marten and 51 of their hybrids were sampled. The hybrids were identified based on osteological signs—the ratio of skull measurements and the number of caudal vertebrae (Gashev and Ageshin 2003).
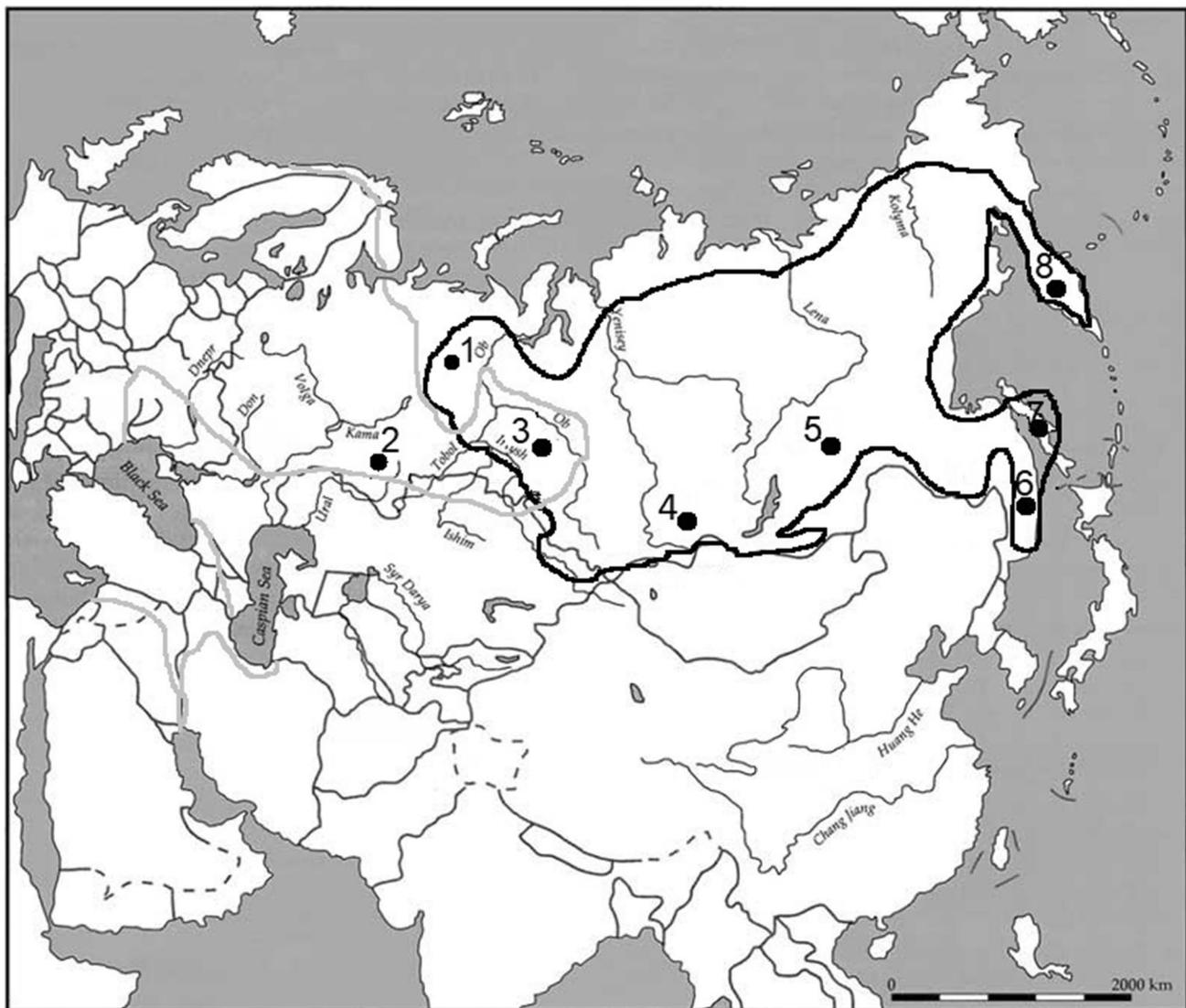
Fig. 1 Sample collection sites of the sable, the pine marten and their hybrids: 1—The North Urals; 2—The South Urals; 3—Western Siberia; Eastern Siberia: 4—The Sayany mountains; 5—Yakutia; The Far East: 6—The Amur River basin; 7—Sakhalin Island; 8—The Kam-chatka Peninsula. The black line shows the current distribution area of the sable. The gray line shows the boundary of the pine marten distribution

DNA extraction and laboratory procedures

Total nucleic acids were extracted from cardiac muscle tissue fixed in 70% ethanol and from dried skin samples using the Diatom DNA Prep100 kit for DNA extraction (Laboratoria Izogen Ltd, Moscow, Russia).

A fragment of the mitochondrial DNA (mtDNA) cytochrome b gene was used as a marker to compare genetic variability in the sable, the pine marten and their hybrids. The mtDNA variation was characterized by Restriction Fragment Length Polymorphism (RFLP) analysis in accordance with the methodology of Balmysheva and Solovenchuk (1999) with slight modifications. The cytochrome b

gene fragment 1300 bp in length was amplified by polymerase chain reaction (PCR) using sequences 5′-GAAAAA CCA(C/T)CGTTGT(A/T)ATTCAACT-3′ and 5′-GTTTAA TTAGAAT(C/T)T(C/T)AGCTTTGGG-3′ as forward and reverse primers, respectively. PCR was performed in 20 μL of the reaction mixture composed of IQ supermix (Bio-Rad), 2.5 mM of each primer, and 10–100 ng of total DNA extracts. The reaction conditions included 94 °C for 5 min.; followed by 33 cycles of 94 °C for 1 min, 51 °C for 1 min, 72 °C for 1 min 45 s; and 72 °C for 2 min. The amplified segments of DNA were screened for restriction site polymorphism using four endonucleases: Hae III, BstN I, Taq I and RSA I. The choice of these enzymes was determined by

the presence of the corresponding restriction endonuclease recognition sites within the sable and the pine marten mitochondrial genome (Koepfli et al. 2008). Standardization of DNA concentrations was performed before this analysis. The digested samples were separated by means of electrophoresis in 2.5% agarose gel in $1 \times$ TAE buffer. The fragment sizes were determined using the GeneRuler™ DNA Ladder mix (Fermentas, Lithuania) as a molecular size marker. Composite haplotypes were designated by four letters, representing the different profiles for each of the four restriction endonucleases. Samples of all rare and new haplotypes were genotyped at least twice.

Data analysis

The RFLP data were computed using the STRUCTURE software (Pritchard et al. 2000). This analysis was run for 10,000 generations after 10,000 of burn-in, with the clusters number equaled the number of sampling localities. To change the optimal clustering we made 10 runs of the program with the K values (number of clusters) from 1 to 9. The NETWORK 5.0.0.1 software (Bandelt et al. 1999) was used to construct a median-joining (MJ) network of mtDNA haplotypes from *M. martes*, *M. zibellina* and their hybrids.

Results

We analysed 241 samples of the sable, the pine marten and their hybrids by RFLP techniques and identified nine composite haplotypes (Table 1). Four haplotypes (Z30, Z5, AK23 and AK29) were typical for the pine marten, whereas seven haplotypes (Z28, Z30, Z31, Z5, AK23, UC1 and AC27) were found in the sable. Haplotypes Z28, Z30 and Z31 correspond to the sable haplotypes A, B and C described by other authors (Balmysheva and Solovenchuk 1999). These three haplotypes were found in the sable from the Far East. Haplotypic diversity was poorer in Eastern Siberia, where we found only two haplotypes—Z28 and Z30. The greatest variety of mtDNA lineages was found in the Western Siberian sable. Haplotype Z28 (AAAA) was most common in the sable populations from the Far East and Eastern Siberia, but it was ten times rarer in populations of the sable from Western Siberia. The sable from the Kamchatka Peninsula and Sakhalin Island were monomorphic in haplotypes Z28 and Z30, respectively.

Some haplotypes in the sable populations from Western Siberia (AK23, Z5) were more commonly found in the pine marten. At the same time, one of the sable haplotypes (Z30) was found in the pine marten with a frequency 10%. Hybrids *M. zibellina* $\times$ *M. martes* had mtDNA haplotypes of both parental species (Table 2).

Table 1 Composite haplotypes[a] frequencies of the mtDNA cytochrome b gene in the sable, the pine marten and their hybrids

A group of animals	Locality	Sample size	Z28 AAAA	Z30 BBBB	Z31 BABB	Z5 CBAB	AK23 AACA	AC27 CBBB	UC1 AABA	AK29 BBAB	AK55 CBCB
M. martes	The South Urals, the Belaya River basin	13	0	0.154	0	0.231	0.154	0	0.077	0.231	0.154
	Western Siberia, Tyumen and Omsk region	32	0	0.100	0	0.350	0.100	0	0	0.450	0
Hybrids	Western Siberia, Tyumen region	51	0	0.326	0.087	0.196	0.326	0	0	0.022	0.043
M. zibellina	The North Urals, the Sos'va River basin	3	0	0	0	0	0	0	1.000	0	0
	Western Siberia, Tyumen region	97	0.030	0.619	0.227	0.031	0.052	0.041	0	0	0
	Eastern Siberia, Yakutia	9	0.222	0.778	0	0	0	0	0	0	0
	Eastern Siberia, the Sayany mountains	12	0.500	0.500	0	0	0	0	0	0	0
	The Far East, the Amur River basin	13	0.308	0.615	0.077	0	0	0	0	0	0
	The Far East, Sakhalin Island	12	0	1.000	0	0	0	0	0	0	0
	The Far East, The Kamchatka Peninsula	12	1.000	0	0	0	0	0	0	0	0

[a] Composite haplotypes are designated by four letters corresponding to four restriction endonucleases Hae III, BstN I, Taq I and RSA I

**Table 2** The frequencies of haplotypes derived from another species

A group of animals	The percentages of haplotypes from	
	M. martes	*M. zibellina*
M. martes	–	10
Hybrids	54.4	41.3
M. zibellina	8.3	–

The results from STRUCTURE analysis of RFLP data show that some individuals from Western Siberian sable population are clustered with the pine marten, while another part—with the eastern sable populations (Fig. 2). There was little genetic structure among other groups of the *M. zibellina*. 'Pure' (phenotypically normal) martens formed a separate cluster (4).

Three individuals of the sable from the Ural had unique haplotype UC1. This haplotype was not found in other sable populations (Table 1). The haplotype UC1 (AABA) differs by two mutational steps from the haplotype Z28 (AAAA) that is the most common in sable populations from Eastern Siberia, and by one mutational step from the haplotype Z31 (BABB), characteristic for the Western Siberian sable (Fig. 3).

Discussion

The present mtDNA data effectively indicate introgressive hybridization process between the sable and the pine marten. In fact, the Western Siberian sable has a mixed origin. As our data show, the Western Siberian sable is more polymorphic compared to other sable subspecies, particularly in mitochondrial markers. Only one haplotype (BBBB) was identified in the Sakhalin sable. Another single haplotype (AAAA) was detected in the Kamchatka
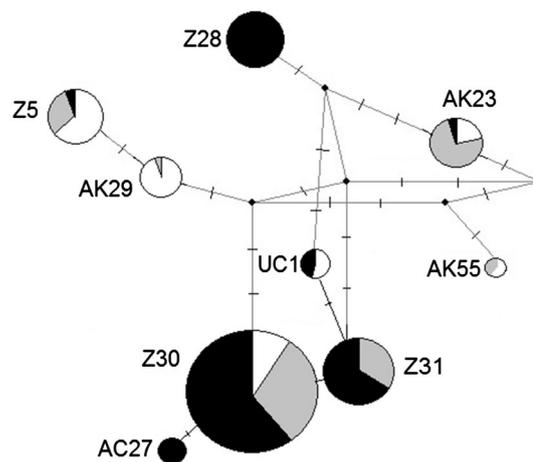
Fig. 3 Median-joining network of the sable *M. zibellina* and the pine marten *M. martes* mtDNA haplotypes. The size of the circle is proportional to the haplotype frequency. Pie-charts indicate relative frequencies in various groups: *M. martes* (in white), *M. zibellina* (in black), hybrids (grey). The number of mutations between haplotypes is designated

sable, while three haplotypes were found in the continental sable populations from the Far East. A low level of genetic variability of some sable subspecies (*M. z. sahalinensis*, *M. z. kamtschadalica*) may be due to the "founder effect" and be the result of genetic drift in island populations (Balmysheva et al. 2002). Our data are consistent with the data of other researchers. Petrovskaya (2007) studied 444 samples from three regions of the Far East and found three mtDNA haplotypes. The same three haplotypes were detected in all the studied eastern sable populations (Balmysheva and Solovenchuk 1999; Malyarchuk et al. 2010). Fifty samples of the sable from the Kamchatka Peninsula were monomorphic on the haplotype A (Petrovskaya 2007). The Western Siberian sable had all of these
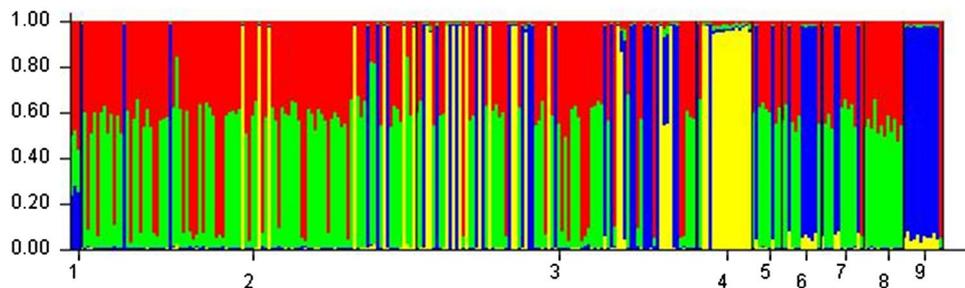
Fig. 2 Results from STRUCTURE analysis of RFLP data from the sable, the pine marten and their hybrids: 1—*M. zibellina* from the North Urals; 2—*M. zibellina* from Western Siberia, 3—hybrids from Western Siberia, 4—*M. martes* from Western Siberia; 5—*M. zibellina* from Yakutia, 6—*M. zibellina* from the Sayany mountains; 7—*M. zibellina* from the Amur River basin, 8—*M. zibellina* from Sakhalin Island, 9—*M. zibellina* from the Kamchatka Peninsula. Four parental types (K = 4) correspond to the three main phylogenetic lines of the sable (haplotypes Z28 (AAAA), Z30 (BBBB), Z31 (BABB)—in blue, red, and green, respectively) and the marten line (in yellow). (Color figure online)

haplotypes as well as two haplotypes typical for the pine marten. The high diversity of mtDNA haplotypes found in modern populations of the Western Siberian sable may be due to the introgression of mitochondrial genes from the pine marten as, in many cases, hybridization causes high heterozygosity and high haplotype diversity. The frequency of "martens" haplotypes in the sable was about 8.3%. At the same time, a typical "sable" haplotype was found in 10% of the pine marten. This suggests a symmetrical interspecific introgression of genes.

Only 'pure' (phenotypically normal) martens were not introgressed (Fig. 2). Little genetic structure among other *M. zibellina* can be explained by the migration processes within the region and population restoration due to reintroduction carried out in the same regions. Haplotype Z28 (AAAA) is frequent in the Eastern Siberian sable populations but is occasional in the Western Siberian sable. This haplotype marks a young phylogenetic group A occurred in late Pleistocene (Malyarchuk et al. 2010). The presence of this haplotype may be the result of reintroduction of the Barguzin sable *M. z. princeps* to Western Siberian territory (Kassal and Sidorov 2013; Zhigileva et al. 2014b).

The Barguzin sable *M. z. princeps* was introduced in the last century to speed up the recovery of local Western Siberian sable populations. There were several introductions events, a total of 1000 sable individuals were delivered (Bobrov et al. 2008, 2011). It was assumed that the Barguzin sable, having valuable dark fur, could improve the fur quality of the local sable subspecies. However, for several decades, there has been a change from the phenotype characteristic for the eastern subspecies to the phenotype of the local subspecies (Ranyuk and Monakhov 2011). Perhaps the Barguzin sable was not enough adapted to local conditions. The low frequency of mtDNA haplotype AAAA (3%) compared to other haplotypes indicates a small contribution of the Eastern mitochondrial lines to the gene pool of the current sable populations in Western Siberia.

The unique mtDNA haplotype (UC1) was detected in *Marten* population from the Urals. This haplotype could persist in the Ural Mountains refugia because of the isolation. The presence of cryptic northern glacial refugia for *M. martes* in Europe was assumed (Ruiz-González et al. 2013). We hypothesized that this haplotype might mark the most ancient mitochondrial DNA line of *Marten*, because it is intermediate between haplotypes typical for the pine marten, on the one hand, and the sable, on the other hand (Fig. 3). There are numerous paleontological finds of *Martes* sp. (sable-marten like) from the Urals, where, according to one of the hypotheses, is the center of their origin. These data are also consistent with data on the highest haplotype diversity of sable from the Urals (Rozhnov et al. 2013). Moreover, some populations of these ancient 'martens' could persist in the Ural refugiums even during the ice age. However, due

to the small number of samples from the Urals tested in this research, this issue needs to be studied further.

The nuclear markers data did not give strong evidence regarding nuclear genes introgression between the sable and the pine marten, due to a lack of suitable species-specific markers among the taxa examined (Zhigileva et al. 2014a). Nevertheless, the genetic comparison between *M. zibellina* and *M. martes* has revealed high similarity of nuclear markers in these species. This fact, in addition to the same number of chromosomes in both species compared (2n = 38), causes the ease of hybridization between the pine marten and the sable. This indicates that the process of species divergence has not gone far enough and hard reproductive barriers have not been formed, as *M. martes* and *M. zibellina* diverged quite recently (Sato et al. 2003). Thus in Western Siberia, a place of secondary contact of the sable and the pine marten after the Ice Age, a vast zone of hybridization has formed.

This conclusion is confirmed by other authors' data, based on morphology and biogeography (Kassal and Sidorov 2013), as well as on sequencing the genomes of the sable and the pine marten (Malyarchuk et al. 2010; Rozhnov et al. 2010; Ruiz-González et al. 2013). Furthermore, Davison et al. (2001) found "sable" haplotypes in the pine marten population from Europe where the sable does not dwell at the present time. In other research (Malyarchuk et al. 2010), haplotype B identical to that in the sable from the Far East was found in one individual of *M. martes* from Sweden. Therefore, these authors stick to the hypothesis of ancient introgressive hybridization between these species in Northern Europe.

Due to the absence of genetic research on the sable before critical reducing its numbers in the late 19th century, we can not say how this depopulation affected the introgression intensity. Nevertheless, observation of the current state of the *Marten* populations indicates that the proportion of hybrids increases with the expansion of the area due to a lack of conspecific partner. The pine marten has occupied the ecological niche vacated after the drastic reduction in the number of the sable. The area of distribution of the pine marten has expanded and the proportion of interspecific hybrids has increased (Kassal and Sidorov 2013). As the population size of the sable and the pine marten as the cyclic species varies periodically, the hybridization process could occur many times since the Pleistocene. This supports the hypothesis that the proportion of the pine marten genes in the Western Siberian sable gene pool was historically large.

Despite the frequent occurrence of hybrids *M. zibellina* x *M. martes* and backcrosses in natural populations of martens in Western Siberia and the Urals, the gene pool of both species is maintained. Reduced fertility of hybrids is a mechanism of regulation of their numbers and boundaries of a hybrid zone in this area. The genetic uniqueness of the sable

from different parts of the distribution area can be traced despite the influence of natural and artificial migrations (Kashtanov et al. 2015). This situation differs from that of the pine marten in England, where there was a loss of gene pool of relict populations as a result of the reintroduction of animals from continental Europe and the hybridization with the American marten *M. americana* (Jordan et al. 2012).

These findings are of great importance for the conservation of genetic resources of the sable. Overhunting of the sable as a more fur valuable species than the marten can lead to violation of the dynamic equilibrium between genetic systems of these related species. This may lead to the loss of a unique gene pool of the sable.

The combination of mtDNA and nuclear data sets appears to show that the sable and the pine marten are very closely related species. Evidence of symmetric introgression of mitochondrial genes between the sable and the pine marten has been detected. Frequency of marten haplotypes in the sable was 8.3%, while sable haplotype was found in 10% of martens. Higher similarity of nuclear markers of hybrids *M. zibellina* × *M. martes* to the sable than to the pine marten has been observed. The low frequency of mtDNA haplotype A indicates a comparatively low portion of Eastern lines in the current sable populations in Western Siberia.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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