

Genetic aspects of interspecies hybridization between sable and pine marten based on microsatellite loci data

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Conflicts of Interest

The authors declare no conflict of interest.

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Abstract

Individuals with intermediate phenotype of the sable (*Martes zibellina*) and pine marten (*Martes martes*) are regularly observed in the sympatry zone of these species' ranges. Presumably, these offspring are hybrids of sable and pine marten. We studied 246 animals, identified by morphological characters as 20 of pine martens and 226 of sables. We surveyed within areas focused on sympatry and identified neighboring territories based on genetic markers. In 6 out of 11 geographical localities of sable, we found individuals (N=10) with a significant portion of pine marten's genotype. Among 20 samples of pine martens, we found one individual with a significant proportion of the sable's genotype. Thus, accurate identification of sable and pine marten hybrids by morphological characters was practically impossible: in sympatric



populations, some animals morphologically defined as sable or pine marten may be hybrids of these species.



Abstract photo. *Pine marten (Martes martes, left) photo by Alexander Gos'kov and sable (Martes zibellina, right) photo by Evgeniy Zakharov.*

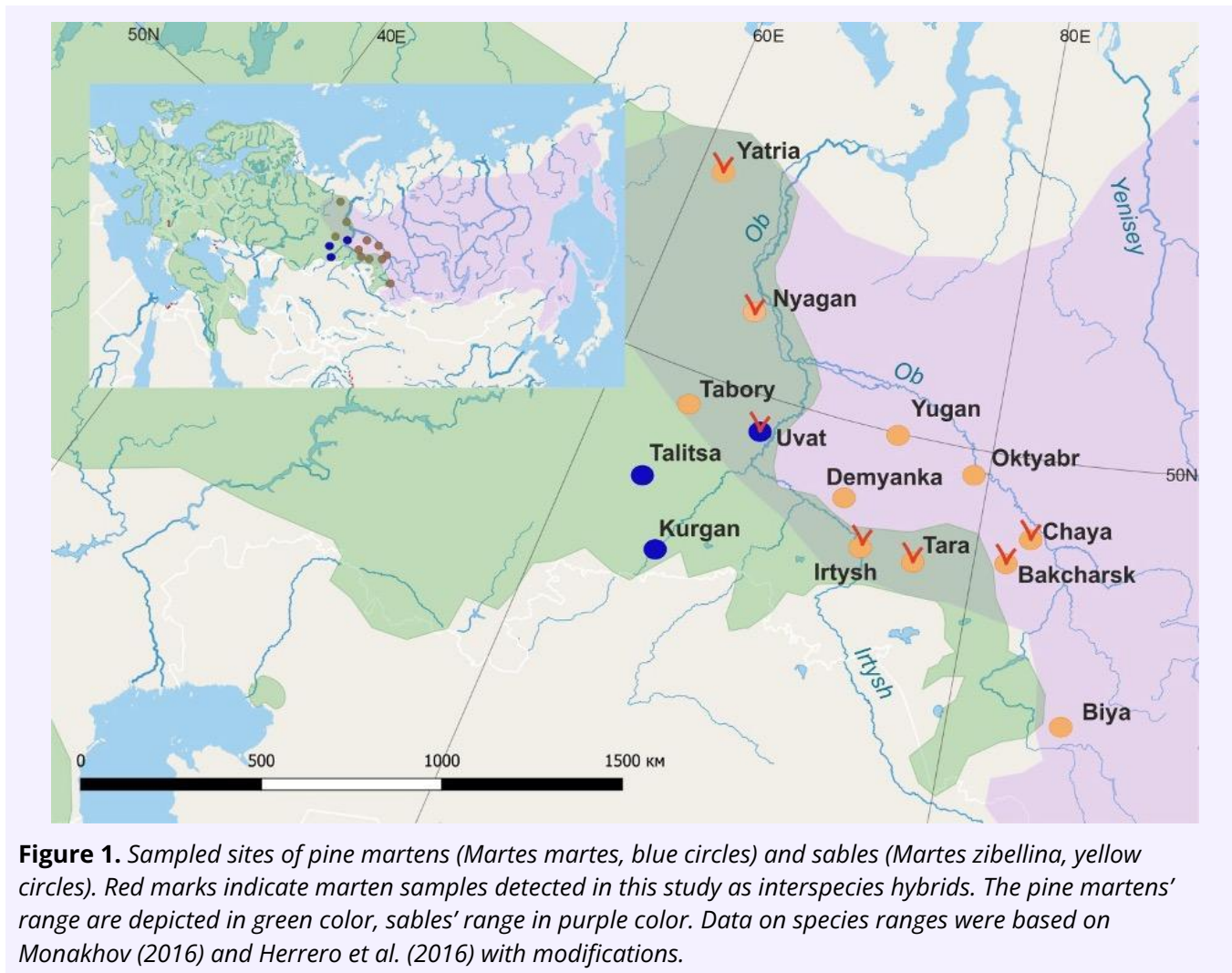
Keywords: *sable, pine marten, hybrid, kiduses, sympatry zone, microsatellite loci*

Introduction

Sable (*Martes zibellina*) and pine marten (*Martes martes*) are two closely related species of the genus *Martes*, with genetic divergence about 1-2 Ma ago (Koepfli et al. 2008; Sato et al. 2012; Law et al. 2018). It has been assumed that sable originated in the Far East (Monakhov 1976), and the pine marten in Western Europe, possibly in the Alps (Grakov 1981). The modern range of the pine marten covers all of Europe, from the British Isles on the west to the Ural Mountains and the south of Western Siberia on the east. The sable range is mainly located in Asia, with the western edge of the northern Urals, and the eastern edge on the Far East, including the Kamchatka Peninsula and Okhotsk Sea islands. In the present, range of sympatry of the two species is located on the Northern Urals and on the



southwestern part of Western Siberia (Fig. 1). It has been hypothesized that the range of the sable extended far to the west, reaching Scandinavia (Jurgenson 1956; Bakeyev et al. 2003; Monakhov 2022), and the pine marten in the east could have reached the basins of the Taz and Yenisei rivers (Monakhov 2022).



Despite the fact that sable and pine marten are well distinguished by external features (shape and coloration of the head, shape of the throat spot, tail length, fur of paws, Fig.2, Table 1) animals with intermediate phenotypic characteristics are often found in areas where both species are found together. Usually, such animals are identified as hybrids. The first



references about the hybrid of sable and pine marten are in the late 18th century in the works of Pallas (1786), but a detailed description of the morphology and ecology of hybrids appears only in the first half of the 20th century (Manteifel 1934; Skalon et al. 1940, etc.). The first experiments on crossbreeding sable and pine marten in captivity were organized at the same time (Ponomarev 1946; Grakov 1974, 1981, 1993) when the first hybrid generations were obtained. The results of breeding experiments were inconsistent. In some cases, infertility of hybrids were described, and the phenomenon of heterosis was observed, when a hybrid male was much larger than parents (Ponomarev 1946). Other authors describe partial fertility of hybrids and intermediate characteristics of skull and fur size (Portnova 1941; Grakov 1974, 1981). Based on contradictory data on the description of wild hybrids, often referred to as kiduses in some journals (e.g., Monakhov and Uspenskaya 2013), some have concluded the scale of hybridization between sable and pine marten was an overestimate, and hybrids of sables or pine martens would occur with a phenotype different from the majority of animals (Pavlinin 1963).

In previous studies, genetic markers, particularly microsatellites, have been used to identify hybrids (Pischulina 2013; Modorov et al. 2020). In this study, we attempt to assess the presence of hybrids in sympatric populations of sable and pine marten based on multiplex analysis of 11 microsatellite loci of nuclear DNA (Modorov et al. 2020).

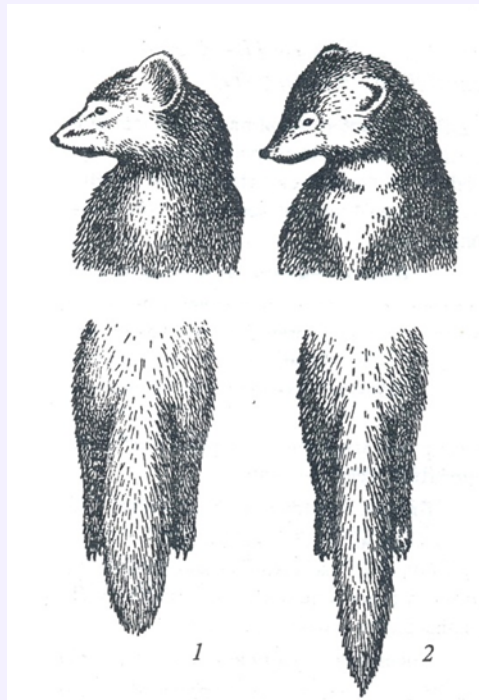


Figure 2. Throat spot and tail of the sable (1) and pine marten (2). Picture from Kuznetsov (1975).

Methods and Materials

This study was based on tissue samples (muscle or skin) of 216 hunted or trapped sables and 30 pine martens. None of the authors were involved in hunting, and no animal was killed with the aim of collecting samples for this work. All samples were obtained directly from licensed hunters. Species identification was made by hunters and based on morphological species-specific characteristics. Our samples included both new material (95 specimens) and individuals already analyzed in previous studies (Modorov et al. 2020; Ranyuk et al. 2021). Martens and sables were sampled at 14 sites of the study area (Fig. 1). DNA was extracted using the DNA-extran-2 Kit for Animals (Sintol, Russia). All the samples were genotyped at 11 microsatellite loci (Modorov et al. 2020). The sets of primers were chosen on the basis of already known microsatellite loci in the sable: Mzf51 and Mzf56 (Zhu et al. 2017); *Martes americana* and *Gulo gulo* Ma1, Ma3, Ma8, Ma15, and Ma19 (Davis & Strobeck 1998); *Martes foina* Mf8.7 and Mf8.8 (Basto et al. 2010); and *Neogale vison*, *Mustela erminea*



Mvis72 and Mvi2243 (Fleming et al. 1999; Vincent et al., 2003). The selected microsatellite loci were located in different linkage groups (Modorov et al. 2020). The PCR was carried out as described by Modorov et al. (2020). PCR products were analyzed via automated capillary electrophoresis on an ABI 3130 (Applied Biosystems) genetic analyzer. Allele sizes were scored against an internal size standard S-550 Lys (Gordiz) in GeneMapper v3.7 (Applied Biosystems).

Table 1. *Morphologic characteristics of sables and pine martens*

Characteristic	Pine marten	Sable
Fur coloration	The coloration of the head and back is about the same	The color of the head is lighter than the body
Throat spot	light yellow or orange, large, well-defined, passes between the front legs	slightly expressed, yellowish, rarely white, with blurred lines, often absent at all
Winter fur on the paws	Paws lightly furred and claws are exposed	Paws completely furred, claws are hidden
Tail length	The length of the tail is longer than the length of the extended hind legs	Tail slightly protrudes beyond the ends of the extended hind legs
Baculum	Baculum with a closed ring at the distal end	The end of the baculum is unclosed and with fork shape

The observed (N_a) and effective (N_e) number of alleles per locus and observed (H_o) and expected heterozygosity (H_e) (Nei, 1977) for the samples were estimated, and the analysis of molecular variance was performed using GenALEx 6.5 (Peakall & Smouse 2006, 2012).

We used STRUCTURE for accurate analysis of admixture-affected population structure. The program implements a model-based clustering method to infer population structure. We used Bayesian clustering realized in STRUCTURE v.2.3.4 (Pritchard et al. 2000) to infer gene pools (sets of alleles in a population) and for genotype assignment. The number of potential genetic clusters (K) was assessed via five individual runs for each



K value ranging from 2 to 12 with a burn-in length of 10,000 and 100,000 iterations of each chain in accordance with the admixture model along with the assumption of correlated allele frequencies among groups (Falush et al. 2003). We examined the optimal number of clusters (K) by using two alternative approaches based on the change of mean log likelihoods of the data: LnP(D) of independent runs for K (Pritchard et al. 2000) and rate of change in the LnP(D) , ΔK , between successive K values (Evanno et al. 2005). The outputs of 10 independent runs for optimal K values were integrated using CLUMPAK (Kopelman et al. 2015). The main pipeline function was used for the summation and graphical representation of the results obtained in STRUCTURE. For this research we identified individuals as “hybrid” if proportion of other species genotype (Q) at the K=2 was more than 0.1 (10%). This relatively low threshold value proved to be highly effective in previous studies of mammalian hybridization with microsatellites markers (van Wyk et al., 2017; Szatmári et al., 2021).

Results

For all 11 loci, no unidirectional deviations of the observed frequencies genotype from the expected frequencies according to the Hardy-Weinberg equilibrium were observed. Therefore, no loci were excluded for analyzing the genetic structure of the population.

The lowest values of the effective number of alleles per locus and heterozygosity were obtained for the pine marten sample (Table 2).

We provide Bayesian clustering results ($K = 1-12$) in Figure 3. The mean similarity score at $K = 2-12$ in the CLUMPAK main pipeline was high (0.89–0.99). Three genetic clusters were detected using Evanno's method (the best $K = 3$). The highest value of LnP(D) detected for $K = 4$.



Table 2. *Geographic locations of the populations analyzed in this study and a summary of genetic diversity metrics. Abbreviations: N, the number of individuals; CI95, confidence interval 95% (low bound - upper bound); Na, the mean number of alleles per locus; Ne, the effective number of alleles per locus; Ho, observed heterozygosity; He, expected heterozygosity. Three geographic locations of pine martens were pooled in one sample "pine marten" because of small number of individuals for Uvat (N=3) and Kurgan (N=3)*

Sample ID	Sampling site	N	Proportion of hybrids CI ₉₅	Na	Ne	Ho	He
Pine marten							
Pine marten (Talitsa, Kurgan, Uvat)	Talitskiy district in Sverdlovsk Oblast, Dalmatovskiy district in Kurgan Oblast, Uvatskiy district in Tyumen Oblast, Russian Federation (RF)	20	1 0.05 (0.001-0.25)	4.55	2.54	0.42	0.47
Sable							
Yatria	Basin of Yatria river in Khanty-Mansiysk Autonomous Okrug, RF	9	2 0.22 (0.03-0.6)	5.45	4.12	0.74	0.72
Nyagan	Oktyabrskiy district in Khanty-Mansiysk Autonomous Okrug, RF	20	2 0.1 (0.01-0.32)	6.27	4.13	0.68	0.72
Tabory	Basin of Tabory river in Sverdlovsk Oblast, RF	12	0 0 (0-0.26)	5.36	3.43	0.63	0.68
Yugan	Basin of Yugan river in Khanty-Mansiysk Autonomous Okrug, RF	28	0 0 (0-0.12)	6.36	3.95	0.70	0.71
Oktyabr	Alexandrovsky district in Tomsk Oblast, RF	10	0 0 (0-0.31)	5.55	3.58	0.68	0.67
Demyanka	Basin of Demyanka river in Tyumen Oblast, RF	33	0 0 (0-0.11)	6.55	4.06	0.71	0.72
Irtysh	Basin of Irtysh river in Omsk Oblast, RF	27	2 0.07 (0.01-0.24)	6.55	3.93	0.69	0.71
Tara	Basin of Tara river in Novosibirsk Oblast, RF	27	2 0.07 (0.01-0.24)	6.91	4.52	0.70	0.73
Bakcharsk	Bakcharsky district in Tomsk Oblast, RF	24	1 0.04 (0.001-0.21)	6.73	4.21	0.68	0.71
Chaya	Chayinsky district in Tomsk Oblast, RF	20	1 0.05 (0.001-0.25)	6.82	4.27	0.72	0.71
Biya	Basin of Biya river in Altai Krai, RF	16	0 0 (0-0.21)	6.64	4.33	0.70	0.72



At $K = 2$, pine marten samples were separated from sable populations (Fig. 3). At the same time, individuals with more than 10% of the “pine marten” genotype were found in sable populations. Such individuals were found in samples Yatria, Nyagan, Irtysh, Tara, Bakcharsk and Chaya (Fig. 1 and 3). One individual with a high level of “sable” genotype was found in pine martens’ sample (Fig. 3). At $K = 3$ and $K = 4$ the population structure of the sable begins to differentiate where populations from the territory between Ob and Irtysh rivers are separated from others (Yugan, Oktyabr, Demyanka, Irtysh, Tara, Bakcharsk and Chaya).



Figure 3. Individual-level membership of gene pools based on the STRUCTURE analysis. The columns represent the proportion of membership assigned to each gene pool ($K = 2, 3, 4$) in each individual.



Discussion

Considerable debate occurs regarding what defines a species (e.g., Dobzhansky 1935), but it has been argued that the biological definition of a species includes morphological, geographical, ecological, behavioral, and molecular information (Mayr 1996). Here, we explore molecular information to provide an assessment for two species - sable and pine martens.

Hybridization in a wild Mustelidae family has been recorded. There is genetic evidence of hybridization between two close related species of badgers *Meles meles* and *M. leucurus* in the contact zone (Kinoshita et al. 2018), natural hybrids of two polecat species, *Mustela eversmanii* and *M. putorius* were identified in the sympatric area (Szatmari et al. 2021). Interspecies hybridization was identified in two zones of contact between North American martens *Martes americana* and *M. caurina* (Colella et al. 2019).

The information about hybridization between the species of our study, Eurasian martens *M. martes* and *M. zibellina* dating back to the 18th century (Pallas 1786). There is even a special name for such hybrids - kidas or kidus. In the 21st century, not only genetic evidence of natural hybridization of these two close species appeared (Pischulina 2013, Modorov et al. 2020), but also the ability of such hybrids to produce fertile offspring were identified (Manakhov, 2022).

Sable and pine marten are typically thought to be well-distinguished by external features - head shape, paw's fur, tail length, fur coloration and properties (Fig. 2, Table 1). Craniological, osteological and odontological characters have a large zone of overlapping for sables and pine martens and generally are not considered suitable for individual species identification (Gasilin, Kosintsev 2013; Gimranov, Kosintsev 2015; Ranyuk, Monakhov 2016). Genetic markers, particularly microsatellite loci and mtDNA, can be used as additional evidence to differentiate species (Rozhnov et al. 2010; Modorov et al. 2020).



The multiplex of 11 microsatellite loci used in this study was quite successful in separating species from each other (Fig. 3). Pine marten has a low genetic variability compared to sable (Table 2). Similar results have been obtained previously for other genetic markers (Manakhov 2022) and morphological traits (Monakhov 2021). This could be due to differences in species ecology where the pine marten may be adapted to a temperate climate, whereas the sable appears more adapted to cold and extreme climates. Another difference could be that sables were described with specific intraspecies genetic structure in the species' range (Ranyuk et al. 2021), whereas pine marten from the whole East European Plain formed one genetic group (Manakhov 2022). Massive translocations carried out in the middle of the 20th century, when sables were moved from the Baikal area to Western and Eastern Siberia (Pavlov et al. 1973) could additionally increase the genetic diversity of sables.

Population structure of the sable was also revealed in our study when according to Bayesian clustering the samples from West Siberian Plain formed the one genetic cluster at $K=3$ and $K=4$ (Fig. 3). Presumably rivers Ob and Irtysh play the role of some landscape barriers for dispersal ability of the animals. Samples from Yatria, Tabory and Biya formed an opposite genetic cluster (Fig. 3). Sable showed a high level of the genetic variability in common and it can be related to high migration activity of the species (Bakeyev et al., 1980; Chernikin, 2006). Previous studies of the sable's genetic structure showed positive autocorrelation occurs in the Mantel correlogram in 300–600 km distance class (Ranyuk et al. 2021). Samples Yatria and Tabory from the western bank of Ob River and population from the basin of Biya River were separated from each other about 1500 km and their presence in the common genetic cluster cannot be explained by migrations only. All these samples are from the autochthonous sable's populations so translocations could not influence the genetic structure of these samples. Intraspecies structure of the sable is a very complicated and interesting problem and to bring light to this question we need more geographic samples and additional genetic markers.

Here, we compared animals identified to species by experienced hunters based on morphological characteristics as pine martens or sables. According to our genetic analysis in 6 geographic regions, samples of 'sable' individuals also exhibited a significant level of the pine marten



genotype, which may suggest that these are interspecific hybrids. Our sampled animals did not differ in morphology from the sables harvested on the same territory. Among the pine martens sampled, an individual with a high part of the sable genotype also was found. Our data confirm the results of a previous genetic study of sables and pine martens from the Northern Urals where it was difficult to identify specific individuals in the sympatry zone of the pine marten and sable by physical characteristics, since the individuals of parental species deviated in morphological traits (Pischulina 2013). Some genetic hybrids, on the contrary, did not differ from one of the parental forms. Genetic methods identified up to 20% of individuals in the sympatric population of the Northern Urals as hybrids, but the results of phenotypic and genetic identification of hybrids did not coincide in 37% of cases (Pischulina 2013). In our study we included individuals with morphological characters of “pure” species and interspecies hybrids were found in half of geographic samples with proportion from 4% (Bakcharsk) to 22% (Yatria). Thus, accurate identification of sable and pine marten hybrids by morphological characters is practically impossible: in sympatric populations, some animals morphologically defined as sable or pine marten may be hybrids of these species, while some individuals morphologically identified as hybrids may be representatives of one of the species.

In the IUCN Red List, pine marten and sable have been assigned to the ‘Least Concern’ category (LC) (Herrero et al., 2016; Monakhov, 2016). However, these two *Martes* species are hunted, and there is always the threat of over-harvesting of certain populations. The sable’s and marten’s populations from the sympatry zone are unique and following the strategy of biodiversity conservation at the intraspecific level, special attention should be paid to the martens and sables in Ural, Western Siberia and Altai Krai.

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Author Contributions

Maryana N. Ranyuk: laboratory work, data analysis, manuscript preparation; Makar V. Modorov: laboratory work, data analysis, manuscript preparation; Vladimir G. Monakhov: collection of material, manuscript preparation.

Data Availability

Data and R code will be made available upon request.

Transparent Peer Review

Results from the Transparent Peer Review [can be found here](#).

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