Genetic connectivity between Caucasian and Northern Velvet Scoter *Melanitta fusca* populations and its importance for the long-term survival of the species in the Caucasus

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Abstract

Historical data suggest that the Velvet Scoter *Melanitta fusca* once had a widespread breeding distribution throughout the Caucasus region, but recent studies have revealed that this population has declined significantly and is now restricted to a single small breeding site at Lake Tabatskuri in Georgia. This population was considered a distinct relict group, likely isolated from the continuously distributed population across the northern forest, alpine and arctic regions of western Eurasia because of its geographic isolation. Until now, however, there was no information available about the genetic structure of the potentially isolated Caucasian population and its connectivity to the rest of the more continuously distributed northern Velvet Scoter population. Here, we analysed mitochondrial cytochrome b (hereafter *cyt b*) sequences and nuclear genotypes at nine microsatellite loci to evaluate: (1) genetic differentiation among the Caucasian and circumpolar populations, and (2) the genetic diversity of the local population. Our analysis revealed no significant genetic differentiation between these two populations based on both genetic markers, indicating that these two regions may represent a single panmictic population. These results are important for planning future conservation measures to maintain the Velvet Scoter population in the Caucasus.

Key words: Baltic, Caucasus, connectivity, conservation, population genetic structure, Velvet Scoter.

The Velvet Scoter *Melanitta fusca* is a globally declining sea duck (BirdLife International 2020) which has led to an International Union for Conservation of Nature (IUCN) classification of Vulnerable. The probable causes for these declines include climate change (Drever *et al.* 2011), reduction in abundance of molluscs (Dagys & Žydelis 2002; Steinacher *et al.* 2009; Dagys & Hearn 2018), bycatch in fishing gear (Dagys & Žydelis 2002; Žydelis *et al.* 2013; Dagys 2016; Carboneras *et al.* 2020; Morkūnas *et al.* 2022), invasive species (Almquist *et al.* 2010; Dagys 2016), and predation and disturbance (Mikola *et al.* 1994; Nordström *et al.* 2002; Traylor *et al.* 2006). Although the Velvet Scoter inhabits most of the Holarctic region of western Eurasia (Carboneras *et al.* 2020), there is a small disjunct Caucasian population in the Western Palearctic area (BirdLife International 2020). This small, isolated relict population (Dagys 2016; Carboneras *et al.* 2020) consisted of 25–35 breeding pairs in the Caucasus region throughout the years 2017–2020 (Paposhvili 2018, 2021), which likely winter in the Caspian and Black Sea areas (Dagys 2016; BirdLife International 2020). The small population size and its geographical isolation from the main breeding areas is of conservation concern, and more information is needed to fill gaps in knowledge of its biology if we are to be able to implement effective conservation strategies.

The main nesting habitat of the Velvet Scoter ranges more or less continuously along the Baltic coasts, through the boreal forest, arctic and alpine habitats of western Eurasia, from Norway to the River Yenisey in western Siberia (hereafter called "Northern population"). In winter it occurs mainly in north and northwest Europe, where it numbers 141,000–268,000 mature individuals (Cramp & Simmons 1977; BirdLife International 2020). The estimated size of the Caucasian population was < 1,500 individuals in the mid-1990s, and a more recent revision using midwinter counts suggests a range of 240–420 wintering birds in the Black and Caspian Seas (Wetlands International 2020). However, the population has disappeared from all but one part of the Caucasus due to human disturbance, population fragmentation and habitat loss in recent years (Adamian & Klem 1997; Kirwan *et al.* 2014; BirdLife International 2020; Ömral Ünsal Özkoç, pers. comm.). Currently, Lake Tabatskuri in Georgia holds the last breeding concentration of Velvet Scoters (< 100 individuals) in the Caucasus (Paposhvili 2021), where breeding success is quite low. Bycatch and disturbance from fishing activities, competition with Armenian Gull *Larus armenicus* for nesting habitat, and the predation of young Velvet Scoters by Armenian Gull are the main factors affecting breeding success (Paposhvili 2021). Now that this population teeters on the very brink of possible extinction, it is vital that we establish the degree to which the Caucasian Velvet Scoters are genetically unique and isolated from the Northern population, in order to develop appropriate conservation and management strategies to maintain its viability into the future. In the present study, we provide the first genetic assessment of the Caucasian Velvet Scoter population and compare it with samples taken from Northern population birds to estimate the degree of genetic differentiation. The

results obtained from this study will also provide useful information for assessing population connectivity, predicting the potential response of the species to possible future environmental changes and optimising conservation and management strategies to prevent the extirpation of Velvet Scoter in the Caucasus.

Methods

Sample collection

Samples were grouped according to their origin: the Northern and Caucasian populations. Samples of the Caucasian population were collected from Velvet Scoters breeding at Lake Tabatskuri (41°39'N, 43°38'E) Georgia throughout the summer seasons (July–August) of 2015–2019. These samples were taken from nesting females caught for ringing (2–3 wing covert feathers; $n = 9$), from the membrane of hatched eggs ($n = 3$, each of which were from different nests) and from unhatched nestlings found dead in eggs (tissue samples, $n = 13$, each of which was from different nests). The samples of the Northern population were collected during the wintering season from drowned Velvet Scoters caught in gillnets (tissue samples, $n = 22$) in Lithuanian coastal waters on the Baltic Sea from November 2015 to April 2016, provided voluntarily by coastal commercial fishermen.

DNA isolation and amplification

DNA was extracted from all samples (feather and tissue) using QIAGEN's DNeasy Blood & Tissue Kit (QIAGEN, Germany), according to the manufacturer's protocol. Extracted DNA was eluted in 100 µl volume. Overall, we analysed 25 samples from Lake Tabatskuri and 22 samples from the Baltic Sea.

The mitochondrial partial *cyt b* gene of 14 Velvet Scoters (seven Caucasian and seven Northern) were amplified using L15369 and H15915 primer pairs (Fu 2000). Polymerase chain reaction (PCR) was conducted in 20µl total reaction volume consisting of 3µl template DNA, 1U Promega Taq polymerase, 1X green Flexi buffer, 0.4 mmol/L dNTP mix, 0.5 mmol/L of each primer and 2.5 mmol/L of MgCl2. PCR reactions took place under the following cycling conditions: 5 min initial denaturation at 94°C, followed by 35 cycles at 94°C for 30 sec, 50°C for 30 sec and 72°C for 1 min, and at the final step, the reaction was held at 72°C for 10 min for the final extension. 5µl of each PCR product was run on 1% agarose gel for assessing the amplification success. The amplicons were sequenced from both directions on the automatic sequencer ABI 3130XL using the same PCR primers, and BigDye Terminator v. 3.1. Sequences were aligned and edited with Geneious (ver. 8.1.9). The unique sequences were deposited to GenBank (accession #OQ842598-OQ842600).

Genotypic data were analysed for nine microsatellite loci. Four loci designed for Mallard *Anas platyrhynchos* [Apl26, Apl23, Apl36 and Caud13 (Denk *et. al.* 2004; Huang *et. al.* 2005)] and five loci known to variable in other waterfowl species [Aph02, Aph4 and Aph7 (Maak *et al.* 2003), Bca11 (Buchholz *et al.* 1998) and Sfi11 (Sonsthagen *et al.* 2019)] were polymorphic in Velvet Scoters. These nine loci were amplified in three multiplex PCR reactions with forward

primers labelled at the five ends with VIC, NED and FAM dyes. PCR was performed using the QIAGEN Multiplex PCR Kit (QIAGEN, Germany). PCR amplification conditions for Aph02, Aph04, Apl23 and Apl36 were as follows: 95°C 15 min; 93°C 30 sec, 60°C 30 sec, –0.2°C per cycle, 72°C 1 min for 30 times; 60°C 30 min, 10°C 10 min. For loci Apl26, Sfi11, Bca11, Aph07, Caud13 PCR conditions were as follows: 95°C 15 min; 93°C 30 sec, 58°C 30 sec, –0.3°C per cycle, 72°C 1 min for 20 times; 93°C 30 sec, 55°C 30 sec, 72°C 1 min for 15 times; 60°C 30 min, 10°C 10 min. Amplified DNA was run on ABI 3130XL, using deionized Formamide and Genescan size standard LIZ 500 (Applied Biosystems Inc., Foster City, CA, USA). Genotypes were screened using Genemapper v5.0 software package (Perkin Elmer, Waltham, MA, USA).

Genetic diversity and population structure

We calculated basic population genetic indices sing ARLEQUIN version 3.5 (Excoffier & Lischer 2010): number of haplotypes for *cyt b* and number of alleles, allele frequencies, and deviations from the Hardy-Weinberg equilibrium (HWE) for microsatellite loci were determined. Allelic richness was calculated using software FSTAT (ver. 2.9.4). In addition, an unrooted phylogenetic tree for *cyt b* was constructed in NETWORK 10.2.0 (Fluxus Technology Ltd.) using the median-joining approach (Bandelt *et al.* 1999).

For the microsatellite dataset, the degree of population subdivision was assessed between Northern and Caucasian Velvet Scoters by calculating a pair-wise fixation index (F_{ST}) and a locus-by-locus analysis of genetic differentiation using 20,000 permutations in ARLEQUIN. We further used three approaches to explore the genetic partitioning of genetic variation between and within Northern and Caucasian regions. First, we used analysis of molecular variance (AMOVA) to assess the hierarchical partitioning of genetic variation in ARLEQUIN. Second, we visualised genetic structure using a Principal Component Analysis (PCA) using the IBM SPSS Statistics software (version 29.0.1.0). For PCA, we plotted only the first two principal components. Lastly, we used a Bayesian clustering approach implemented in the software STRUCTURE (Pritchard *et al.* 2000) to detect genetic structure in our dataset without the prior identification of sub-populations. The software infers and delineates the most likely number of genetically homogenous (*i.e.* panmictic) groups of sampled individuals from their genotypes at multiple loci and assigns the individuals to the inferred groups that maximise the Hardy-Weinberg equilibrium and minimise the linkage disequilibrium. We used the admixture model and the option of correlated allele frequencies between populations, setting the burn-in period and the length of MCMC to 100,000 each. We tested the range of Ks (*i.e.* the number of genetic clusters or populations in a dataset) from 1 to 5. To quantify the statistics of the posterior probability of population structure for a given K, we performed 10 independent runs for each K. The most likely K value was identified using the LN P(D) of Structure Harvester (Earl & von Holdt 2012).

Recent immigration rates analysis

We estimated population immigration rates over the last several generations between Northern and Caucasian Velvet Scoters as well as determine immigration ancestry of each individual (non-migrant or 1st or 2nd generation migrant) using the programme BayesAss 3.0 (Wilson & Rannala 2003). This algorithm allows for estimating the probability of allochthonous origin for each genotyped individual using allelic frequency data and does not assume that populations are in migration-drift or Hardy-Weinberg Equilibrium. We ran the programme 10 times, with different random number seeds, with the number of iterations to discard as burn-in equal to 100,000 and the number of iterations for MCMC equal to 10,000,000. We selected the run with the highest Bayesian deviance value using the script developed by Merimans (2014).

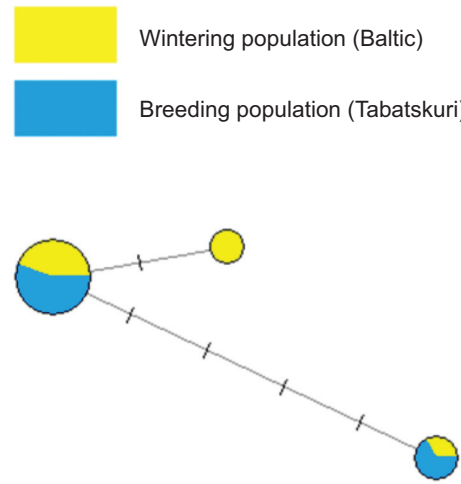

Figure 1. Median-joining network (using the methods of Bandelt *et al.* 1999) linking the haplotypes of the individual Velvet Scoters breeding at Lake Tabatskuri (Caucasian population) and those wintering in the Baltic Sea (Northern population). Size of circle is proportional to the frequency of each haplotype observed.

Results

Genetic diversity and population structure

Three mitochondrial haplotypes were revealed from the 470 bp segment of *cyt b* sequences. All haplotypes were present in the wintering Northern population (seven samples), while only two haplotypes were found in the Caucasian breeding population (seven samples). Even the most diverged haplotype (five variable sites from the central haplotype) included individuals from both populations (Fig. 1).

Numbers of alleles per microsatellite locus in both populations varied from 3 to 19. The mean allelic richness was 5.15 for the Caucasian (n = 25) and 5.2 for the Northern population (n = 22). No significant deviations from the Hardy-Weinberg equilibrium were observed in either of the populations.

We found no significant population differentiation based on microsatellite genotype data (F_{ST} = 0.012, P = 0.08, n.s.). The results of AMOVA analysis (Table 1), where the proportion of variance explained by the differences between the populations, among the individuals within populations and within individuals, was 1.1, 3.7 and 95.1%, respectively. In agreement with population level analysis, the individual-based STRUCTURE and PCA analysis suggested that our dataset consisted of a single population. STRUCTURE analysis suggested the most likely number of genetic

Table 1. Output from the analysis of molecular variance (AMOVA), based on the microsatellite profiles of Velvet Scoter samples taken from Northern (Baltic) and Caucasian (Lake Tabatskuri) individuals.

Source of variation	Degrees of freedom	Sum of squares	Variance components	Percentage of variation
Among populations	1	2.83	0.02 Va	1.13
Among individuals within populations	45	84.16	0.07 Vb	3.74
Within individuals	47	81.50	1.73 Vc	95.14
Total	93	168.49	1.82	

clusters was K = 1. The first two PCA axes explained 33% of the total variation. Ordination of these two axes did not separate individuals from Tabatskuri and Baltic populations from each other (Fig. 2).

Recent immigration rates analysis

BayesAss 3.0 simulation suggested that 31.5% of the Lake Tabatskuri population are migrants from the Baltic Sea, but only 5.1% of the Baltic Sea population are migrants primarily from Lake Tabatskuri (per generation). All Lake Tabatskuri samples had a high probability that these individuals are 1st or 2nd generation migrants from the Baltic Sea, suggesting that there is very little or no internal recruitment in this population. Only two individuals (31, 37) in Baltic samples had a high probability to be 2nd generation migrants from Lake Tabatskuri (see Fig 3.).

Discussion

The analyses of mtDNA and microsatellite revealed no significant genetic differentiation or population structure between the Northern and Caucasian populations of Velvet Scoter. Moreover, according to this study, the Northern and Caucasian populations act as a source and a sink, respectively, with very little or no internal recruitment in the Caucasian population. These results do not support the hypothesis of genetic isolation of the Caucasian population and confirm considerable intermixing between the two populations, indicating a single panmictic population in the western Palearctic. Incomplete lineage sorting can also produce a similar pattern suggesting panmixia and, given the more recent coalescent times of microsatellite makers and the general observation of male-biased dispersal in waterfowl, a more genomic approach may be necessary to determine the contributions of gene flow and incomplete lineage to the observed patterns.

Similar results were found in two different populations of Whooper Swans *Cygnus cygnus* breeding in Iceland and continental Europe, where connectivity was

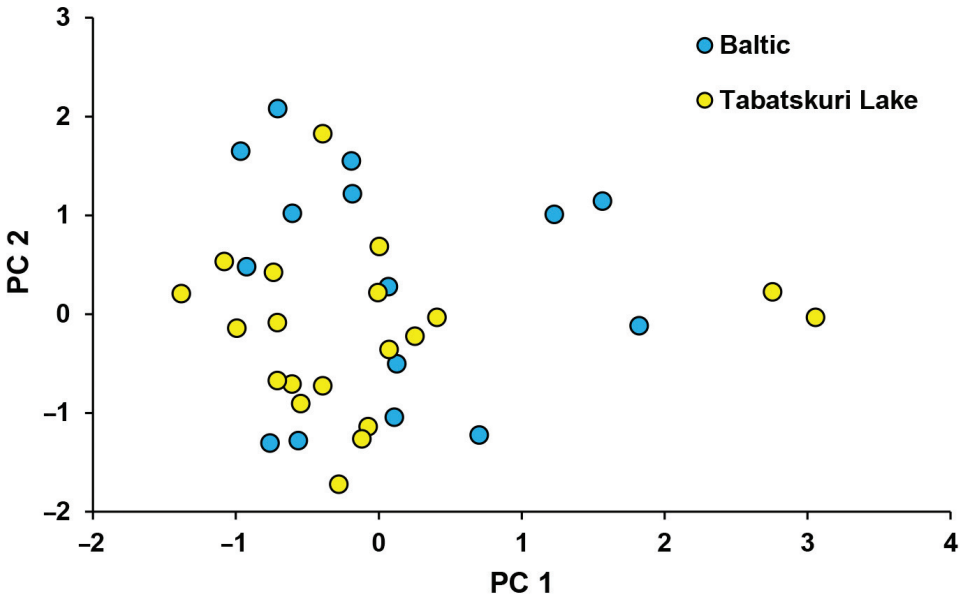

Figure 2. Ordination of the individual microsatellite genotypes along the first and the second Principal Component Analysis (PCA) axes.

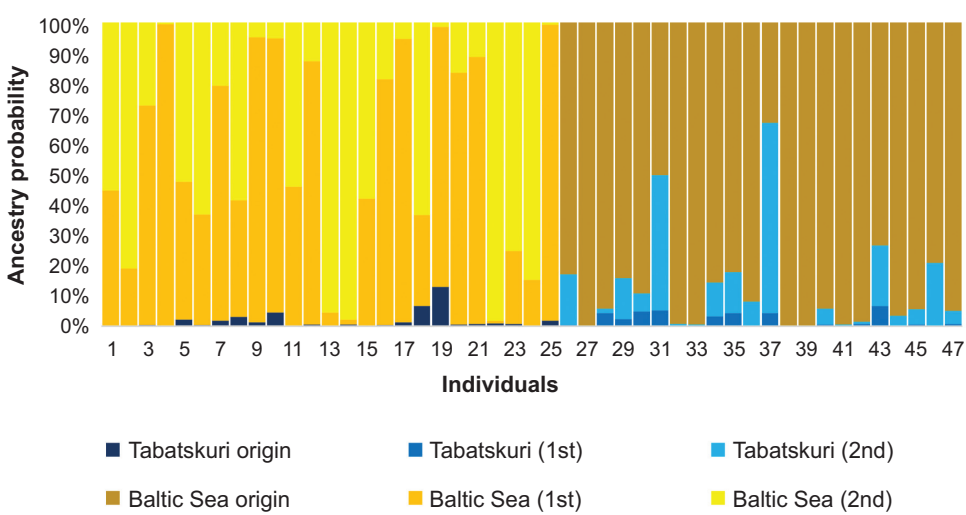

Figure 3. Individual ancestries of Velvet Scoters from Lake Tabatskuri and the Baltic Sea, respectively, inferred from BayesAss 3.0 Bayesian analysis (the first 25 samples are from Lake Tabatskuri and the remaining 22 from the Baltic Sea).

observed between populations despite separate breeding and wintering locations (Butkauskas *et al.* 2012; Brides *et al.* 2023). Our findings suggest that: (1) individuals in these two populations disperse frequently and the long geographic distance between the nesting sites does not represent a barrier, and/or (2) gene exchange across these two populations takes place at wintering sites where the birds from different populations congregate together and form pairs. Contrary to the second assumption, Brown & Fredrickson (1997) report that White-winged Scoters *Melanitta deglandi* pair during spring migration or soon after arrival at the nesting area. However, five years of observing and surveying Velvet Scoters breeding at Lake Tabatskuri suggested that the birds return to the lake in pairs in late April or May (Paposhvili 2021) and courtship and pair-bonding most likely take place at or near wintering areas (N. Paposhvili, pers. comm.). Given the fact that female sea ducks in general show fidelity to breeding sites, as well as to wintering areas (Anderson *et al.* 1992; Robertson & Cooke 1999; Mabry *et al.* 2013), and female Velvet Scoter nesting at Lake Tabatskuri showing a high fidelity as well (N. Paposhvili, pers. comm.), we can assume that the genetic connectivity between these two populations are most likely due to male dispersal.

Gene flow between populations can have a significant impact on population viability by enhancing genetic diversity within populations. This helps limit the negative impacts of inbreeding, thereby enhancing the stability and resilience of populations against environmental challenges (Sonsthagen *et al.* 2019). The major component enabling gene flow between the Northern and Caucasian populations is likely attributed to the existence of common wintering grounds. The wintering area where these two populations intermix is likely the Black Sea (Delany *et al.* 1999; Dagys 2016; BirdLife International. 2023). It is challenging to determine the origin of individual Velvet Scoters recorded on the Black Sea, as we currently lack sufficient data from ringing recovery or tracking data to make such inferences. However, according to data available on the eBird.org portal, there are indications of Velvet Scoters migrating to the Black Sea in numbers exceeding those that can be accounted for at Lake Tabatskuri, and there are also regular wintering records of other Arctic and northern nesting species (*e.g.* Common Scoter *Melanitta nigra* and Long-tailed Duck *Clangula hyemalis*) in the Black Sea region (eBird. 2023). Based on recent estimates, > 95% of the Northern population of Velvet Scoter winters in the Baltic and adjacent NW Europe (BirdLife International 2020; Wetlands International 2020), although this does not exclude single individuals occurring in the Black Sea, where the seasonal migrations of Velvet Scoter for wintering could cause the admixture of individuals in Northern and Caucasian populations. Contact between a few migrants per generation is sufficient to prevent genetic drift from causing populations to become genetically differentiated.

Based on the evidence, it is now doubly important to identify, preserve and protect important wintering sites in the Black Sea in coordination with the protection of nesting sites in order to conserve this population.

Habitat loss is widely recognised as one of the most important causes of species extinction, and recent experiences with the degradation and loss of historical nesting sites for the Velvet Scoter in Turkey, Armenia and Georgia have been a bitter reminder of this (Adamian & Klem 1997; Kirwan *et al.* 2014; Paposhvili 2018). For this reason, Lake Tabatskuri and its island have assumed an even higher conservation value because today only this site meets the breeding requirements of Velvet Scoters in the entire Caucasus, and it is clear that as long as the lake continues to provide these conditions, the Velvet Scoter will remain part of the biodiversity of the Caucasus.

Therefore, despite the lack of genetic differentiation, we consider that it is crucial to develop a long-term management strategy and undertake further conservation efforts to protect the entire habitat at Lake Tabatskuri, not just the Velvet Scoter population. As a result of restricting human access to islands on Lake Tabatskuri during the breeding season, there has been a rapid increase in the abundance and numbers of nesting pairs from six nesting pairs in 2017 to 39 pairs in 2022. Such growth is an example of the importance of maintaining and improving habitat quality and, in the short term, may also support the influx of new individuals from the north. Although this high population growth rate immediately prior to 2022 may simply be due to the high number of fully fledged young in 2020 (39 ducklings fledged), it does not rule out immigration of individuals from the Northern population as a contribution to population increase. For this reason, it would be worth increasing the sample size and using a more genomic approach such as double digest restriction associated DNA sequence (ddRAD), which may provide higher resolution in detecting subtle genetic structure and distinguish between past and present connectivity between these Caucasian and Northern breeding populations. In a study conducted using ddRAD between Northern Velvet Scoter and American White-winged Scoter *Melanitta deglandi*, individuals were almost exclusively assigned to species-specific clusters (Sonsthagen *et al.* 2019).

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Photograph: Male Velvet Scoter at Lake Tabatskuri, Georgia, by Oksana Bystritskaia.