Phylogeography and Conservation of the Caucasian Population of Velvet Scoter (Melanitta fusca)

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The doctoral thesis is submitted to the Faculty of Natural Sciences and Medicine at Ilia State University to earn the degree of Doctor in Ecology

Doctoral Programme:Ecology

Supervisors: Professor Alexander Gavashelishvili and Associate Professor Zurab Javakhishvili

Ilia State University

Tbilisi 2025

Statement

As the author of the submitted dissertation, I declare that this work is my original creation and does not include materials previously published, accepted for publication, or submitted for defence by other authors that are not mentioned or cited in accordance with the appropriate rules.

Nika Paposhvili ------------------------------ ნ.პაპოშვილი ------------------------------ 17.11.2025

აბსტრაქტი

გარიელის (Melanitta fusca) რიცხოვნობა გლობალურად მცირდება. ბუნების დაცვის საერთაშორისო კავშირის მიერ გარიელი კლასიფიცირებულია, როგორც მოწყვლადი სახეობა. კავკასიაში გარიელი წარმოადგენს ზღვის იხვების ერთადერთ მობუდარ წარმომადგენელს, რომლის გავრცელება წარსულში მოიცავდა სომხეთს, თურქეთსა და საქართველოს. თუმცა, ბოლო ათწლეულებში სახეობის რიცხოვნობა და გავრცელების არე მკვეთრად შემცირდა, და საქართველოში გარიელის მობუდარი პოპულაცია მხოლოდ ტაბაწყურის ტბაზეა შემორჩენილი.

მიუხედავად იმისა, რომ ტაბაწყურზე კონსერვაციული ღონისძიებები 2017 წლიდან ხორციელდებოდა, გარიელის პოპულაციური ტენდენციების, ბუდობის წარმატების, იზოლაციისა და შემცირების გამომწვევი ფაქტორების შესახებ არსებული ცოდნა ძალიან მწირი იყო. შესაბამისად, წარმოდგენილი სადოქტორო კვლევა მიზნად ისახავდა ამ ხარვეზის შევსებას და კავკასიაში გარიელის ეკოლოგიური და გენეტიკური მდგომარეობის კომპლექსურ შეფასებას. შესაბამისად, კვლევის ძირითადი ამოცანები მოიცავდა: (1) ტაბაწყურის ტბაზე გარიელის სეზონური სიმრავლისა და ბუდობის წარმატების შეფასებას; (2) ბუდობის ქცევასა და წარმატებაზე მოქმედი ფაქტორების იდენტიფიცირებას; (3) კავკასიურ და ჩრდილოეთ პოპულაციებს შორის გენეტიკური კავშირის დადგენას; (4) ისტორიული გავრცელების არეალის შემცირების, ძირითადი საფრთხეების და რეგიონული ხელახალი კოლონიზაციის პოტენციალის შეფასებას. კვლევები განხორციელდა 2020-2025 წლებში და მოიცავდა საველე და ლაბორატორიულ სამუშაოთა ფართო სპექტრს: ტაბაწყურის ტბისა და გარიელის საბუდარი კუნძულის მონიტორინგს; ადგილობრივი მოსახლეობის გამოკითხვას; მობუდარი წყვილების, ბუდეებისა და ბუდობების აღრიცხვასა და მონიტორინგს; გენეტიკური ანალიზისთვის სინჯების შეგროვებას როგორც ტაბაწყურზე, ისე ბალტიის ზღვაში; ისტორიული ჩანაწერებისა და ყოფილი საბუდარი ტერიტორიების (საქართველო, სომხეთი, თურქეთი) შეფასებასა და ანალიზს.

შედეგებმა აჩვენა, რომ კავკასიაში დღეს მხოლოდ ტაბაწყურის ტბაზეა შემორჩენილი მცირე, მოწყვლადი მობუდარი პოპულაცია, რომლის რიცხოვნობა 25-35 წყვილიდან, კვლევების პარალელურად განხორციელებული კონსერვაციული ღონისძიებების შედეგად, ბოლო წლებში გაიზარდა და ამჟამად 40-50 მობუდარ წყვილს შეადგენს. თუმცა, რეპროდუქციულ წარმატებაზე მნიშვნელოვან ზემოქმედებას ახდენს მტაცებლობა, განსაკუთრებით სომხური თოლიის (Larus armenicus) მხრიდან, და საბუდარი ტერიტორიის სიმცირე, რომელიც გამოწვეულია მხოლოდ ერთი პატარა საბუდარი კუნძულის არსებობითა და აქ არსებული ხშირი ბუჩქნარით.

გენეტიკურმა ანალიზებმა არ აჩვენა არსებითი განსხვავება კავკასიურ და ჩრდილოეთ პოპულაციებს შორის, რაც მიუთითებს, რომ შესაძლოა ისინი წარმოადგენენ ერთ პანმიქტურ პოპულაციას. ისტორიული გამრავლების არეალის დაახლოებით 90%-ით შემცირება და მობუდარი ინდივიდების გაქრობა სომხეთსა და თურქეთში სავარაუდოდ გამოწვეულია მტაცებლობით, კვერცხების შეგროვებით, სათევზაო ბადეებში დაჭერით, რეკრეაციული და თევზჭერის აქტივობებით გამოწვეული შეწუხებითა და ჰაბიტატის დეგრადაციით.

წარმოდგენილი კვლევა წარმოადგენს კავკასიაში გარიელის პოპულაციის პირველ ყოვლისმომცველ ეკოლოგიურ და გენეტიკურ შეფასებას. მიღებული შედეგები ქმნის სამეცნიერო მტკიცებულებებზე დაფუძნებულ საფუძველს გარიელის კონსერვაციის გრძელვადიანი სტრატეგიის შესამუშავებლად და მოიცავს რეკომენდაციებს საბუდარი და გამოზამთრების ადგილების დაცვაზე, მტაცებლობის მართვაზე, საბუდარი ტერიტორიის გაფართოებაზე და ჰაბიტატის აღდგენაზე სახეობის რეინტროდუქციისა და გრძელვადიანი გადარჩენის უზრუნველსაყოფად კავკასიაში.

ძირითადი საძიებო სიტყვები: გარიელი, Melanitta fusca, ტაბაწყური, კავკასია, ფილოგეოგრაფია, სახეობათაშორისი ურთიერთქმედება, რეპროდუქცია, პოპულაციის შემცირება, კონსერვაცია.

Abstract

The Velvet Scoter (Melanitta fusca) is declining worldwide and is listed as Vulnerable by the IUCN. In the Caucasus, it is the only breeding sea duck and was once widespread across Armenia, Turkey, and Georgia. In recent decades, both its population size and range have drastically decreased, leaving only a single breeding population at Lake Tabatskuri in Georgia. Although conservation efforts started in 2017, there is still limited knowledge about the species' population trends, breeding success, isolation, and reasons for its decline. Therefore, this doctoral research aimed to fill these gaps by: (1) assessing seasonal abundance and reproductive success at Lake Tabatskuri; (2) identifying factors affecting nesting behaviour and success; (3) analysing genetic connectivity between Caucasian and northern populations; and (4) evaluating range contraction, population decline, threats, and recolonization potential. Fieldwork at Lake Tabatskuri (2020-2025) included local interviews, ongoing monitoring of the lake and nesting island, and systematic observation of pairs, nests, and broods. Genetic samples were gathered from Lake Tabatskuri and the Baltic Sea, while historical distribution and threats were assessed through past records and field surveys at former breeding sites in Georgia, Armenia, and Turkey.

Results indicate that only Lake Tabatskuri supports a small, vulnerable breeding population - initially 25-35 pairs, which increased to about 40-50 pairs during the study due to conservation efforts. However, reproductive success remains limited by predation, mainly from Armenian Gulls (Larus armenicus), and by scarce nesting space caused by dense vegetation and the presence of only one small island. Genetic analyses showed no significant differences between Caucasian and northern populations, indicating they may constitute a single panmictic population. Nevertheless, the species has lost nearly 90% of its original breeding range in the Caucasus, disappearing completely from Armenia and Turkey. The main causes of decline likely include predation, egg collection, bycatch, human disturbance from fishing and recreational activities, and habitat loss.

Overall, this research is the first comprehensive ecological and genetic assessment of the Velvet Scoter in the Caucasus. Its findings offer a scientific basis for long-term conservation efforts. Key recommendations include protecting breeding and wintering habitats, managing gull predation, expanding nesting areas, and restoring historical breeding sites to support potential reintroduction and ensure the species' long-term survival in the region.

Keywords: Velvet Scoter, Melanitta fusca, Tabatskuri, Caucasus, phylogeography, interspecific interaction, nesting behaviour, reproductive output, population decline, conservation.

Acknowledgments

The true reason behind this work was never just about science. It was a quiet reminder to myself and others that nature still breathes all around us, delicate and alive, and every step we take leaves a mark on its ongoing story.

I want to sincerely thank my supervisors, Professor Alexander Gavashelishvili and Zurab Javakhishvili, for their invaluable support, guidance, and encouragement throughout my doctoral studies and the preparation of this dissertation. Their ongoing mentorship since 2010 has been crucial in shaping my academic and professional growth, guiding me from an ordinary hunter to a dedicated ornithologist and conservationist.

I am deeply grateful to the Faculty of Natural Sciences and Medicine at Ilia State University, as well as all the professors and lecturers whose expertise and teaching have greatly contributed to my development. I also sincerely thank Dean Elene Zhuravliova, the faculty office, Ia Gurchiani, and Marta Taktakishvili for their administrative and technical support during my Ph.D. journey.

My sincere thanks to my thesis reviewers and committee members for their time, insightful comments, and constructive feedback on my dissertation.

I am thankful to Niko Kerdikoshvili, Nika Budagashvili, Sopio Kiknavelidze, Lika Gogaladze, Nika Melikishvili, Luka Tkemaladze, Dachi Shoshitashvili, Saxon Bosworth, Nana Devidze, Mariam Papashvili, Ömral Ünsal Özkoç, Ilia Berdzenishvili, Gagik Papikian, and Hrant Muradyan for their invaluable help with fieldwork; and to Professor David Tarkhnishvili, Professor Marine Murtskhvaladze, Professor Natia Kopaliani, Levan Ninua, Davit Dekanoidze, Alexander Abuladze, Tamar Beridze, Vasil Metreveli, Natia Barateli and Zurab Janiashvili for their advice and assistance with laboratory analyses and working on articles/thesis. I am also very grateful to Professor Anthony David Fox and Ib Krag Petersen for their professional guidance, hospitality, and the opportunity to be at Aarhus University, where I gained essential experience in advanced waterfowl survey techniques. My thanks also go to Julius Morkunas for his help collecting samples from bycaught birds in the Baltic Sea. I also want to recognize the many individuals who supported me during fieldwork, laboratory work, and data analysis.

I extend my appreciation to all collaborators, co-authors, and field assistants whose efforts made the publications included in this dissertation possible. I am also grateful to the Agency for Protected Areas of Georgia for providing research permissions and facilitating fieldwork on Lake Tabatskuri.

Finally, I want to express my deepest gratitude to my beloved family - my wife, Marina Piduashvili, and my sons, Alexander and Daniel Paposhvili for their unwavering support, patience, and understanding throughout this demanding journey. This dissertation is dedicated to my mother, Ketevan Khvedelidze, who, despite earning her master's degree in biology and having the opportunity to pursue a doctorate, chose instead to dedicate her life to her children.

Financial support: This research and conservation effort was made possible thanks to the generous financial support of the Conservation Leadership Programme, the Rufford Foundation, the Shota Rustaveli National Science Foundation of Georgia, the Caucasus Nature Fund , the Institute of Ecology at Ilia State University, NGO Garieli ("Garieli" is the Georgian name for the Velvet Scoter - aims to research and conserve wildfowl in Georgia), and my family's small business, Garieli Wine, which donates more than 40% of its proceeds to the research and conservation of the Velvet Scoter (Melanitta fusca).

Contents

List of Tables

Chapter 2

Chapter 3

Chapter 4

List of Figures

Abbreviations

AM - Armenia

AMOVA - Analysis of Molecular Variance

CR - Critically Endangered

DNA - Deoxyribonucleic acid

GE - Georgia

GPS - Global Positioning System

HWE - Hardy-Weinberg Equilibrium

IUCN - International Union for Conservation of Nature

mtDNA - Mitochondrial DNA

PCA - Principal component analysis

PCR - Polymerase Chain Reaction

TR - Turkiye

VU - Vulnerable

List of Publications

Özkoç, Ö., Paposhvili, N., Agbayani, K., Petersen, I., & Fox, A. (2025). Contraction of range, declines in abundance and site-based threats to Velvet Scoter (Melanitta fusca) breeding in the Caucasus. Wildfowl, 74, 159–184.

Kiknavelidze, S., Kopaliani, N., Budagashvili, N., Melikishvili, N., Javakhishvili, Z., Gavashelishvili, A., & Paposhvili, N. (2024). Nesting behaviour and factors affecting reproductive success of Velvet Scoter (Melanitta fusca) breeding at Lake Tabatskuri, Georgia. Wildfowl, 74, 179–192.

Paposhvili, N., Morkunas, J., Ninua, L., Beridze, T., Kerdikoshvili, N., Dekanoidze, D., Murtskvaladze, M., Javakhishvili, Z., & Gavashelishvili, A. (2023). 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. Wildfowl, 73, 250–261.

Paposhvili, N. (2021). Seasonal abundance and breeding biology of the Velvet Scoter (Melanitta fusca) at Lake Tabatskuri, Georgia. Wildfowl, 71, 221–233.

General Introduction

The Mergini tribe, part of the Anatidae family, mainly consists of diving ducks adapted to high-latitude ecosystems (Kear, 2005). There are 20 known Mergini species in the Northern Hemisphere, most of which breed in tundra habitats or northern boreal forests and mainly spend winter in coastal waters (Johnsgard, 2010; Savard et al., 2015). Among these sea ducks, Velvet Scoter (Melanitta fusca, in the western Palearctic), Stejneger's Scoter (Melanitta stejnegeri, in the eastern Palearctic), and White-winged Scoter (Melanitta deglandi, in the Nearctic) - three closely related species, form a "super-species", mainly breeding in boreal regions of the Northern Hemisphere and migrating southward to coastal habitats for winter (Collinson et al., 2006).

The Velvet Scoter breeds more or less continuously across Eurasia from Norway to the Yenisey River in western Siberia and winters mainly in northern and northwestern Europe (Cramp & Simmons, 1977; Rogacheva, 1992; Carboneras et al., 2020; Keller et al., 2020). Although the Velvet Scoter inhabits most of the Holarctic region of western Eurasia, there is a small, isolated relic Caucasian population persisting in the Western Palearctic, that likely winters in the Caspian and Black Sea areas (Cramp & Simmons, 1977; Delany & Scott, 2006; Skov et al., 2011; Dagys, 2016; Carboneras et al., 2020).

The Velvet Scoter is listed as Vulnerable (VU) on the International Union for Conservation of Nature Red List (IUCN) due to an estimated breeding population decline of about 32-46% over the past three generations, now numbering approximately 141,000 to 268,000 mature individuals (BirdLife International, 2020). However, outside the Velvet Scoters' primary breeding areas in the northern boreal forest, the Caucasian population - estimated at around 1,500 individuals in the mid-1990s (Wetlands International, 2020) - has declined rapidly, bringing this geographically restricted population to the brink of extinction (Paposhvili, 2018; Keller et al., 2020). Recent estimates from Georgia indicate only 25-35 breeding pairs of Velvet Scoters remain (Paposhvili, 2018), and the species is now considered critically endangered (CR) in the region (Georgian Biodiversity Database, 2025).

The decline of the global Velvet Scoter population has been attributed to multiple factors, including climate change (Drever et al., 2011), reduced food availability (Dagys & Žydelis, 2002; Steinacher et al., 2009; Žydelis et al., 2009; Žydelis et al., 2013; Dagys, 2016; Carboneras et al., 2018), bycatch - entanglement or drowning in fishing nets (Dagys, 2016), oil pollution (del Hoyo et al., 1992; Kear, 2005), avian influenza and other diseases (Melville & Shortridge, 2006), hunting (Bregnballe et al., 2006), and high duckling mortality caused by disturbance and predation (Mikola et al., 1994; Traylor et al., 2006). Additionally, habitat degradation plays a significant role (Garthe & Huppop, 2004; Kear, 2005; Skov et al., 2011; Dierschke et al., 2016; Dagys, 2016).

Historical information on the Velvet Scoter's breeding population in the Caucasus is limited, making the causes of its rapid decline difficult to determine. However, records show that in the second half of the 20th century, the Velvet Scoter still nested in Armenia, Georgia, and Turkiye (Janashvili et al., 1960; Kutubidze, 1985; Adamian & Klem, 1997; Jordania et al., 1999; Matcharashvili et al., 2004; Gavashelishvili et al., 2005; Kirwan et al., 2014). But, by the end of the 20th century and into the early 21st century, the species had disappeared from most lakes in the region. In Armenia, it has been suggested that a rapid drop in water levels at Lake Sevan during Soviet times caused the loss of nesting habitat, leading to the species' local extinction (Adamian & Klem, 1997). In Turkiye, habitat loss, human disturbance, and global warming are believed to have contributed to its disappearance as a breeding species in Turkiye (Kirwan et al., 2014). In Georgia, the reasons for the decline are not well understood, but they are likely due to a combination of the same pressures affecting global populations. However, it is known that Lake Tabatskuri is the last surviving breeding site for the species in Georgia, possibly in the entire Caucasus (Paposhvili, 2018), and it is clear that the last population of the Velvet Scoter teeters on the brink of extinction. There is an urgent need to fill knowledge gaps in its biology and population isolation, develop appropriate conservation and management strategies to ensure the long-term survival of the last remaining breeding population, and facilitate potential recolonization of formerly occupied sites elsewhere in the Caucasus. Therefore, the doctoral research aimed to study the breeding biology of the Velvet Scoter, determine the level of isolation of the Caucasian population, evaluate past and current threats, and analyse the potential for regional recolonization. All of these are crucial to preventing the species' extinction in the Caucasus region.

Chapter 1. Seasonal abundance and breeding biology of the Velvet Scoter Melanitta fusca at Lake Tabatskuri, Georgia

The Velvet Scoter (Melanitta fusca), a sea duck found across the circumpolar regions, is classified as Vulnerable by the International Union for Conservation of Nature (IUCN) due to its ongoing global decline (BirdLife International, 2020). This species breeds nearly nonstop throughout Eurasia, from Norway to the Yenisey River in western Siberia, and mainly winters in northern and northwestern Europe, where its population is estimated at 202,000 to 384,000 individuals (Cramp & Simmons, 1977; BirdLife International, 2020). A small, isolated relic population remains in eastern Turkey, Georgia, and Armenia, likely wintering along the Black and Caspian seas. However, its overall abundance and yearly distribution are still not well understood (Dagys, 2016). In the mid-1990s, this group was estimated to total fewer than 1,500 birds, with more recent assessments suggesting a further decline to 240-420 birds, based on winter sightings (Wetlands International, 2020). In Armenia, the Velvet Scoter became extinct as a breeding species after a sharp drop in Lake Sevan's water level during the Soviet era, which caused the complete loss of its nesting habitat (Adamian & Klem, 1997). Similarly, in Turkey, habitat destruction, increased human disturbance, and climate change are believed to have caused the disappearance of breeding populations (Kirwan et al., 2014). By the late 20th century, the Velvet Scoter was breeding on nearly all major lakes of the Javakheti Plateau in southern Georgia (Janashvili et al., 1960; Kutubidze, 1985; Jordania et al., 1999; Matcharashvili et al., 2004; Gavashelishvili et al., 2005). However, during the early decades of the 21st century, the species disappeared from key waterfowl habitats in the Samtskhe-Javakheti region, including Lakes Madatapa, Bughdasheni, Khanchali, and Kartsakhi. Several factors likely contributed to this decline: (1) habitat degradation caused by increased water withdrawal for agricultural irrigation;

(2) mowing of vegetation on peninsulas and islands previously used for nesting; (3) egg collection, resulting in direct nest loss and disturbance; (4) eutrophication and pollution from agricultural intensification and wastewater discharge into lakes; (5) overfishing, which reduces food

availability and causes accidental bycatch; and (6) excessive hunting pressure from illegal shooting. Today, Lake Tabatskuri is considered the last remaining breeding site for the Velvet Scoter in Georgia and neighbouring countries (Paposhvili, 2018).

A comprehensive survey conducted in 2017 across all potential breeding lakes for the Velvet Scoter on the Javakheti Plateau, Georgia, revealed that nesting activity (25-35 pairs) was limited to a single, traditionally occupied site, Lake Tabatskuri (41°39’N, 43°38’E; Paposhvili, 2018). Since that year, regular spring and summer visits to all potential breeding locations on the plateau have confirmed the species' absence elsewhere. Furthermore, no Velvet Scoters were recorded during surveys in mid-August 2018 at four Turkish lakes where the species historically bred, Aktaş (41°13’N, 43°13’E), Çıldır (41°03’N, 43°14’E), Aygır (40°46’N, 43°00’E), and Kuyucuk (40°44’N, 43°27’E), as documented by BirdLife International. Collectively, these observations, supported by expert consultations and recent publications, indicate that Lake Tabatskuri now constitutes the only remaining active breeding site for the Velvet Scoter within this formerly widespread range. To identify potential causes of the species’ regional decline and promote the long-term survival of the last existing breeding population, a systematic monitoring program was started in 2017 at Lake Tabatskuri. The study reports the preliminary findings of this monitoring effort and discusses possible mitigation strategies to protect this relict population.

Methods

Study area

Lake Tabatskuri sits at an elevation of 2,000 meters above sea level on the Javakheti Plateau in southern Georgia. The lake spans 14.2 square kilometres, with a maximum depth of 43 meters and an average depth of 15 meters. It is known for its clear, unpolluted waters. The region endures long, cold winters, with snow cover lasting up to 150 days annually. Average daily temperatures range from -8°C in January to 12°C in July. The lake is bordered by two villages, one of which extends onto a small peninsula that juts into the water. In the northern part of the lake lies a one-hectare island, currently the only breeding site for the Velvet Scoter in the entire Caucasus. About one-quarter of the island is covered with shrubs, interspersed with a few pine (Pinus), maple (Acer), and birch (Betula) trees, habitats that Velvet Scoters tend to avoid for nesting.

Breeding surveys

Weekly surveys of Velvet Scoters at Lake Tabatskuri were conducted from late April to November each year starting in 2017. These surveys aimed to count the number of birds to assess changes in local abundance, record the adult sex ratio, and gather data on reproductive success (Figs. 1 & 2). The scoters begin laying eggs at the site in mid-June. By late June, most (if not all) breeding females are already incubating eggs. Every summer, 2-3 observers walking closely together searched the entire island intensively for nests from late June to early July. GPS coordinates were recorded for all nests found (Fig. 3), along with the number of eggs in each clutch (Supporting Materials Table S1).

In 2019 and 2020, 5-6 camera traps were placed at nests where vegetation allowed monitoring without disturbing the sitting females (Fig. 4a,b,c). During the post hatching period, mainly in the first half of August, nests found in June or July were rechecked, and the hatched and addled eggs in each nest were counted. The entire island was surveyed weekly to find any nests that might have been missed earlier. After hatching, daily observations were made of all broods for the first three weeks after they moved to water; then, once a week until late October, to track how many fledged, whether broods used different parts of the lake, and to identify major threats to the species. It is important to note that in 2017, due to inexperience, it is highly likely that: (1) locating all present nests may have failed (the island was only checked once after hatching), and (2) the number of fledged birds was underestimated due to difficulties in distinguishing adult females from fully fledged young at long distances without prior experience. Consequently, the data from 2018-2020 are more reliable than those from 2017.

Results

During the initial surveys at Lake Tabatskuri in 2017, the Velvet Scoter population peaked at 92 individuals on June 10 (Fig. 1), with females making up 36% of the total (Fig. 2). Subsequent weekly counts recorded between 25 and 32 birds from July 5 to September 10, 2017, with the proportion of females ranging from 49% (July 5) to 39% (July 22), averaging slightly below 50% throughout this period and most of the breeding season. In 2018, the first count on April 15 occurred before the species arrived; however, 54 individuals were present by April 25. Numbers peaked at 77 on May 5 and remained high with 76 individuals recorded on May 15 (Fig. 1). Unlike in 2017, there was no clear increase in the proportion of males in late May and early June. The proportion of females averaged 45% (range = 43-46%) from June 10 to July 26, increasing to 68-69% from August 10 to August 29 (Fig. 2). In 2019, the maximum count of 87 Velvet Scoters was recorded on May 24 (Fig. 1), with females comprising 46% of the total (Fig. 2). Eighty-six individuals persisted until June 5, after which numbers declined, but the proportion of females stayed steady at an average of 46% (range = 29-55%) through August. In 2020, peak counts of 79 individuals were recorded on May 31 and June 11 (Fig. 1), with 46% being females (Fig. 2). After that, the sex ratio shifted to being more male-biased, with females averaging only 25% (range = 22-30%) from July 2 to July 19, likely due to females staying on nests during incubation. The proportion of females then increased to an average of 54% (range = 51-56%) from August 6 to August 24, before dropping again from September 4 to October 7 (average = 39%, range = 29-67%), and only two females were recorded remaining into November (Fig. 2).

The spatial distribution and nesting results of individual Velvet Scoter nests are shown in Figure 3, with colour codes indicating breeding success. In 2017, all six identified nests were successful, although some nests may have gone unnoticed. In 2018, 17 of 23 nests were successful (74%), while one nest was predated, four were abandoned, and one was classified as a “dump nest” - a nest lacking down feathers or an incubating female, in which all eggs failed to hatch. During 2019, 17 of 33 nests were successful (52%), with 11 predated, three abandoned, and two

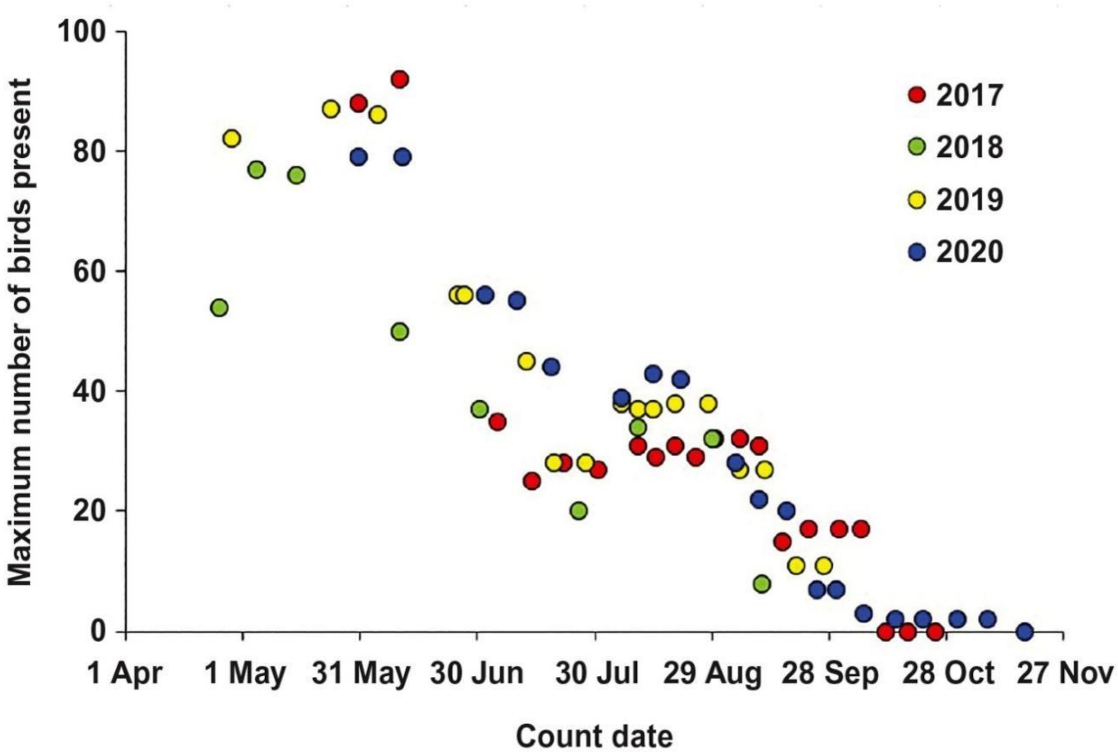

Figure 1. Annual seasonal variations in the number of Velvet Scoters observed on Lake Tabatskuri, Georgia, during regular counts conducted throughout the breeding season in the summers of 2017-2020.

dump nests, both of which failed completely. In 2020, out of 31 recorded nests, 23 were successful (74%); however, three females were killed while incubating, two nests were predated, two abandoned, and one dump nest with 22 eggs - briefly incubated - failed entirely by August 5. No significant differences were found among years in either the proportion of eggs per nest that hatched successfully or overall hatching success (Kruskal-Wallis tests: $H = 4.89$, d.f. = 3, $P = 0.18$ and $H = 6.13$, d.f. = 3, $P = 0.11$, respectively; n.s. in each case).

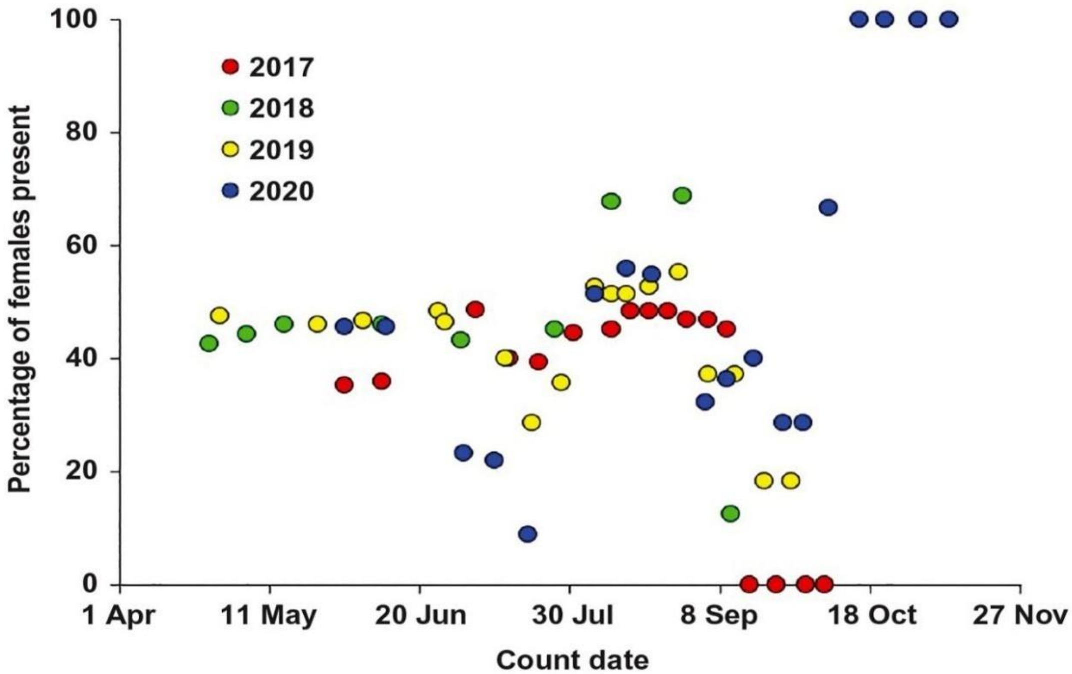

Figure 2. Annual seasonal changes in sex ratio (shown as the percentage of adults that are females), based on data collected during regular counts throughout the breeding season in summers 2017-2020.

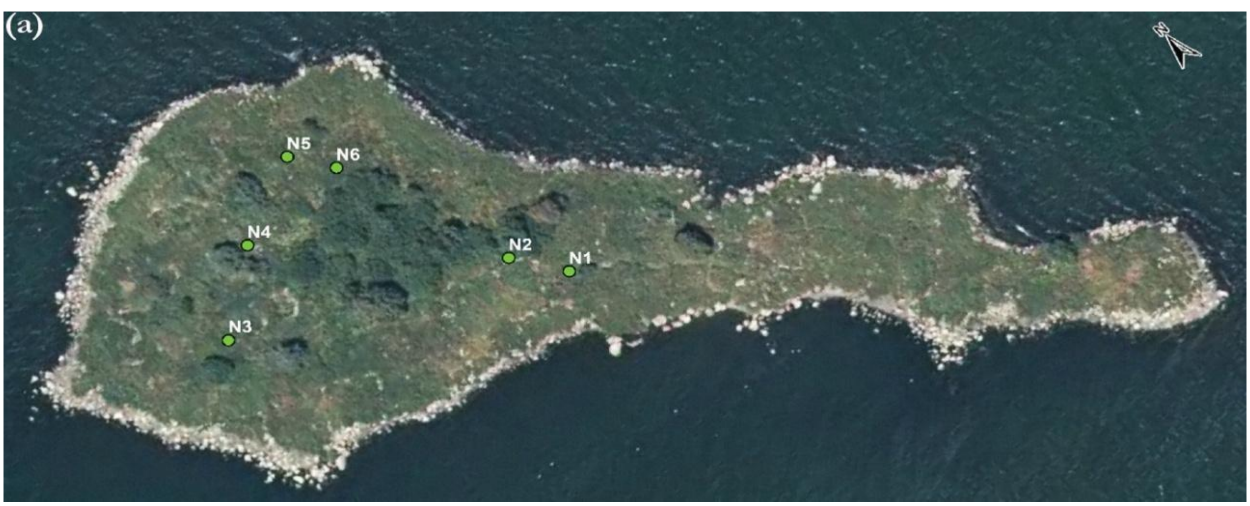

Figure 3 (continued below)

Figure 3 (continued). Aerial survey images showing the locations of individual Velvet Scoter nests on the island in Lake Tabatskuri during: (a) 2017, (b) 2018, (c) 2019, and (d) 2020. Green points = successful nests; yellow = predated nests; blue = abandoned nests; violet = dump nests; red = nests with predated females.

Analysis of data from three camera traps monitoring females with known incubation start dates confirmed that the incubation period lasted 28 to 30 days. During this time, incubating females usually left the nest once per day for feeding, spending on average two hours away, although both the timing and duration of absences varied among individuals. Hatching began on July 18 among the camera-monitored nests and was mostly finished by August 5, although in some cases, ducklings hatched as late as the second half of August (Fig. 4c). After the first hatchling emerged, females stayed on the nest for an additional 15 to 42 hours until the remaining eggs hatched, then led the ducklings to the lake. No instances of active egg predation by Armenian Gull (Larus armenicus), Hooded Crow (Corvus cornix), or Eurasian Magpie (Pica pica) were recorded at monitored nests during incubation. These species were only seen consuming addled eggs after hatching or from abandoned nests. However, two cases of egg predation by Marsh Harrier (Circus aeruginosus) were observed among 11 active nests during incubation. Although no camera traps were present on the three nests where incubating females were killed in 2020, field evidence and frequent Marsh Harrier activity at monitored nests strongly suggest that this species was the predator in all three cases (Fig. 4d). Supporting Materials Table S1 provides detailed data on clutch size and hatching success across all four years. In 2017, 48 eggs were recorded in six nests, with 17 failing to hatch, resulting in a hatching rate of 65%. While individual duckling survival rates could not be determined, the 31 successfully hatched eggs produced nine fledglings, indicating a 29% fledging rate and an overall 19% success rate from eggs laid. It is likely that not all nests were found that year, and the number of fledged young may have been overestimated. In 2018, when all nests were confidently located, 213 eggs were recorded in 23 nests, with 99 failing to hatch, leading to a 54% hatching rate. The 114 hatched eggs resulted in only four fledged young, with a 4% fledging rate and a 2% overall success rate. In 2019, 280 eggs were recorded across 33 nests, with 180 failing to hatch (36% hatching rate). The 100 hatched eggs yielded five fledged young, reflecting a 5% fledging rate and a 2% overall success rate. In 2020, 296 eggs were documented in 31 nests, with 150 failing to hatch, producing a 49% hatching rate. The 146 hatched eggs led to 39 fledged young, a 27% fledging rate and a total success rate of 13% for that year.

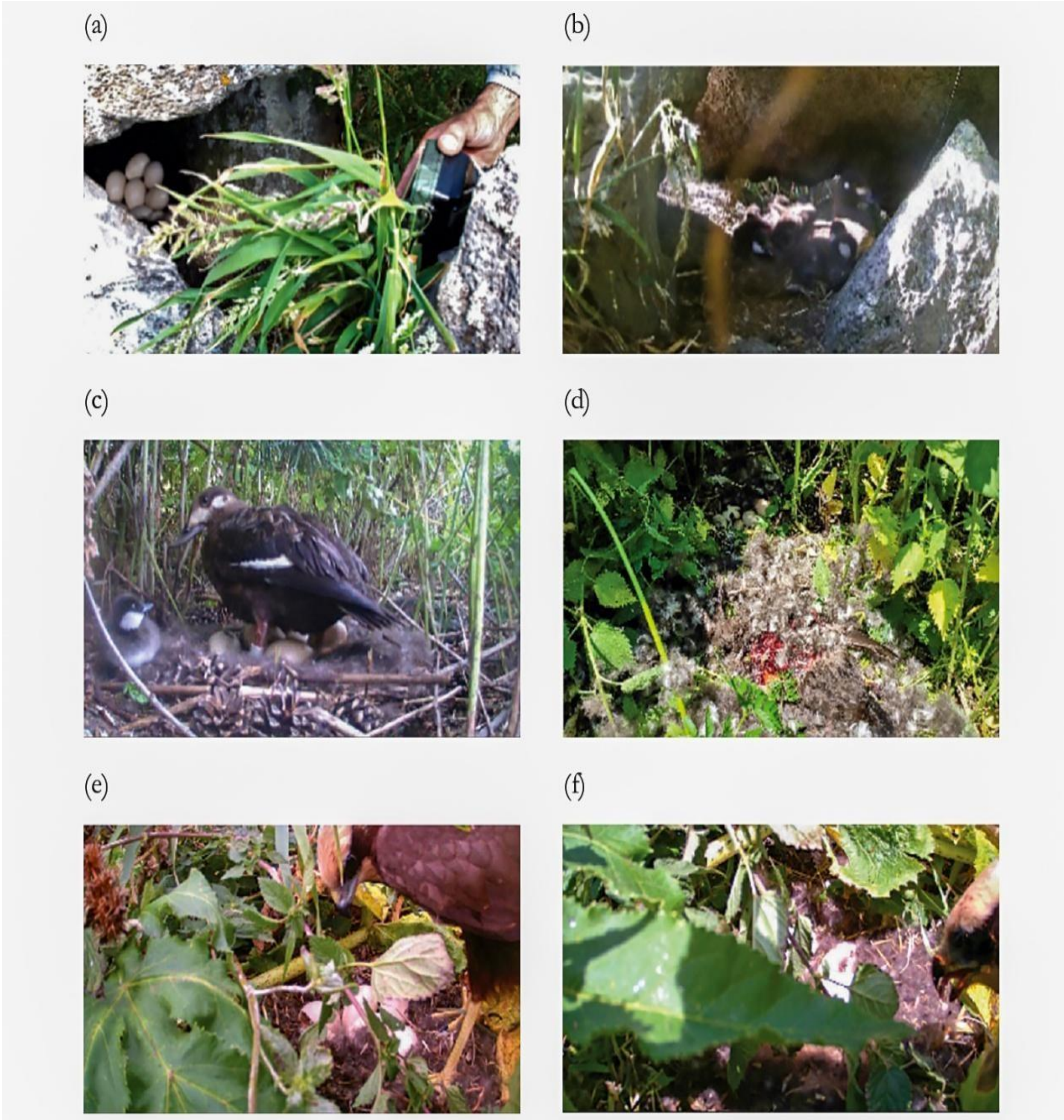

Figure 4 (continued below).

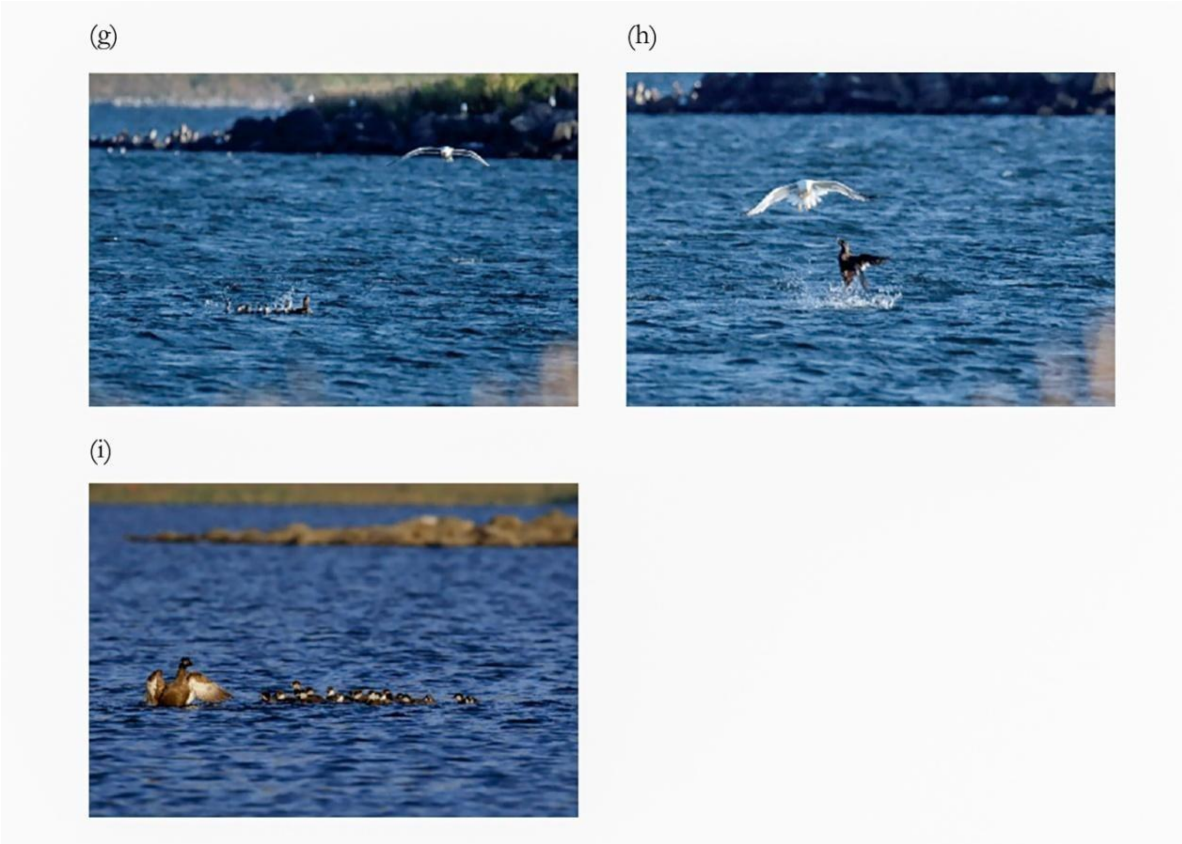

Figure 4 (continued). Velvet Scoters at Lake Tabatskuri, Georgia, during the breeding season, illustrating: (a, b, c) suitable nests for deployment of camera traps, (d, e) predated females, (e, f) egg predation, (g) an Armenian Gull Larus armenicus attacking a brood, (h) a parent Velvet Scoter defending a brood (such defence behaviour does not always result in duckling survival, particularly when attacking gulls operate as a team), and (i) female protecting her own brood in a creche with ducklings of other females. Photographs by Nika Melikishvili and Nika Paposhvili.

A spatial map showing the combined use of Lake Tabatskuri by Velvet Scoter broods, based on their recorded locations and movements during 2019-2020, is presented in Supporting Materials Figure S1. Consistent with Paposhvili (2018), adult birds with broods of different ages and sizes used only about 25% of the total lake area during the summer, avoiding the remaining 75%, which is likely too deep for good feeding conditions (local fishermen, pers. comm.). The northern part around the island was used most intensively by the broods. In the first two weeks after hatching, broods mainly foraged along the shoreline before gradually expanding their activity into nearby shallow waters (shown in red on Figure S1). Despite daily movements, the broods consistently returned to the island at dusk to roost and left again at dawn toward the northwest coast, where they did most of their daytime feeding. The distance from the island to the feeding area along the shore ranged from 600 to 800 meters. Disturbances mainly came from Armenian Gulls (Larus armenicus) and local fishermen. After about 40-45 days, the broods moved to the northeastern part of the lake, which is the open-water zone used regularly by moulting males in all study years (marked in blue on Figure S1). They stayed there until shortly before leaving the breeding site.

Discussion

Observations from 2017 to 2020 showed that each year, between 6 and 33 female Velvet Scoters settled at Lake Tabatskuri to nest, though slightly higher numbers of pairs were typically present from May to mid-June. Over the four years of monitoring, the number of nesting females on the island gradually and steadily increased, reaching 31-33 individuals in 2019-2020. In 2017, a notably higher number of females was recorded early in the season (33 individuals) compared to the smaller numbers later in the year (10-17 females from July to September), likely reflecting high nesting failure rates, possibly caused by egg collection by locals. Females that failed early, like most males, probably left the lake by late July to moult elsewhere. During 2018-2020, late season counts of female Velvet Scoters ranged from 8 to 27 individuals, indicating improved nesting success compared to 2017. In 2020, some females appeared unable to leave for moulting sites early in September because of the presence of unfledged ducklings; thus, a few stayed at Lake Tabatskuri with their broods until November (Fig. 1).

In 2017, it was initially assumed that some Velvet Scoters observed at Lake Tabatskuri during May and early June were temporarily staging before migrating to breeding sites in Turkey. However, four years of subsequent monitoring showed that all the birds recorded during this period were part of the resident breeding population at Tabatskuri. After pairing up, most males left the lake to reach their moulting sites, while a smaller number typically between 11 and 19 males stayed at Lake Tabatskuri each year. These males, likely looking for chances to mate with unpaired females, moulted in August-September in the northeastern part of the lake. They generally left for their wintering grounds by late September. During all study years, Velvet Scoters of both sexes arrived at Lake Tabatskuri in pairs shortly after the ice melted in April, with peak numbers consistently between late May and early June.

Throughout all four years of the study, nesting was limited exclusively to the single island within Lake Tabatskuri. Velvet Scoters rarely reused the same nesting sites in successive years; only one female was observed nesting in the same spot for two consecutive breeding seasons, using a cavity beneath a large stone. Annual nesting success, defined as at least one egg hatching per nest, varied over the four years 65% in 2017, 54% in 2018, 36% in 2019, and 49% in 2020. These success rates were notably lower than the 67-92% reported by Brown and Brown (1981) and the 72-89% reported by Traylor et al. (2004) for the North American White-winged Scoter (M. f. deglandi). Fledging success among hatchlings was also low (29%, 4%, 5%, and 27% in 2017-2020, respectively), likely due to predation by Armenian Gulls and Marsh Harrier, as well as incidental drowning of ducklings in fishing nets. As a result, the overall reproductive success defined as the proportion of eggs that produced fledged young remained low across the study period (19%, 2%, 2%, and 13% for 2017-2020, respectively). The breeding success of Velvet Scoters at Lake Tabatskuri was therefore lower than that reported for populations in Finland, which are exposed to significant human disturbance, or for North American populations under similar anthropogenic pressures (Mikola et al., 1994). However, it was comparable to some North American sites where gull predation greatly contributed to duckling mortality, resulting in fledging success rates of only 5-10% of eggs laid (Traylor & Alisauskas, 2006).

In 2017, direct field observations combined with information gathered from interviews with local residents revealed that one of the main factors negatively impacting Velvet Scoter productivity at Lake Tabatskuri was egg collection by local fishermen. To address this problem and raise community awareness, informational brochures and posters were distributed in nearby villages. These materials included details about the conservation status of the Velvet Scoter, the major threats to its survival, and practical ways local people could help reduce these threats. As a result of these outreach efforts, human disturbance on the nesting island significantly decreased, and by 2019, egg collection had effectively stopped. This success initially seemed like a major step toward solving the conservation problems facing the species. However, despite this progress, breeding success remained low, only four ducklings fledged in 2018 and five in 2019. Continued monitoring showed that predation on ducklings by Armenian Gulls, which are abundant at Lake Tabatskuri, had become the main cause of duckling deaths. Although broody females often tried vigorously to defend their young, most ducklings were predated within the first few days after hatching. Another significant source of disturbance was fishing activity, which not only disturbed broods but also caused incidental duckling mortality when they were caught and drowned in fishing nets. Observations indicated that gull attacks were much more successful when broods were disturbed by boats than when they were left undisturbed. In several cases, boat activity forced females to leave their ducklings briefly, during which gull predation occurred. In recent years, the Armenian Gull population has grown substantially, and by 2020, its range extended across the entire Javakheti Plateau, where thousands of birds were recorded compared to only a few seen three or four decades earlier (A. Abuladze, pers. comm.). The reasons for this population increase remain unclear, but it may be related to the growth of landfill sites in the region, which offer abundant and easily accessible food resources for gulls.

In 2020, steps were taken to reduce the local impact of fishing activities on Velvet Scoters at Lake Tabatskuri. Three key local fishermen were financially compensated to join the conservation effort, ensuring no fishing took place within the main duckling feeding area during August 2020. Although fishing continued at the main moulting site, an area also used by mature birds, this measure effectively lowered human disturbance and bycatch risk during the critical duckling development period. Starting in mid-September, intensive fishing usually picks up again in the moulting zone, greatly increasing the chance of bycatch-related deaths. Restricting fishing at that time is impractical, as it provides the main income for many local residents. Interestingly, in 2020, many Armenian Gulls left the lake earlier than usual, probably because there were fewer chicks to feed on the island. Possibly due to this decrease in gull activity and the fishing restrictions, 39 Velvet Scoter ducklings fledged that year - a significant improvement over the previous year. Although gull predation persisted, it was much lower than in previous breeding seasons. Additional factors that may affect the Velvet Scoter population at Lake Tabatskuri include weather conditions and food availability. Unfortunately, there is currently no data available on the species' diet or the composition and abundance of potential food sources within the lake. Meteorological conditions showed little variation over the four study years, although 2020 was slightly warmer and drier than previous years.

It seems that the low reproductive success of Velvet Scoters at Lake Tabatskuri is caused by a combination of predation and human disturbance. The main predator of ducklings at the site is the Armenian Gull, whose population has grown rapidly in recent years. This species now has a significant negative impact on the already small and isolated breeding population of Velvet Scoters in the Caucasus. Therefore, controlling the gull population might help improve scoter reproductive success. However, further studies are needed before implementing such measures to avoid unintended ecological effects. In 2020, three incubating females were likely predated on their nests by Marsh Harriers. This may have been linked to the reduced presence of nesting gulls on the island, which usually provide indirect protection by mobbing approaching raptors. The decrease in gull activity could have increased the vulnerability of nesting Scoters to bird predators. Conversely, poor grass growth on the island that year might have also made predator detection easier by reducing vegetative cover. From a demographic standpoint, losing breeding adult females has a greater impact on the population than losing ducklings, due to the high natural mortality of ducklings and their relatively low survival rate in the first winter. Still, the overall effect must also consider the much higher number of ducklings taken by gulls, even if predation occurs in a short period after hatching. It is crucial to improve duckling survival to reinforce the positive effects of other management actions, such as stopping human egg collection. Sustaining and expanding these efforts are vital for ensuring the long-term survival of the remaining Velvet Scoter population at Lake Tabatskuri.

Chapter 2. Genetic connectivity between Caucasian and Northern Velvet Scoter Melanitta fusca populations and its importance for the long-term survival of the species

Although the Velvet Scoter (Melanitta fusca) inhabits much of the Holarctic region of western Eurasia (Carboneras et al., 2020), a small, isolated population remains in the Caucasus within the Western Palearctic (BirdLife International, 2020). In recent decades, this population has disappeared from nearly all parts of the region, mainly due to human disturbance, habitat loss, and population fragmentation (Adamian & Klem, 1997; Kirwan et al., 2014; BirdLife International, 2020; Ömral Ünsal Özkoç, pers. comm.). Currently, Lake Tabatskuri in Georgia hosts the last remaining breeding group of the species in the Caucasus, fewer than 100 individuals, with consistently low reproductive success (Paposhvili, 2021). Major threats to breeding include bycatch and disturbance from fishing, competition with the Armenian Gull (Larus armenicus) for nesting sites, and predation of ducklings by the same species (Paposhvili, 2021). With the population now nearing extinction, it is essential to assess whether the Caucasian Velvet Scoter is genetically distinct and isolated from the Northern population to guide effective conservation efforts. This study provides the first genetic evaluation of the Caucasian Velvet Scoter population, comparing it with individuals from the Northern population to assess genetic differences. The findings will help improve understanding of population connectivity, predict the species' response to environmental changes, and support the development of strategies to ensure the Velvet Scoter's long-term survival in the Caucasus.

Methods

Sample collection

Samples were categorized by their geographic origin into two groups: the Northern and Caucasian populations. Specimens representing the Caucasian population were collected from breeding Velvet Scoters at Lake Tabatskuri, Georgia (41°39′N, 43°38′E), during the summer months (July-August) of 2015-2019. These included 2-3 wing covert feathers from nesting females captured for ringing (n = 9), eggshell membranes from hatched eggs (n = 3, each from a different nest), and tissue samples from unhatched embryos found dead inside eggs (n = 13, each from a separate nest). The samples of the Northern population were collected during the winter season from drowned Velvet Scoters caught in gillnets (tissue samples, n = 22) in Lithuanian coastal waters of the Baltic Sea from November 2015 to April 2016, provided voluntarily by coastal commercial fishermen.

DNA isolation and amplification

Genomic DNA was extracted from all feather and tissue samples using the DNeasy Blood & Tissue Kit (QIAGEN, Germany), following the manufacturer's protocol. DNA was eluted in a final volume of 100 μl. In total, 47 samples were analysed, including 25 from Lake Tabatskuri and 22 from the Baltic Sea.

A fragment of the mitochondrial cytochrome b (cyt b) gene was amplified in 14 Velvet Scoter individuals (seven from the Caucasian and seven from the Northern population) using the primer pair L15369 and H15915 (Fu, 2000). Polymerase chain reactions (PCRs) were carried out in 20 μl volumes containing 3 μl of template DNA, 1 U of Promega Taq polymerase, 1× Green Flexi buffer, 0.4 mmol/L dNTP mix, 0.5 mmol/L of each primer, and 2.5 mmol/L $MgCl_2$. The thermal cycling profile comprised an initial denaturation at 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 1 min, with a final extension at 72 °C for 10 min. Amplification success was verified by electrophoresis of 5 μl of each PCR product on a 1% agarose gel. Amplicons were sequenced bidirectionally on an ABI 3130XL automated sequencer using the same PCR primers and BigDye Terminator v3.1 chemistry. Sequence alignment and editing were performed in Geneious v8.1.9, and unique haplotypes were deposited in GenBank under accession numbers OQ842598–OQ842600.

Genotypic variation was assessed across nine polymorphic microsatellite loci. Four loci originally developed for the Mallard (Anas platyrhynchos) - Apl26, Apl23, Apl36, and Caud13 (Denk et al., 2004; Huang et al., 2005) and five loci known to be variable in other waterfowl species Aph02, Aph04, and Aph07 (Maak et al., 2003), Bca11 (Buchholz et al., 1998), and Sfi11 (Sonsthagen et al., 2019) were successfully amplified in Velvet Scoters. The nine loci were amplified in three multiplex PCR reactions using forward primers fluorescently labelled at their 5′ ends with VIC, NED, or FAM dyes. PCRs were conducted with the QIAGEN Multiplex PCR Kit (QIAGEN, Germany).

Thermocycling conditions for loci Aph02, Aph04, Apl23, and Apl36 included an initial denaturation at 95 °C for 15 min; 30 cycles of 93 °C for 30 s, 60 °C for 30 s (with a 0.2 °C decrement per cycle), and 72 °C for 1 min; followed by a final extension at 60 °C for 30 min and a hold at 10 °C for 10 min. For loci Apl26, Sfi11, Bca11, Aph07, and Caud13, the conditions were 95 °C for 15 min; 20 cycles of 93 °C for 30 s, 58 °C for 30 s (with a 0.3 °C decrement per cycle), and 72 °C for 1 min; followed by 15 cycles of 93 °C for 30 s, 55 °C for 30 s, and 72 °C for 1 min; with a final extension at 60 °C for 30 min and a hold at 10 °C for 10 min.

Amplified fragments were separated on an ABI 3130XL genetic analyser using deionized formamide and the GeneScan LIZ 500 size standard (Applied Biosystems, Foster City, CA, USA). Genotypes were scored and verified using the GeneMapper v5.0 software package (Perkin Elmer, Waltham, MA, USA).

Genetic diversity and population structure

Basic population genetic parameters were calculated using ARLEQUIN v3.5 (Excoffier & Lischer, 2010). For the mitochondrial cyt b dataset, the number of haplotypes was determined, while for microsatellite loci, the number of alleles, allele frequencies, and deviations from Hardy-Weinberg equilibrium (HWE) was estimated. Allelic richness was calculated in FSTAT v2.9.4. To visualise relationships among haplotypes, an unrooted phylogenetic network was constructed in NETWORK v10.2.0 (Fluxus Technology Ltd.) using the median-joining algorithm (Bandelt et al., 1999).

For the microsatellite dataset, the degree of population subdivision between Northern and Caucasian Velvet Scoters was quantified by estimating pairwise fixation indices (FST) and conducting locus-by-locus analyses of genetic differentiation with 20,000 permutations in ARLEQUIN. To further explore patterns of genetic structure between and within the two populations, three complementary analytical approaches were employed.

First, Analysis of Molecular Variance (AMOVA) was performed in ARLEQUIN to assess the hierarchical distribution of genetic variation. Second, Principal Component Analysis (PCA) was used to visualise genetic clustering in IBM SPSS Statistics v29.0.1.0, with the first two principal components plotted to illustrate population differentiation. Third, a Bayesian clustering analysis was conducted in STRUCTURE (Pritchard et al., 2000) to infer population structure without prior information on population origin. STRUCTURE identifies the most likely number of genetically homogeneous (panmictic) groups by maximising Hardy-Weinberg equilibrium and minimising linkage disequilibrium across loci.

The admixture model with correlated allele frequencies was applied, using a burn-in period of 100,000 iterations followed by 100,000 Markov Chain Monte Carlo (MCMC) repetitions. The number of potential clusters (K) was tested from 1 to 5, with 10 independent replicates conducted for each K. The most likely K value was determined based on the posterior probability [LN P(D)] using Structure Harvester (Earl & von Holdt, 2012).

Recent immigration rates analysis

Population immigration rates between Northern and Caucasian Velvet Scoters over the past several generations were estimated, and the immigration ancestry of each individual (non-migrant, first-generation, or second-generation migrant) was determined using BayesAss v3.0 (Wilson & Rannala, 2003). This algorithm estimates the probability of allochthonous origin for each genotyped individual based on allelic frequency data and does not assume migration–drift or

Hardy–Weinberg equilibrium. The program was executed ten times with different random number seeds, using 100,000 iterations as burn-in and 10,000,000 iterations for the MCMC run. The run with the highest Bayesian deviance value was selected using the script developed by Merimans (2014).

Results

Genetic diversity and population structure

Three mitochondrial haplotypes were identified from the 470 bp fragment of cyt b sequences. All three haplotypes were detected in the wintering Northern population (n = 7), whereas only two haplotypes were found in the breeding Caucasian population (n = 7). Notably, the most divergent haplotype, differing by five variable sites from the central haplotype, contained individuals from both populations (Fig. 1).

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

Microsatellite genotype data revealed no significant genetic differentiation between the two populations (FST = 0.012, P = 0.08, n.s.). Results of the AMOVA (Table 1) indicated that variance among populations, among individuals within populations, and within individuals accounted for 1.1%, 3.7%, and 95.1% of the total variation, respectively. Consistent with these findings, both the STRUCTURE and PCA analyses supported the absence of population subdivision. STRUCTURE results identified a single genetic cluster (K = 1), while the first two PCA axes together explained 33% of the total genetic variation. The ordination plot showed no separation between individuals from the Tabatskuri (Caucasian) and Baltic (Northern) populations (Fig. 2).

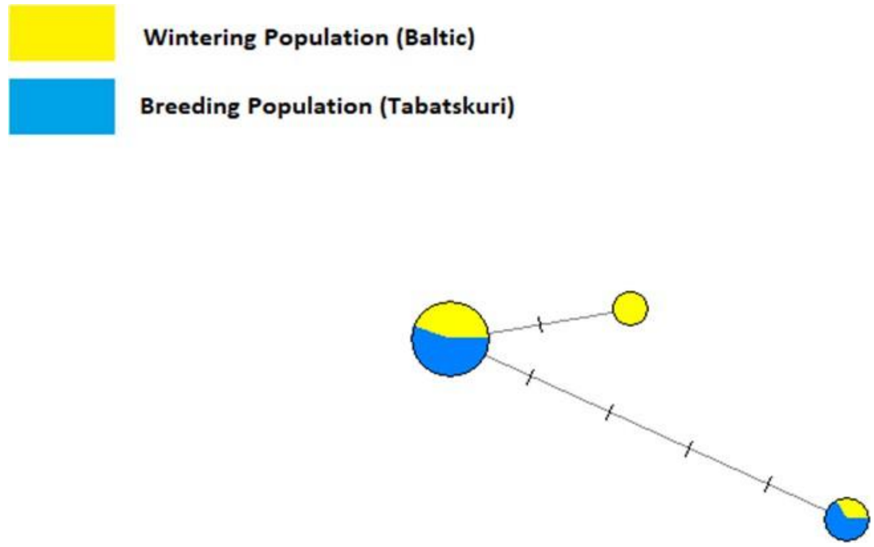

Figure 1. Median-joining network (using the methods of Bandelt et al. 1999) linking the haplotypes of the individual Velvet Scoters breeding at Lake Tabatskuri (Caucasian population) and those wintering in the Baltic Sea (Northern population). Size of circle is proportional to the frequency of each haplotype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

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	

Recent immigration rates analysis

BayesAss 3.0 simulations indicated that 31.5% of individuals in the Lake Tabatskuri population were migrants originating from the Baltic Sea, whereas only 5.1% of the Baltic population represented migrants primarily derived from Lake Tabatskuri (per generation). All samples from Lake Tabatskuri showed a high probability of being first- or second-generation migrants from the Baltic Sea, suggesting minimal or absent internal recruitment within this population. In contrast, only two individuals (31 and 37) from the Baltic samples displayed a high probability of being second-generation migrants from Lake Tabatskuri (Fig. 3).

Discussion

Analyses of both mtDNA and microsatellite data revealed no significant genetic differentiation or population structure between the Northern and Caucasian populations of the Velvet Scoter. The findings indicate that these populations function respectively as a source and a sink, with the Caucasian population exhibiting very limited or no internal recruitment. Consequently, the results do not support the hypothesis of genetic isolation of the Caucasian population but instead confirm a high degree of genetic intermixing, suggesting that the species forms a single panmictic population across the western Palearctic. A similar genetic pattern may also result from incomplete lineage sorting. Given the relatively recent coalescence times of microsatellite markers and the generally male-biased dispersal observed in waterfowl, a broader genomic approach may be required to disentangle the effects of gene flow and incomplete lineage sorting on the observed genetic homogeneity.

Comparable results have been reported for two geographically distinct populations of the Whooper Swan (Cygnus cygnus) breeding in Iceland and continental Europe, where genetic connectivity was observed despite the separation of breeding and wintering ranges (Butkauskas et al., 2012; Brides et al., 2023). Our findings suggest that (1) individuals from the Northern and

Caucasian populations disperse frequently, and the considerable geographic distance between nesting sites does not act as a barrier to movement; and/or (2) gene exchange occurs at shared wintering sites, where individuals from both populations congregate and form pairs. However, in contrast to the latter assumption, Brown and Fredrickson (1997) reported that White-winged Scoters (Melanitta deglandi) typically pair during spring migration or shortly after arriving at breeding grounds. Observations of Velvet Scoters breeding at Lake Tabatskuri over five consecutive years indicate that pairs return to the lake together in late April or May (Paposhvili, 2021), implying that courtship and pair formation most likely occur at or near wintering areas (N. Paposhvili, pers. comm.).

As female sea ducks generally exhibit strong fidelity to both breeding and wintering sites (Anderson et al., 1992; Robertson & Cooke, 1999; Mabry et al., 2013), and given that female Velvet Scoters nesting at Lake Tabatskuri display similar site fidelity (N. Paposhvili, pers. comm.), the observed genetic connectivity between the two populations is most plausibly driven by male-mediated dispersal.

Gene flow between populations plays a crucial role in maintaining population viability by enhancing genetic diversity and reducing the detrimental effects of inbreeding, thereby increasing population stability and resilience to environmental pressures (Sonsthagen et al., 2019). The primary factor facilitating gene flow between the Northern and Caucasian Velvet Scoter populations is likely the existence of shared wintering areas. The Black Sea is the most probable site where individuals from both populations overlap during the non-breeding season (Delany et al., 1999; Dagys, 2016; BirdLife International, 2020).

Determining the exact origin of individual Velvet Scoters observed in the Black Sea remains challenging, as current data from ringing recoveries or tracking studies are insufficient to make conclusive inferences. Nevertheless, observations reported on the eBird.org platform indicate that the number of Velvet Scoters migrating to the Black Sea exceeds what could be attributed solely to the Lake Tabatskuri population. In addition, the regular presence of other Arctic and northern-nesting sea duck species, such as the Common Scoter (Melanitta nigra) and Long-tailed Duck

(Clangula hyemalis), supports the role of the Black Sea as a wintering area for multiple northern taxa (eBird, 2024).

Recent estimates suggest that more than 95% of the Northern Velvet Scoter population winters in the Baltic Sea and adjacent northwestern European coasts (BirdLife International, 2020; Wetlands International, 2020). However, this does not preclude the occurrence of small numbers of individuals in the Black Sea, where seasonal migrations could facilitate admixture between Northern and Caucasian birds. Importantly, even limited contact such as the exchange of only a few migrants per generation can be sufficient to prevent genetic drift from leading to marked population differentiation.

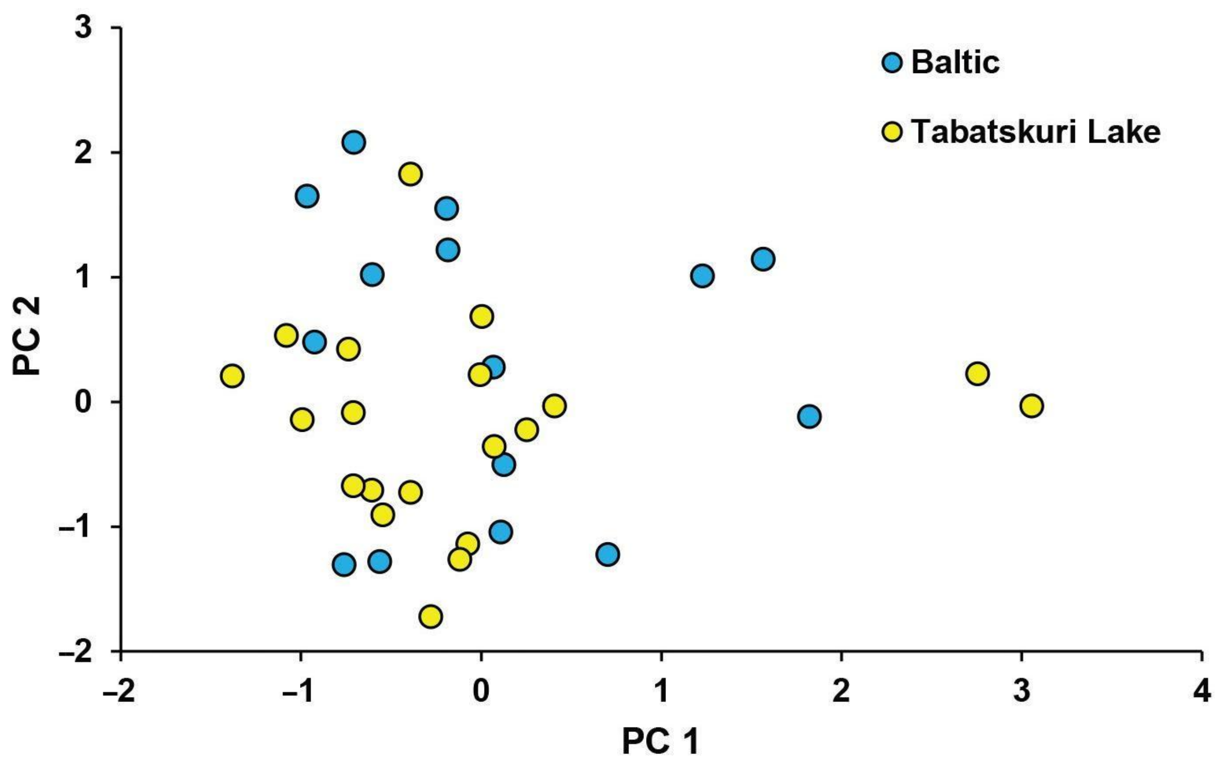

Figure 2. Ordination of the individual microsatellite genotypes along the first and the second Principal Component Analysis (PCA) axes.

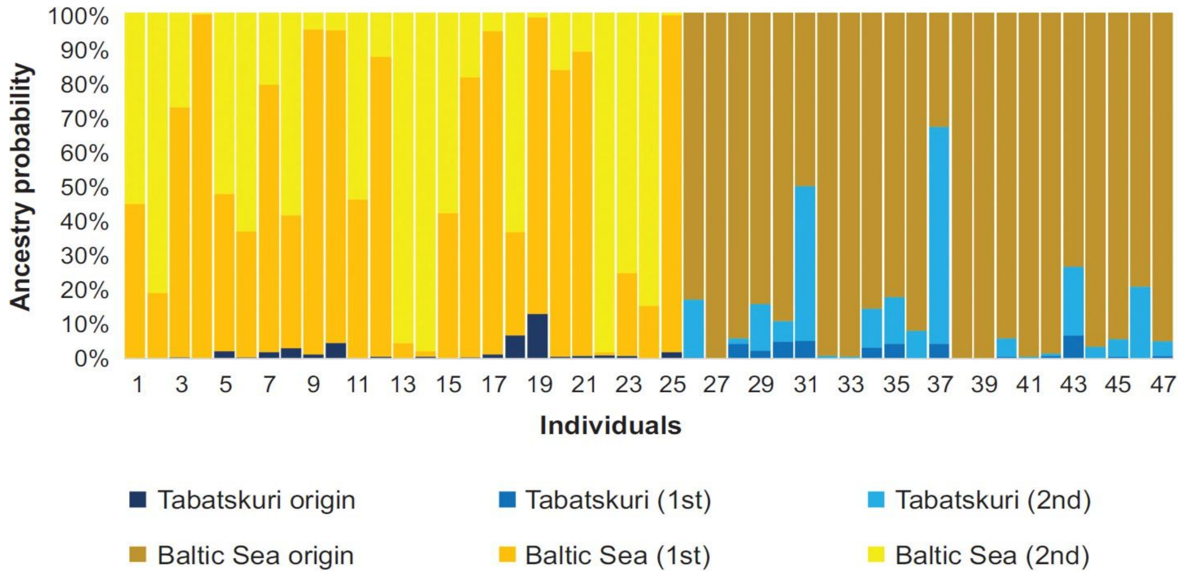

Figure 3. Individual ancestries of Velvet Scoters from Lake Tabatskuri and the Baltic Sea, respectively, inferred from BayesAss 3.0 Bayesian analysis (the first 25 samples are from Lake Tabatskuri and the remaining 22 from the Baltic Sea).

The evidence presented underscores the urgent need to identify, preserve, and protect key wintering areas in the Black Sea in coordination with the protection of breeding habitats to ensure the long-term conservation of the Velvet Scoter population. Habitat loss is widely recognised as one of the principal drivers of species extinction, and the recent degradation and disappearance of historical Velvet Scoter breeding sites in Turkey, Armenia, and Georgia serve as stark reminders of this threat (Adamian & Klem, 1997; Kirwan et al., 2014; Paposhvili, 2018). Consequently, Lake Tabatskuri and its island have acquired exceptional conservation significance, as they currently represent the only location in the entire Caucasus that fulfils the species' breeding requirements. As long as these ecological conditions are maintained, the Velvet Scoter will continue to persist as part of the region's biodiversity.

Despite the absence of pronounced genetic differentiation between the Northern and Caucasian populations, it remains essential to implement a long-term management strategy and to strengthen conservation actions aimed at protecting the entire ecosystem of Lake Tabatskuri, rather than focusing solely on the Velvet Scoter population. Following the restriction of human access to the islands during the breeding season, the number of nesting pairs at Lake Tabatskuri increased markedly from six pairs in 2017 to 39 pairs in 2022. This growth highlights the importance of maintaining and enhancing habitat quality and may, in the short term, also reflect immigration of individuals from northern populations. Although this increase may be partly explained by a strong reproductive output in 2020 (39 fledged ducklings), the possible contribution of migrants from the Northern population cannot be excluded.

To better understand the mechanisms driving this recovery and to clarify the degree of connectivity between the Caucasian and Northern populations, further genetic analyses with larger sample sizes and higher-resolution methods are warranted. The application of genomic techniques such as double-digest restriction-associated DNA sequencing (ddRAD) could provide finer resolution for detecting subtle population structure and distinguishing between historical and contemporary gene flow. A previous study employing ddRAD to compare Northern Velvet Scoters and American White-winged Scoters (Melanitta deglandi) successfully identified distinct, species-specific genetic clusters (Sonsthagen et al., 2019), demonstrating the potential value of this approach for future research.

Chapter 3. Nesting behaviour and factors affecting reproductive success of Velvet Scoter Melanitta fusca breeding at Lake Tabatskuri, Georgia

Historical data on the breeding numbers of the Velvet Scoter in the Caucasus remain limited. Recent field observations indicate that multiple factors including habitat degradation, hunting, egg collection, entanglement and drowning in fishing nets, as well as predation pressure may all contribute to the species' low reproductive success. This is likely the main factor behind its rapid population decline (Paposhvili, 2021). Research conducted at Lake Tabatskuri, Georgia showed that the overall reproductive output of the Velvet Scoter was negatively affected by low nesting success. This may result from a combination of factors such as human disturbance, predation, competition within and between species (for example, gulls Larus sp. and other Scoters occupying nesting sites), the age and health of breeding females, and possibly other unknown influences. A full understanding of these ecological factors affecting nesting success is urgently needed to improve conservation efforts. These efforts should focus on increasing breeding success and helping the species recolonize historically used sites across the Caucasus. To address this, the study combines direct nest observations with remote monitoring tools particularly camera traps that offer continuous surveillance of nesting activity to identify the main factors influencing the nesting success of the Velvet Scoter at Lake Tabatskuri.

Methods

Study area

Lake Tabatskuri (41°39'N, 43°38'E) lies on the Javakheti volcanic plateau at an elevation of about 2,000 meters above sea level in Georgia. It is situated along the border between the Borjomi and Akhalkalaki municipalities, in the northern part of the Samsari Mountain Range. The lake is part of the Ktsia-Tabatskuri Protected Area, managed by the Borjom-Kharagauli Protected Areas Administration, and is bordered by two settlements Tabatskuri and Moliti. Covering an area of 14.2 km², the lake reaches a maximum depth of 45 meters (with an average depth of 15 meters) and is known for its clear, unpolluted waters. The regional climate features cold winters, with snow cover lasting up to 150 days each year.

A small island about 1 hectare in size, located in the northern part of the lake (Supporting Materials Fig. S1), currently serves as the only nesting site for the Velvet Scoter in Georgia and across the Caucasus region (Paposhvili, 2021). This island seems to provide especially favourable breeding conditions for the Scoters, likely because of the presence of both deep and shallow waters around it, which support clear, food-rich zones suitable for foraging by adults and later by ducklings. The island's dense vegetation offers secure nesting sites for waterfowl, effectively protecting them from land-based predators. Additionally, the presence of breeding Armenian Gulls (Larus armenicus) may help protect nesting scoters by deterring bird predators through the gulls' defensive behaviours around their own nests.

Nest surveys

Each summer from 2019 to 2021, systematic nest surveys were carried out on the island, during which two or three observers walked in close parallel lines to thoroughly search the entire area for nests throughout June and July (Supporting Materials Figs. S2 & S3). The island was surveyed three times each breeding season to find any nests that might have been missed during earlier visits. For each nest, the geographic coordinates (latitude and longitude; Fig. 1), clutch size, and egg fate were recorded. Camera traps were set at nests where surrounding vegetation did not block visibility (Supporting Materials Fig. S4) and were placed at different nest sites across the island in each study year: seven in 2019, four in 2020, and five in 2021 (Fig. 2). All camera traps in photo mode were installed 70-90 cm from the nest, while a single video mode camera trap was placed less than 35 cm away. These motion activated devices were installed not during the first survey but during subsequent visits. In total, 131,219 photographs were taken and later analysed.

During the post hatching period (August), all nests were revisited to record the number of hatched, unhatched, and/or predated eggs in each clutch (Supporting Materials Figs. S5 & S6). These data were used to calculate the proportion of successfully hatched and predated eggs per nest, thereby estimating overall hatching and nesting success. All unhatched eggs were opened to determine whether they were addled or contained dead embryos (Supporting Materials Fig. S7). For nests monitored by camera traps, additional behavioural and environmental data were collected, including records of species visiting the nest, daily defensive displays of female scoters (e.g., bill opening and hissing directed at approaching intruders), the frequency of egg turning and positional adjustments by incubating females, periods when nests were left unattended, the duration of the entire nesting period, instances of egg predation, and ambient air temperatures derived from the camera trap data (Supporting Materials Figs. S8-S11).

Data analysis

It was hypothesised that egg predation, year, presence of camera traps, and air temperature could influence the proportion of successfully hatched eggs within a clutch (hereafter referred to as hatching success). The inclusion of the camera variable was necessary, as the presence of camera traps might have caused disturbance to incubating females, potentially leading to nest abandonment. Data for all variables were derived from field observations conducted in 2019, 2020, and 2021 (Supporting Materials Table S1a–c). To identify which factors most strongly affected hatching success, linear models (LMs) were constructed using R software, version 4.3.2 (R Core Team, 2023), with the predictor variables specified in Table 1. All possible combinations of predictors and their interaction terms were examined to determine the most parsimonious model. Model selection was based on the Akaike Information Criterion (AIC). The same modelling approach was applied to assess which predictor variables influenced the proportion of predated eggs per clutch.

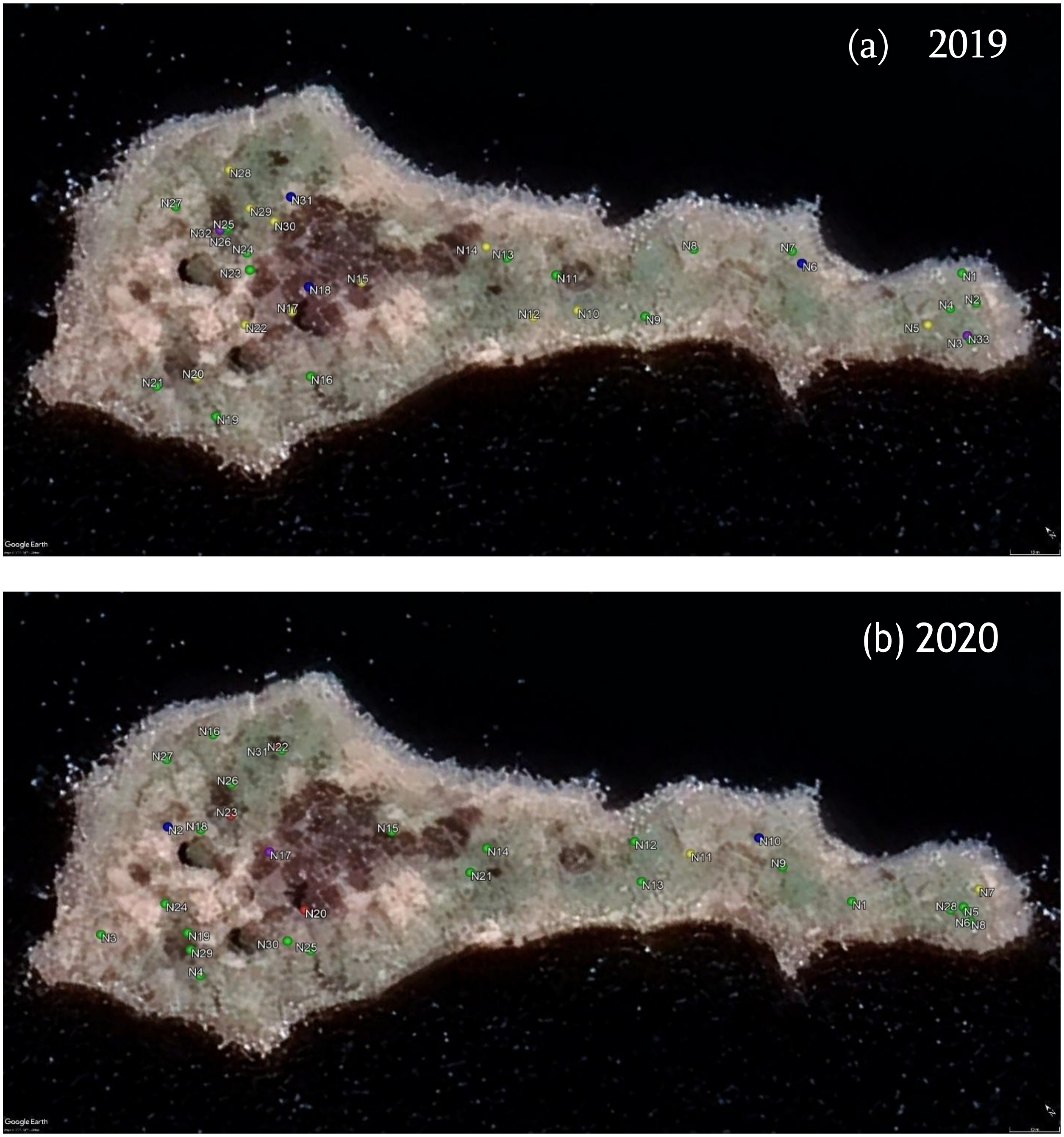

Figure 1 (continued below).

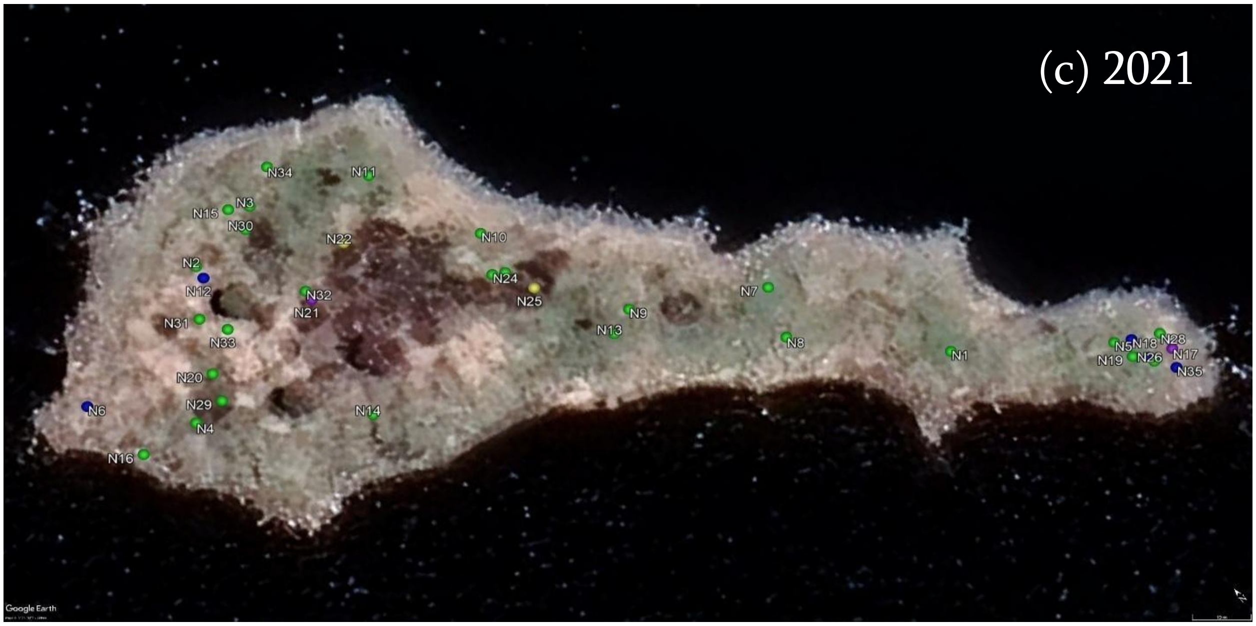

Figure 1. Aerial survey images showing the location of individual Velvet Scoter nests on the island in Lake Tabatskuri during: (a) 2019, (b) 2020 and (c) 2021. Green points = successful nests; yellow = predated nests; blue = abandoned nests; violet = dump nests; red = nests with predated females.

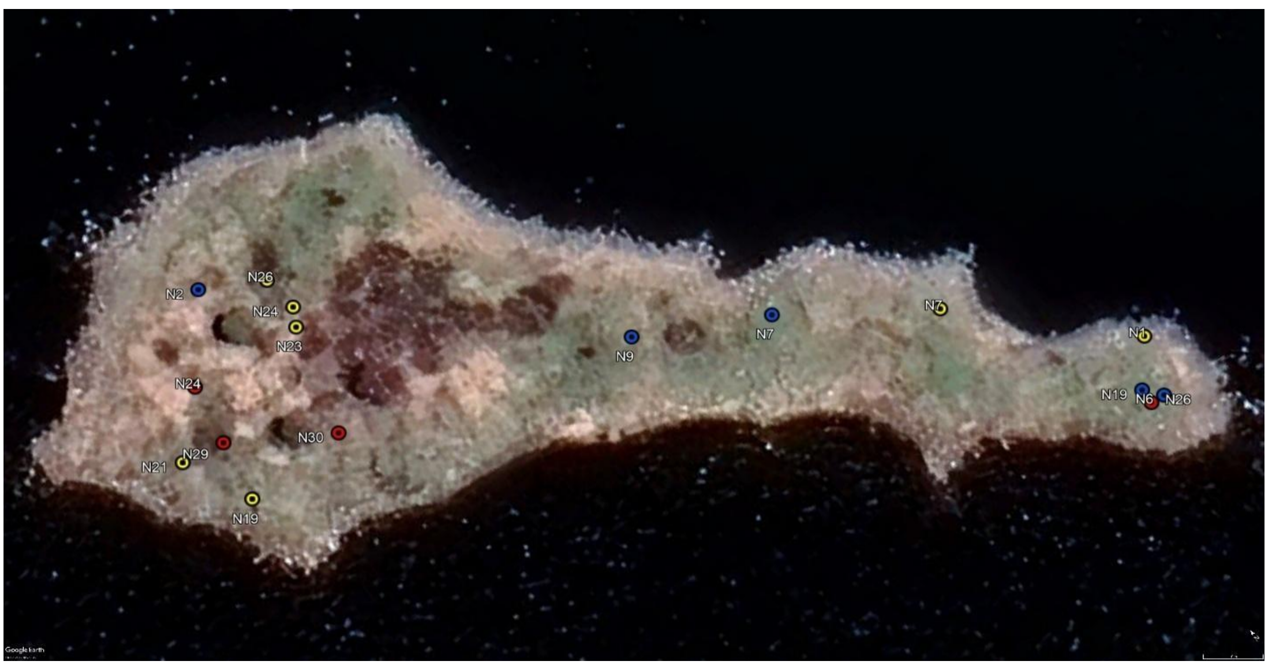

Figure 2. Aerial survey images showing the location of individual Velvet Scoter nests on the island in Lake Tabatskuri where camera traps were deployed in summers 2019–2021. Yellow points = 2019 (at 7 nests); red = 2020 (4 nests); blue = 2021 (5 nests).

Results

Nest surveys

A total of 99 nests with clutches were recorded over the three-year study period: 33 in 2019, 31 in 2020, and 35 in 2021. Throughout all years, breeding pairs often chose similar nesting sites, although not necessarily the exact same nest bowl, with most new nests situated within 2-3 m of the previous year's location. In 2019, of the 33 recorded clutches, 52% were successful (i.e., at least one egg hatched), 33% were completely predated, 9% were abandoned (containing addled eggs), and 6% were classified as dump nests - nests without an incubating female, which consequently failed to hatch (Table 2; see also Paposhvili, 2021). Among 280 eggs found in these nests, 36% hatched successfully, 32% were addled, 3% contained dead embryos, and 29% were predated (Table 3). The mean clutch size (± s.d.) in successful nests was 8.47 ± 1.37 eggs, with an average of 5.88 ± 2.20 eggs hatching per nest (Table 3). In 2020, 74% of the 31 clutches were successful, 16% were predated (including three cases where females were killed on the nest), 6% were abandoned, and 3% were laid in dump nests containing 22 eggs that were briefly incubated but ultimately failed to hatch by 5 August (Paposhvili, 2021; Table 2). That year, 296 eggs were recorded, with 49% hatching, 41% being addled, 5% suffocated, and 5% predated (Table 3). The mean clutch size for successful nests was 9.26 ± 2.09 eggs, with an average of 6.34 ± 1.92 eggs hatched (Table 3). In 2021, 74% of the 35 clutches were successful, 6% were predated, 14% were abandoned, and 6% were dump nests without incubating females, all failing to hatch (Table 2). Among 325 recorded eggs, 55% hatched successfully, 31% were addled, 5% were suffocated, and 9% were predated (Table 3). The average clutch size of successful nests was 8.88 ± 1.03 eggs, with an average of 6.80 ± 1.86 eggs hatching per nest (Table 3).

Table 1. Variables included on modelling the hatching success of Velvet Scoters breeding at Tabatskuri Lake, Georgia.

Variable	Description
Nest success	The proportion of nests in which ≥ 1 egg hatched
Hatching success	Percentage of hatched eggs in a successful clutch
Predation occurrence	Presence or absence of predated eggs in a clutch
Predation rate (%)	Percentage of predated eggs in a clutch
Year	Year of the study
Camera trap	Presence or absence of a camera trap deployed to observe the nest
Air temperature	Mean air temperature (°C) over the nesting period, extracted from camera traps

Table 2. Colony size and fate of Velvet Scoter nests found at Tabatskuri Lake, Georgia in summers 2019–2021.

Nests	Year		
	2019	2020	2021
Initiated	33	31	35
Successful	17	23	26
Predated	11	2	2
Nests with predated females	0	3	0
Abandoned	3	2	5
Dump	2	1	2

Camera trap data

All clutches in nests with camera traps hatched successfully each year of the study (Supporting Materials Table S1a-c). Data from one of the sixteen cameras, specifically the one operating in video mode were excluded from the analysis of factors affecting hatching success because this camera was installed within 35 cm of the nest (compared to 70-90 cm for the others) and was left uncamouflaged, increasing the chance of disturbance (see Supporting Materials Annex S1 for detailed observations from this device).

Model selection using the Akaike Information Criterion (AIC) identified the best fitting model for hatching success as including two categorical predictors: the presence or absence of predation and the presence or absence of camera traps (Table 4, Fig. 3). Nests that did not experience predation showed higher hatching success, and the negative impact of predation seemed to be lessened by the presence of a camera trap. In other words, nests monitored by camera traps demonstrated reduced vulnerability to predation. This model explained 26.4% of the variance in hatching success ($P < 0.001$; Table 4).

The proportion of depredated eggs per clutch was best explained by two categorical variables: year and the absence of camera traps (Table 5, Fig. 4). Lower predation rates were observed at nests where camera traps were installed, while higher levels of clutch depredation occurred in 2019 compared to 2020 and 2021. Females returning to their nests showed different behavioural responses to the presence of camera traps, most often displaying brief curiosity toward the unfamiliar object. Only four females (27%) showed clear threat displays directed at the cameras. However, all females habituated quickly, showing no further reaction to the cameras by the next day. On rare occasions when threat displays were directed at a camera, it could not be ruled out that the behaviour was in response to another, unseen stimulus behind the device (i.e., outside the camera's field of view). To prevent misinterpretation, all threat displays toward cameras were excluded from behavioural analysis.

A total of 2,534 threat displays, recorded from fifteen cameras, were attributed to responses to external stimuli rather than being directed at the cameras themselves. Only 13 of these instances captured the source of disturbance, and all of these were identified as Armenian Gulls (Larus armenicus) (Supporting Materials Fig. S11).

Table 3. Clutch size and nest success for all Velvet Scoter nests found at Tabatskuri Lake, Georgia in 2019–2021, together with the average number of hatched, depredated, addled and suffocated eggs in the nests. Sample sizes for all nests and successful nests each year are in Table 2, with detailed information in Supporting Materials Table S1a,b,c.

Reproductive parameter	Year		
	2019	2020	2021
All nests			
Clutch size (mean ± s.d.)	8.5 ± 2.9	9.6 ± 3.2	9.3 ± 4.0
Nest success (mean ± 95% CI)	0.52 (0.34–0.67)	0.74 (0.59–0.90)	0.74 (0.60–0.89)
Successful nests			
Clutch size (mean ± s.d.)	8.5 ± 1.4	9.3 ±2.1	8.9 ± 1.0
Eggs hatched (mean ± s.d.)	5.9 ± 2.2	6.4 ± 2.0	6.8 ± 1.9
Eggs depredated (mean ± s.d.)	0.2 ± 0.5	0	0.2 ± 0.2
Eggs addled (mean ± s.d.)	1.8 ± 1.6	2.6 ± 1.1	1.4 ± 1.9
Eggs suffocated (mean ± s.d.)	0.6 ± 0.5	0.3 ± 0.5	0.5 ± 1.1

Table 4. Summary of the best linear model of the relationship between the hatching success and predictor variables (see Table 1 for a description of the variables). Reference models used in the analysis were “Depredation: No” and “Camera trap: No”.

Model item	Coefficient	P value
Depredation: Yes	–0.449	< 0.001
Camera trap: Yes	0.110	0.302
Depredation: Yes * Camera trap: Yes	0.467	0.017
Intercept	0.561	< 0.001
Adjusted R2	0.264	< 0.001

Table 5. Summary of the best linear model of the relationship between the depredation percentage and predictor variables (see Table 1 for a description of the variables). “Year 2021” and “Camera trap: No” are the categories used for model references.

Model item	Coefficient	P value
Year: 2020	–0.2988	0.0005
Year: 2021	–0.2619	0.0017
Camera trap: Yes	–0.1884	0.0416
Intercept	0.3876	< 0.0001
Adjusted R2	0.136	0.0007

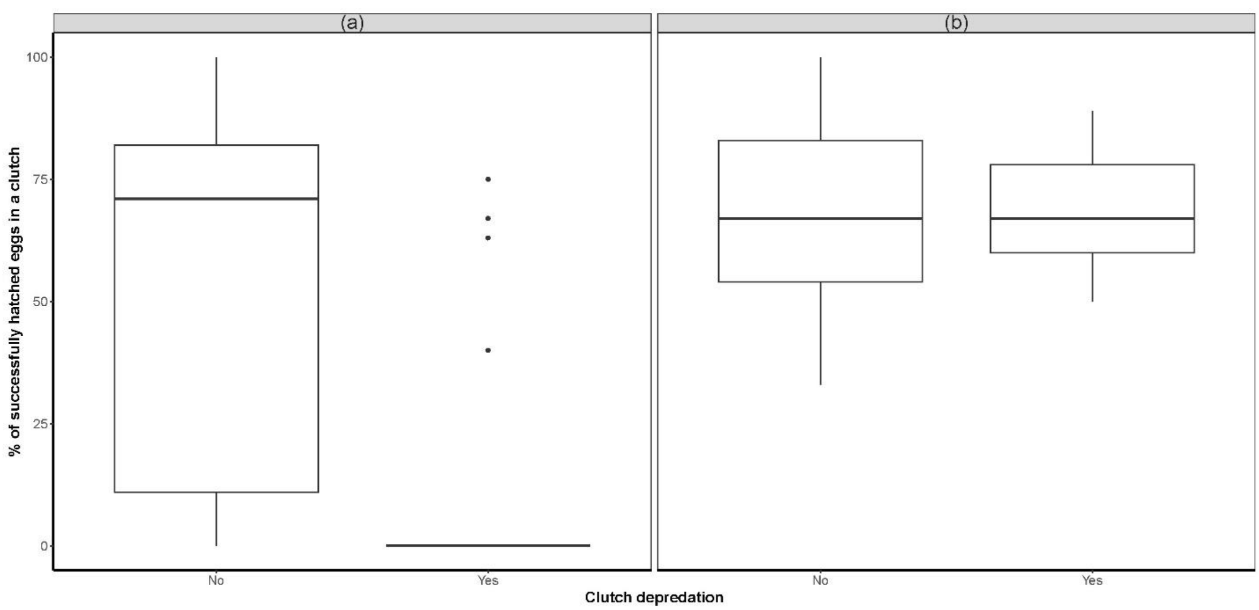

Figure 3. Box plots showing the relationship between the most important predictor variables (listed in Table 1) and hatching success for Velvet Scoters at Tabatskuri Lake, Georgia: (a) with no camera traps installed by the nests, and (b) with camera traps installed.

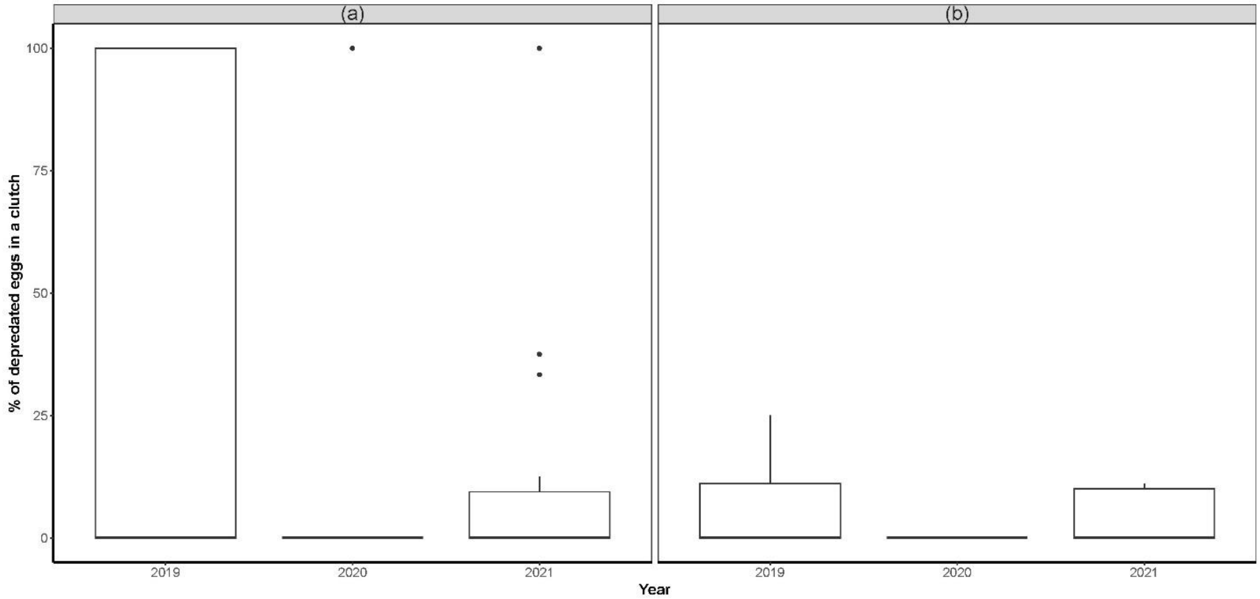

Figure 4. Box plots showing annual variation the percentage of predated eggs in a Velvet Scoter clutch at Tabatskuri Lake, Georgia: (a) with no camera traps installed by the nests, and (b) with camera traps installed, on including other significant predictor variables (listed in Table 1) in the model.

Data collected over the three-year study period, from both direct observations and camera trap recordings, showed that land-based predators were absent on the island. The main avian predators present included Armenian Gulls (Larus armenicus), which nested on the island, and Marsh Harriers (Circus aeruginosus), which bred in wetland areas located in the northeastern and southwestern parts of the lake.

Throughout the 2019-2021 monitoring period, no active predation of Velvet Scoter eggs by Armenian Gulls or Marsh Harriers was observed at active nests during continuous camera surveillance during incubation. Only one camera trap captured two egg predation events by a Marsh Harrier, both at the same nest (21/2019). Despite these predation events, the incubating female did not abandon the nest and eventually hatched four ducklings. The Marsh Harrier visited the nest briefly, for about 10-15 minutes after midday (12:40 h; 14:50 h) on two consecutive days

(24 and 25 August 2021), eating one egg during each visit. On both occasions, the female left the nest safely and returned after three and five hours, respectively (Supporting Materials Fig. S10).

Armenian Gulls, including both adults and juveniles, were observed removing spoiled eggs from a scoter nest where the remaining eggs had already hatched, with such behaviour documented only five times (Supporting Materials Fig. S11). Evidence of scoter egg predation was found during annual nest inspections across the island, with most incidents likely caused by Armenian Gulls, given their high numbers and frequent presence near nests. None of the three nests in 2020 where incubating females were killed on the nest (Supporting Materials Fig. S12) were fitted with camera traps. However, since no other large avian predators were present in the area during summer, these incidents most likely involved Marsh Harriers.

Beyond the predator species, camera trap recordings also captured visits by other Velvet Scoters to active nests on two separate occasions (see Supporting Materials Annex 2 for detailed accounts).

Following successful hatching and the subsequent movement of ducklings to the water, camera trap recordings documented females returning alone to their nests on four occasions. In three of these cases, females returned within one hour of departure, while in the fourth instance, the return occurred the following day. In each case, the returning females, presumably having lost their broods, remained at the nest site for two to three days, apparently anticipating the hatching of any remaining eggs; however, no additional hatching events were observed.

Camera trap data confirmed that the total incubation period lasted 28-29 days for nests with known start dates (n=11). The start of incubation was defined as when the female settled in the nest and stayed there for most of the day, usually at the end of June. Hatching generally happened between July 20 and 25. Across all camera monitored nests, females rolled their eggs an average of 7.07 ± 5.16 times per day (n=155; max=24) and changed their body position an average of 17.87 ± 12.47 times per day (n=164; max=60). In some cases, it was hard to tell the difference between egg-rolling and repositioning, so ambiguous observations were counted as position changes. The real number of egg-rolling behaviours was probably higher than reported.

During the incubation period, females left their nests for an average of 2.38 ± 2.18 hours per day (n = 153). In three cases, the absences were unusually long, lasting between 15 and 24 hours, once during the early incubation stage and twice during the final days before hatching. Conversely, in four cases, females remained continuously on the nest for a full 24 hours, occurring twice during mid-incubation and twice on the day of hatching. Before leaving, females typically covered their eggs with down, although this behaviour was not observed in five recorded instances.

In two cases, a Marsh Harrier visited the same nest shortly after the female's departure. In one additional case, a different Velvet Scoter female with five ducklings visited an unattended nest about 40 minutes after the incubating female left, staying for less than two hours (see Supporting Materials Annex 2). In two other cases, no visits by other birds were recorded during the female's absence; both occurred two to three days before hatching.

One observation documented a female leaving four newly hatched ducklings unattended in the nest, returning after three hours, then leaving again 90 minutes later, and coming back two hours after that. During these absences, the ducklings stayed huddled together and did not leave the nest. After her final return, the female brooded the ducklings for roughly 14 hours before leading them away from the nest site.

Discussion

Observations collected between 2019 and 2021 indicated that the average clutch size of Velvet Scoter nests at Lake Tabatskuri ranged between eight and nine eggs across the three study years, with mean clutch sizes of 8.47, 9.26, and 8.88 eggs in 2019, 2020, and 2021, respectively, for successful nests (i.e., those in which at least one egg hatched). Modal clutch sizes were eight eggs in 2019 and nine eggs in both 2020 and 2021. In 2019, overall clutch size ranged from four to thirteen eggs (mean = 7.94, excluding eggs from dump nests); in 2020, from three to fifteen eggs (mean = 9.13); and in 2021, from two to twelve eggs (mean = 8.48). Each year, a small number of predated or abandoned nests contained only two to six eggs. Only two incubating females were recorded with unusually small clutches: one with six eggs, of which two hatched, in 2019, and another with three eggs, of which one hatched, in 2020. Both cases were likely second nesting attempts, inferred from the small clutch sizes and the continuation of incubation into early August.

Based on these findings, the typical clutch size for Velvet Scoters breeding at Lake Tabatskuri was 8-9 eggs, consistent with values previously reported for taiga and arctic breeding populations of the species (Cramp & Simmons, 1977). This clutch size probably resulted in an average brood size of roughly six to seven newly hatched ducklings.

Hatching success increased significantly with lower levels of predation, which were notably reduced in 2020 and 2021 compared with 2019. This decline in predation was most likely related to the reproductive failure of Armenian Gulls during these two years (N. Paposhvili, pers. obs.). In 2020, many gulls left the lake early after losing their chicks, while in 2021 only a few dozen pairs nested successfully on the island.

The placement of camera traps near nests, within the view of incubating females, had no detectable negative effect on hatching or overall nesting success throughout the study. Although the cameras initially caused increased threat displays in the first few days after installation, this behavioural response diminished over time. The initial concern was that such heightened vigilance might increase energy expenditure and potentially reduce body condition, thereby influencing the female's ability to complete incubation or protect the hatched ducklings from Armenian Gulls while leading them to water (as previously noted by Paposhvili, 2021). However, no direct negative effects on nesting females were observed, and using camera traps was valuable in identifying factors that influence nesting success and female behaviour.

Camera recordings showed that incubating Velvet Scoters generally succeeded in deterring Armenian Gulls from nests through threat displays. Only one instance of direct physical aggression toward an approaching gull was recorded. Threat displays happened daily at all monitored nests; out of 2,534 displays, only thirteen images captured and identified the approaching intruders as Armenian Gulls. In all other cases, the source of the female's defensive posture was unclear, making it impossible to tell if the response was aimed at an actual threat or potentially at the camera itself.

Interestingly, the presence of camera traps seemed to lessen the impact of egg predation on breeding success. This indicates that while Velvet Scoters were mostly unaffected by the cameras, potential predators like Armenian Gulls might have been more cautious or kept away. The reason for this effect remains unknown. Notably, most camera traps were set up in areas with sparse vegetation to improve visibility, which might have made these nests more noticeable and accessible to predators.

Unlike interactions with Armenian Gulls, nesting Velvet Scoter females generally could not repel Marsh Harriers when these raptors approached or attacked the nest. In several instances, females temporarily abandoned the nest when the predator arrived, returning a few hours later to check on the clutch and resume incubation if the nest remained largely intact. In 2020, three incubating females were found to have been killed by Marsh Harriers while on the nest. This predation pattern may have been linked to the early departure of Armenian Gulls from the lake that year, which left Velvet Scoters without the "umbrella" protection normally provided by gull colonies. Typically, nesting Armenian Gulls actively mob raptors approaching the island, offering an indirect defence for nearby scoter nests.

The presence of dump nests also contributed to a decrease in the total number of successfully hatched eggs. Egg dumping is well documented among waterfowl, often seen as a form of conspecific nest parasitism (Weller, 1959) or as a result of nest site limitation under high nesting densities (Morse & Wight, 1969; Kruckenberg, 2019). Other explanations include egg laying by females that have recently lost their own nests to predators or strategies to increase reproductive output by depositing eggs in the nests of other females (Pienkowski & Evans, 1982). Although the exact cause could not be established in this study, dump nests consistently appeared in the same area of the island, the zone with the highest nesting scoter density, across all three study years. Notably, in 2021, when the highest total number of eggs was recorded in dump nests (19 and 26 eggs), it coincided with the largest number of active nests ever observed on the island (Supporting Materials Fig. S13). These findings suggest that high female densities and limited available nesting sites likely contributed to the occurrence of dump nesting behaviour in the Lake Tabatskuri Velvet Scoter population.

The behaviour of a female with five hatched ducklings trying to incubate at another nest is difficult to interpret. One possible explanation is that the visual or olfactory cue of an uncovered clutch, especially one nearing hatch, with eggs starting to pip may have triggered an incubation response. This behaviour could be an adaptive effort to boost reproductive success by increasing brood size through adopting additional hatchlings. Brood merging is known to lower predation risk among waterfowl because larger broods can divide predation risk once on open water.

However, returning to incubate at another nest without her ducklings would have been risky, as unattended broods are highly vulnerable to predators unless they are already lost. Additionally, in this case, the resident female eventually drove off the intruding bird, preventing any potential reproductive benefit. Similar cases where females return alone to nests within 10-30 minutes of leaving, but without their ducklings, have also been observed at other sites; these likely reflect brood losses shortly after hatching. Such losses align with high predation pressure on ducklings during their first day on the water, as confirmed by direct field observations.

This behavioural pattern may also explain why some females were seen covering unhatched eggs with down after leading their broods away from the nest. This action could be an effort to protect the remaining eggs' viability, keeping open the chance of recovering some reproductive effort within the same breeding season.

The nesting success of the Velvet Scoter seems influenced by a complex interaction involving predation pressure, the presence of gulls, and human disturbance levels. Human activities on or near the island often caused incubating females to leave their nests, sometimes without covering the eggs, which negatively impacts the nest's thermal conditions, increasing the chances of egg addling and embryo mortality. Additionally, disturbance events frequently flush gulls into the air above the island, increasing nest visibility and making predation easier.

Local awareness and outreach efforts involving community members, protected area staff, and local fishers have likely helped reduce the impact of disturbances. Consequently, hatching success increased from 52% in 2019 to 74% in 2021, reaching levels similar to those documented for the closely related White-winged Scoter (Melanitta deglandi) in North America, where hatching success ranged from 67-92% (Brown & Brown, 1981) and 72-89% (Traylor et al., 2004).

At Lake Tabatskuri, Armenian Gulls are the main predators of Velvet Scoter eggs and small ducklings (N. Paposhvili, pers. obs.). While their predation can significantly reduce reproductive output, the presence of gull colonies may also deter Marsh Harriers, which can prey on adult females. Gulls typically consume eggs and ducklings during periods when female ducks are distracted by human disturbance, yet many females successfully defend their nests from gull attacks. Conversely, Marsh Harriers have been observed killing incubating females, but only in areas without nearby gulls. Therefore, Armenian Gulls may play a paradoxical but beneficial role by helping reduce adult mortality through territorial exclusion of raptors. Since the death of breeding females has a much greater impact on population dynamics than the loss of eggs or ducklings, maintaining a balanced gull population might be crucial for sustaining scoter recruitment.

Human disturbance demands ongoing management, and gull populations should be regulated to minimize their direct predation on scoter nests while maintaining their indirect “umbrella” protection against raptors. Preserving and improving current habitat conditions at Lake Tabatskuri (Paposhvili et al., 2023) is essential to enhance duckling survival, which remains low (Paposhvili, 2021). Conservation efforts should include strict regulation of human access to and around the island, consistent enforcement of fishing and boating restrictions across the northern lake sector, sustainable lake water management for irrigation, pollution control, and habitat preservation. Collectively, these actions are vital to ensure the long-term survival of the region’s small and isolated Velvet Scoter population.

Chapter 4. Contraction of range, declines in abundance and site-based threats to Velvet Scoter Melanitta fusca breeding in the Caucasus

Over the past twenty years, significant declines have been observed in several sea duck species, including the Velvet Scoter (Melanitta fusca) (Kilpi et al., 2015; Skov et al., 2011). In line with this worldwide trend, the Caucasian population has experienced a severe reduction, bringing this small, isolated group close to extinction. Over the last 60 years, the population has decreased rapidly, and its breeding range has shrunk to just one known site in Georgia (Keller et al., 2020; Paposhvili, 2018; Wetlands International, 2020).

Historical data on breeding abundance and distribution in the Caucasus remains limited, making it harder to determine the specific causes of decline. Nonetheless, recent studies show that hunting, egg collection, accidental bycatch in fishing nets, predation, and habitat degradation have collectively decreased juvenile and adult survival rates and reduced reproductive success, speeding up the population's decline (Paposhvili, 2021). Additionally, climate change is viewed as a major and ongoing threat to the species, both now and in the near future (Drever et al., 2011).

The main goal of the study is to evaluate both historical and recent threats that have caused the Velvet Scoter population in the Caucasus to decline over the last sixty years, and to analyse their combined effects on the species' viability. Another goal is to assess whether abandoned breeding sites can be restored to a healthy ecological state that supports recolonization by the species. This evaluation offers a scientific foundation for considering future reintroduction efforts in the region, based on recent research and conservation experience.

Reintroduction can only succeed if the main causes of local extinction are identified, measured, and addressed. Therefore, it is crucial to understand both the historical and current reasons for population decline at previously occupied sites to guide recovery efforts that are essential to prevent regional extinction. In conservation biology, understanding how past and present pressures combine is key to creating effective long-term strategies. By focusing on these factors, this study aims to develop evidence-based conservation actions to stop further decline and help restore this unique and ecologically important sea duck to its former numbers and range in the Caucasus.

Methods

Geographical scope of the study

The Caucasus Ecoregion, covering about 586,800 km², stretches across various landscapes in Armenia, Azerbaijan, Georgia, the northern Caucasus, northeastern Türkiye, and northwestern Iran. Recognized for its high levels of endemism and species diversity, it is designated as one of the world's major biodiversity hotspots (Zazanashvili, 2009). This study investigated both historical and current breeding sites of the Velvet Scoter in Georgia, Armenia, and the Caucasian part of Türkiye, where the species has bred in recent times. Site selection was based on historical records and the known breeding range of the species. A summary of the lakes studied, along with their key habitat features, is shown in Table 1. During fieldwork, water transparency was assessed, and trophic status was qualitatively evaluated using ecological indicators like the condition and presence of submerged aquatic plants.

In total, thirteen former breeding sites were revisited: six in Georgia, four in Türkiye, one transboundary lake shared by both countries, and two in Armenia (Fig. 1). Areas within the Caucasus regions of Russia and Iran, as well as Azerbaijan, were excluded because there is no record of Velvet Scoter breeding activity.

Compiling historical data

Historical data were compiled from literature sources dating back to 1896 through keyword-based searches using terms such as Velvet Scoter, Melanitta fusca, Caucasus/Caucasia, Armenia, Georgia, Russia, and Türkiye. Searches were conducted across a range of books and academic databases, including Google Scholar and national repositories, in five languages: English, Armenian, Georgian, Russian, and Turkish. These sources were complemented by observational data drawn from the two most widely used regional citizen science ornithological databases - eBird (2024) and Observation.org (2024), as well as the Turkish web-based ornithon photographic platform TRAKUŞ (2024).

The data collection covered the territories of three countries and were consolidated into a comprehensive summary table (Table 1). Historical breeding records were classified according to the highest of the sixteen breeding behaviour codes proposed by Keller et al. (2020), grouped as follows: "A" (codes 1-2; possible breeding), "B" (codes 3-9; probable breeding), and "C" (codes 10-16; confirmed breeding). Category C16 sites represented locations where nests were found and young were either seen or heard.

Table 1. Summary table of the habitat characteristics of the study sites (TR = Türkiye; AM = Armenia; GE = Georgia).

#Site	Site Name (Country)	Coordinates	Altitude (m)	Surface Area (km²)	Average depth (max. depth) (m)	Number of Islets
1	Çıldır (TR)	41°30'N, 43°15'E	1 963	123	30 (42.00)	4
2	Aktaş (TR) / Kartsakhi (GE)	41°13'N, 43°14'E	1 800	14.00 (TR) 13.00 (GE)	0.7 (1.0)	12
3	Aygır (TR)	40°45'N, 43°00'E	2 131	3,7	? (30.00)	0

4	Balık (TR)	39°45'N, 43°34'E	2 254	34	7.00 (37.00)	2
5	Nemrut Caldera (TR)	38°37'N, 42°13'E	2 252	34	100.00 (155.00)	2
6	Arpi (AM)	41°03'N, 43°37'E	2 025	20	4.2 (8.00)	2
7	Sevan (AM)	40°19'N, 45°21'E	1 900	1242	26.00 (79.00)	1
8	Khanchali (GE)	41°15'N, 43°33'E	1 931	6,9	0.5 (1.00)	0
9	Bughdasheni (GE)	41°12'N, 43°41'E	2 045	0,4	0.8 (1.50)	1
10	Madatapa (GE)	41°11'N, 43°47'E	2 112	8,78	0.7 (1.70)	2
11	Saghamo (GE)	41°18'N, 43°44'E	1 999	4,8	1.60 (2.20)	1
12	Paravani (GE)	41°26'N, 43°48'E	2 079	37,5	2.20 (3.30)	4
13	Tabatskuri (GE)	41°39'N, 43°38'E	1 993	14,2	15.00 (45.00)	3

Table 1 continued below

#Site	Site Name (Country)	Habitat on the Islets	Transparency	Trophic state
1	Çıldır (TR)	Human-made Woodland, grassland, shrubs, rocky, stony, ancient ruins	Transparent	Mesotrophic

2	Aktaş (TR) / Kartsakhi (GE)	Scattered trees and shrubs, stony, rocky, grassland	Turbid	Eutrophic
3	Aygır (TR)	No island	Transparent	Mesotrophic
4	Balık (TR)	rocky, stony, grassland	Transparent	Oligotrophic
5	Nemrut Caldera (TR)	Rocky, stony, woodland, shrubs	Transparent	Oligotrophic
6	Arpi (AM)	grassland, shrubs, stony	Turbid	Oligotrophic
7	Sevan (AM)	grassland, shrubs, stony	Transparent	Oligotrophic
8	Khanchali (GE)	No island	Severe algal growth	Eutrophic
9	Bughdasheni (GE)	Grass, two half-dried small trees	Turbid	Mesotrophic
10	Madatapa (GE)	The first, large island is grassy; the second is stony	Severe algal growth	Eutrophic
11	Saghamo (GE)	Grassy, three or four small trees	Turbid	Mesotrophic
12	Paravani (GE)	All four islands are grassy with a few shrubs	Turbid	Mesotrophic
13	Tabatskuri (GE)	The first, large island is grassy, with shrubs and trees; the second is grassy and the third one is stony	Transparent	Oligotrophic

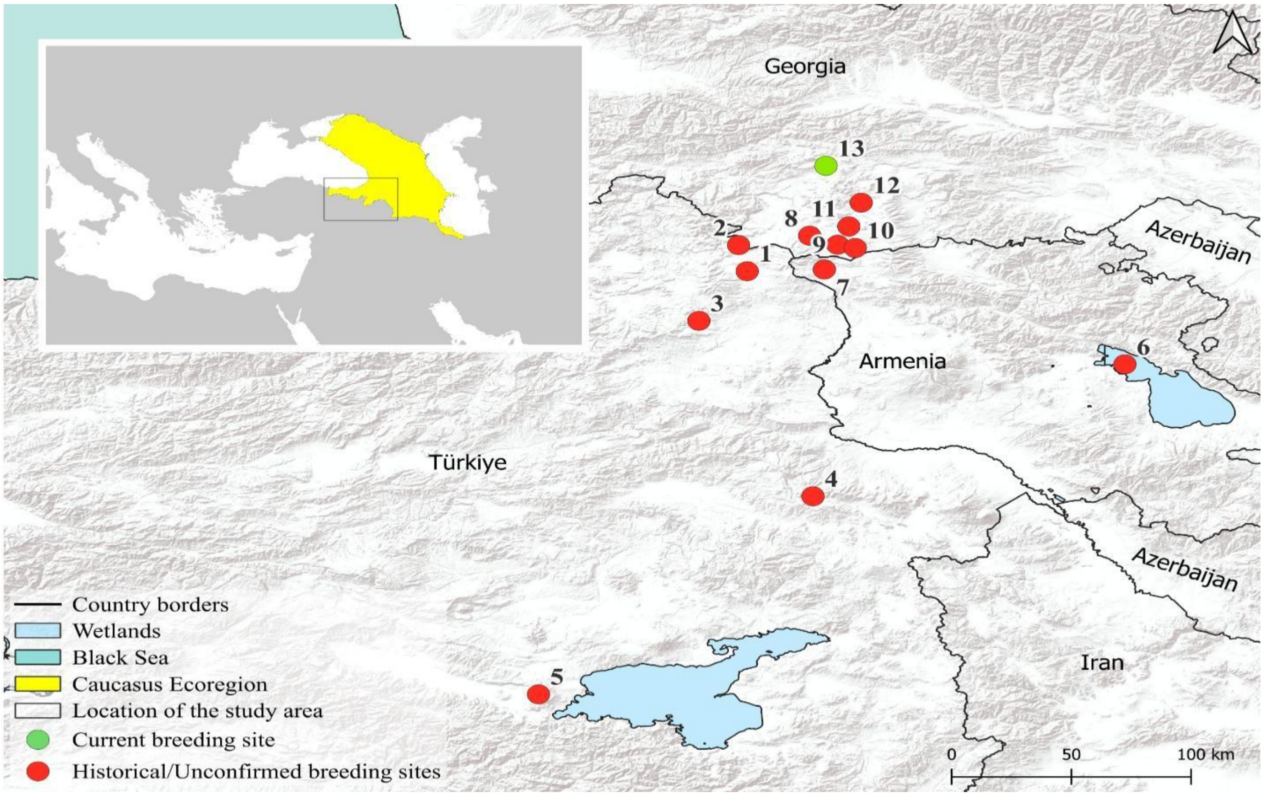

Figure 1. Historical and current breeding sites for Velvet Scoters in the Caucasus and the location of the Caucasus Ecoregion. Site codes (numbers) are listed in Table 1.

Current breeding survey

Current breeding surveys were conducted at both historically occupied and the last remaining active breeding sites of the Velvet Scoter. Field observations followed the point count methodology described by Bibby et al. (2000). Surveys took place in Georgia between 2017 and 2023, in Türkiye during 2016-2018 and 2021-2023, and in Armenia from 2013 to 2024. When multiple breeding-related behaviours were observed at a site, the highest applicable breeding code-based on the sixteen standardized categories defined by Keller et al. (2020) was assigned to indicate the species' definitive breeding status at that location.

Threats analysis

Threats to the Velvet Scoter and its breeding habitats, along with the related stresses caused by these threats, were identified through direct observations made during visits to all target sites and by reviewing the literature listed in Table 2. The classification of threats followed the IUCN–CMP Unified Classification of Direct Threats (Version 4.0) and Stresses (Version 1.0) (Salafsky et al., 2024). The "threat ranking methodology" developed by the Ministry of Agriculture and Forestry (2023) for use in Türkiye was employed to assess and prioritize threats.

Each threat was evaluated based on three criteria: (1) Scope - the proportion of the population or habitat affected; (2) Severity - the extent of impact on the species or its habitat; and (3) Urgency - the urgency of implementing mitigation measures. Threats were ranked individually for each criterion across all study areas collectively, with no distinction between countries. Each criterion was scored on a numerical scale from 1 to 16, where 1 indicated the broadest or most significant impact and 16 the narrowest or least impact. This scale reflected the total number of identified threats. The same scoring method was applied independently for each criterion, with the three scores then summed to determine an overall ranking. The threat with the lowest combined score was identified as the most critical.

Based on the cumulative impact levels, threats were then categorized as "critical," "high," "medium," or "low." The thresholds for these categories were determined through expert consensus, supported by extensive field experience in the region. Finally, the connections between identified threats and their resulting stresses on Velvet Scoters were illustrated using a problem tree diagram created to represent the species' breeding ecology within the Caucasus.

Results

Historical and current breeding distributions

During the surveys, no Velvet Scoters were observed in Türkiye (2016-2023) or Armenia (2013-2024). The only confirmed breeding site was at Lake Tabatskuri, Georgia, with an estimated 45-50 breeding pairs. This site is the last remaining breeding location for the Caucasian Velvet Scoter population, confined to the largest of the three islets in the lake. Of the thirteen sites previously associated with the species, seven were confirmed as former breeding areas, while the others were identified as either historical locations used during pre- or post-nuptial migration or as unconfirmed breeding sites (Table 2).

Table 2. Overview of historical and current data. ? = lack of data. Breeding codes indicate the increasing probability of birds breeding, based on the European Breeding Bird Atlas 2 categories (Keller et al. 2020): A1 = species observed during the breeding season in possible nesting habitat; B3 = pair observed during the breeding season in possible nesting habitat; B4 = territorial behaviour; C12 = recently fledged or downy young observed; C13 = adults entering or leaving the nest site; C15 = nest containing eggs; and C16 = nests with young seen or heard.

#Site	Site Name (Country Code)	Status of the site	Year of		
			Max counts (Year)	Latest observation	Latest breeding attempt
1	Çıldır (TR)	Unconfirmed breeding	14 (2005)	2005	?
2	Aktaş (TR) / Kartsakhi (GE)	Former breeding	725 (1980)	2005	1980
3	Aygır (TR)	Unconfirmed breeding	32 (2001)	2008	1967
4	Balık (TR)	Former breeding	18 (1967)	2008	1985
5	Nemrut Caldera (TR)	Former breeding	21 (1967)	1992	1998
6	Arpi (AM)	Unconfirmed breeding		1998	1969

7	Sevan (AM)	Former breeding	50 (1968)	1969	2004
8	Khanchali (GE)	Former breeding	?	2004	?
9	Bughdasheni (GE)	Unconfirmed breeding	?	2nd half of 20th century	?
10	Madatapa (GE)	Unconfirmed breeding	?	2nd half of 20th century	?
11	Saghamo (GE)	Unconfirmed breeding	21 (2002)	2004	?
12	Paravani (GE)	Unconfirmed breeding	?	2nd half of 20th century	?
13	Tabatskuri (GE)	Current breeding	106 (2023)	2023	2024

Table 2 continued below

#Site	Site Name (Country)	Number	Max Number	Max number	Breeding	References
		of pairs	of ♂ - ♀	of ducklings	Behaviour Code	
1	Çıldır (TR)	?	?	?	A1	1, 2
2	Aktaş (TR) / Kartsakhi (GE)	20–50	?	?	C12	1, 3, 4 - 8
3	Aygır (TR)		?	?	A1	1, 2, 6
4	Balık (TR)	3	3 ♀	15	C12	1, 2, 9
5	Nemrut Caldera (TR)	3-5	5-5	18	C12	1, 2, 9
6	Arpi (AM)	0-1	2-1	0	B4	10

7	Sevan (AM)	?	?	?	C15	11, 12, 13
8	Khanchali (GE)	10-20	?	1	C12	4, 5, 14, 15
9	Bughdasheni (GE)	?	?	?	B3	4, 5
10	Madatapa (GE)	?	?	?	B3	4, 5, 16
11	Saghamo (GE)	4	5-4	?	C13	4, 5, 15, 17
12	Paravani (GE)	?	?	?	B3	4, 5
13	Tabatskuri (GE)	45-50	56-50	39	C16	18, 19, 20

References: 1 = Kirwan et al., 2008; 2 = eBird, 2024; 3 = BirdLife International, 2020; 4 = Janashvili et al., 1960; 5 = Kutubidze, 1985; 6 = TRAKUS, 2024; 7 = van der Ven & Gheyselinck, 1982; 8 = Magnin & Yarar, 1997; 9 = Vielliard, 1968; 10 = Adamian & Klem, 1999; 11 = Lyayster & Sosnin, 1942; 12 = Dahl, 1954; 13 = Margaryan, 1975; 14 = I. Matcharashvili, pers. obs; 15 = BirdLife International, 2020; 16 = Matcharashvili et al., 2004; 17 = G. Darchiashvili, pers. obs.; 18 = Paposhvili, 2018; 19 = Paposhvili, 2021; 20 = Paposhvili et al., 2023.

Analysis of breeding codes assigned to each surveyed site revealed the following: two sites were classified as possible breeding (code A1), four sites as probable breeding (codes B3 and B4), and seven sites as confirmed breeding (codes C12, C13, C15, and C16) (Table 2). The highest estimated numbers of breeding pairs were recorded at Lakes Aktaş/Kartsakhi (Türkiye/Georgia) and Tabatskuri (Georgia), each supporting up to 50 pairs. Based on historical information, the maximum estimated regional population of the Velvet Scoter in the Caucasus was likely fewer than 150 breeding pairs from 1942 to 2025.

Historical records show that the earliest documented breeding occurrence of the Velvet Scoter in the Caucasus dates back to 1896, originating from observations at Lake Tabatskuri (Satunin, 1907). In Türkiye, the most recent record of a Velvet Scoter during the breeding season was in 2008, when a male was sighted at Lake Aygır, while the last confirmed breeding event occurred at the Nemrut Caldera in 1998 (Table 2). In Armenia, the most recent breeding attempt was documented in 2004 at Lake Sevan, where two males displayed territorial behaviour. After the rediscovery of breeding Velvet Scoters at Lake Tabatskuri, Georgia, in 2014 (Toriashvili, 2023), the species was considered extirpated as a breeding bird from the rest of the Caucasus region.

Classification and analysis of threats

A total of eighteen direct threats to the Velvet Scoter and its breeding habitats were identified (Table 3), resulting in six distinct categories of associated stress (Fig. 2). The spatial distribution of threats varied among countries, with sixteen recorded in Georgia, thirteen in Türkiye, and twelve in Armenia; ten of these threats were common to all three. The most frequently documented threats across sites included native species interactions (n = 13), recreational activity (n = 12), and hunting and egg collection (n = 11). Among the surveyed sites, Lakes Paravani and Tabatskuri exhibited the highest number of identified threats (n = 13 each), whereas Lakes Aygır and Balık were subject to the fewest (n = 3 each). The threats categorised as viral diseases and climate change were considered non-site-specific in nature.

Grazing and ranching. In Türkiye and Armenia, cattle grazing on breeding islands has contributed to habitat degradation, resulting in trampling of vegetation and the destruction of nests and eggs. On Lake Çıldır, both cattle and horses were observed grazing on islands. Until 2016, the islets of Aktaş/Kartsakhi Lake were also subject to grazing by Turkish farmers. This activity ceased following the establishment of a Turkish military border post and the designation of the area as a protected zone for breeding colonies of the Dalmatian Pelican (Pelecanus crispus) and the Great White Pelican (Pelecanus onocrotalus).

Hunting and egg collection. Illegal hunting of waterfowl remains a documented threat at breeding sites in both Türkiye and Georgia. At Lake Aktaş/Kartsakhi, eggs of the Greylag Goose (Anser anser) and Mallard (Anas platyrhynchos) were historically gathered for human consumption, and Greylag Goose eggs were also used for incubation with domestic geese. It is highly likely that Velvet Scoter eggs were accidentally or intentionally taken during these activities. The implementation of access restrictions and enhanced protection measures at Lake Aktaş/Kartsakhi has since reduced this threat, and it is no longer considered an active issue at this location. Such practices directly cause adult mortality and decrease overall reproductive success by leading to the loss of eggs and disturbance of nesting females. At Lake Tabatskuri, egg collection was once a major threat; however, this problem has now been largely addressed thanks to targeted conservation efforts and the active cooperation of local communities.

Table 3. Threat categories recorded for each of the study sites.

CLASSIFICATION OF THREATS	STUDY SITES												
	Khanchali (GE)	Bughdasheni (GE)	Madatapa (GE)	Saghamo (GE)	Paravani (GE)	Tabatskuri (GE)	Aktaş (TR) / Kartsakhi (GE)	Çıldır (TR)	Aygır (TR)	Balık (TR)	Nemrut Caldera (TR)	Sevan (AM)	Arpi (AM)
Grazing & ranching													
Hunting & collecting eggs													
Cutting & collecting terrestrial plants													
Fishing													
Recreational activities													
Scientific research													
Abstraction of surface water													

Dams													
Native species interactions													
Invasive non-native species													
Sewage													
Nutrient loads													
Herbicides & pesticides													
Garbage & solid waste													
Agricultural disturbance													
Drought													
*Viral diseases	*Since both are considered hypothetical for the entire geographical scope, they were classified as non-site specific.												
*Climate change													

Cutting and collecting terrestrial plants. Vegetation on several breeding islands was previously cut and baled for livestock fodder. During this process, incubating females were occasionally killed, and vegetation removal caused irreversible habitat degradation for the duration of the breeding season. This activity, once recorded at Lake Aktaş/Kartsakhi, is no longer considered a threat at that site due to the enforcement of access restrictions, which have also eliminated egg collection activities.

Fishing. Fishing activities, including boat operations and associated human presence, create significant disturbance during the breeding season. At Lake Tabatskuri, such disturbance has been particularly problematic, frequently separating broods from attending females and thereby increasing the vulnerability of small ducklings to predation by Armenian Gulls (Larus armenicus). In addition, as a diving species, the Velvet Scoter is highly susceptible to entanglement and accidental capture in set gillnets as well as in lost or abandoned “ghost” nets, resulting in drowning and physical injury (Fig. 3).

Recreational activities. Human presence on breeding islands disrupts incubating females, often resulting in nest abandonment and increasing the risk of eggs being accidentally trampled. Off-road vehicle use, motorboat traffic, and uncontrolled tourist activity further exacerbate disturbance during critical breeding periods. Such disturbances interrupt incubation, feeding, and brood-rearing behaviour, consequently exposing both eggs and ducklings to heightened predation risk.

Scientific research. Research activities have been conducted exclusively at breeding lakes in Georgia. Factors such as the duration of field visits, the size of research teams, and the methods used can temporarily disturb nesting birds. However, researchers consistently apply mitigation measures to reduce such impacts, including covering eggs with down and camouflaging nests after each visit. Based on the number of nests recorded and the counts of Velvet Scoter ducklings in recent surveys, there is no evidence suggesting that research activities have any significant negative effects on the species.

Abstraction of surface water. Excessive extraction of surface water for domestic, agricultural, and industrial purposes has changed hydrological regimes in several Armenian wetlands, leading to substantial declines in water levels. A notable example occurred at Lake Sevan during the 1970s, when lowered water levels turned the former breeding island into a peninsula accessible to land predators (Table 4). This impact was further worsened by the development of a historic monastery complex on the former island for tourism, greatly increasing disturbance.

Dams. The construction of a dam at the end of the 20th century divided Lake Khanchali into two basins. One basin has mostly dried out since then and is now used by local residents for grazing. Before the dam was built, the lake covered about 13.1 km^2; now, its surface area has decreased to 6.9 km^2, leading to major changes in the local ecosystem and loss of suitable breeding habitats for waterfowl.

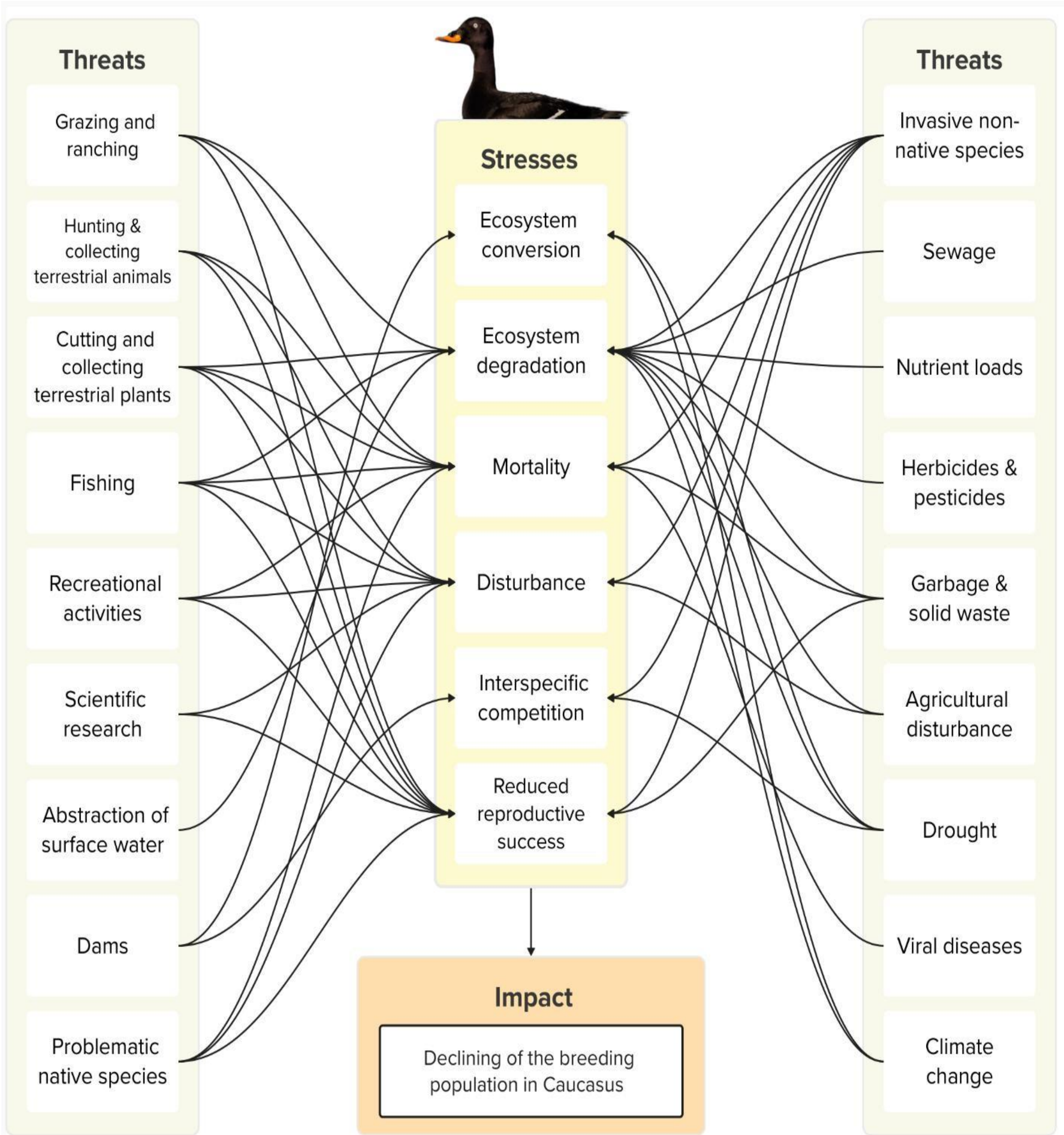

Figure 2. Threat analysis of the declining Velvet Scoter breeding population in the Caucasus.

Figure 3. Two juveniles entangled in a fishing net at Lake Tabatskuri in August 2021, by H. Muradyan.

Table 4. Native predators and their effects on Velvet Scoters. Evidence codes: d = documented by cameras; do = direct observation; p = potential predator).

Predator	Location	Egg	Duckling	Adult	Nesting competition	Level of evidence
Dalmatian pelican Pelecanus crispus	Aktaş/Kartsahki	-	+	+	+	p
White pelican Pelecanus onocrotalus	Aktaş/Kartsahki	-	+	+	+	p

Armenian Gull Larus armenicus	All lakes (except Aygır)	+	+	+	+	d & do
Marsh Harrier Circus aeruginosus	All lakes	+	+	+	+	d & do
Northern Goshawk Accipiter gentilis	Sevan & Arpi	-	+	+	-	do
Brown Rat Rattus norvegicus	Çıldır & Nemrut Caldera	+	+	-	-	p
Least Weasel Mustela nivalis	Sevan	+	+	-	-	do
Eurasian Otter Lutra lutra	Tabatskuri & Çıldır	+	+	-	-	p
Caucasian Badger Meles canesens	Madatapa	+	+	-	-	p
Red Fox Vulpes vulpes	Madatapa, Sevan & Arpi	+	+	-	-	do
Brown Bear Ursus arctos	Nemrut Caldera	+	-	-	-	p

Native species interactions. A total of six mammal and five bird species were identified as confirmed (n = 5) or potential (n = 6) predators of the Velvet Scoter across the study area (Table 4), as illustrated in the Supporting Materials (Fig. S1). At Lake Tabatskuri, Armenian Gulls (Larus armenicus) breed and compete with Velvet Scoters for nesting sites, while also preying on their eggs and ducklings. Marsh Harriers (Circus aeruginosus) were observed at all lakes included in the study; however, Armenian Gulls were the most frequently observed predator at Lake Tabatskuri, the only site with ongoing and systematically monitored Velvet Scoter breeding (Fig. 4). Although nest predation contributed to a smaller portion of overall reproductive losses (estimated at 15–25%), observations indicated that 65-75% of hatchlings that entered the water died within their first day due to gull predation (N. Paposhvili, pers. obs.). Based on these findings, it is likely that similar predation levels occurred historically at other breeding lakes in the Caucasus where large Armenian Gull colonies exist.

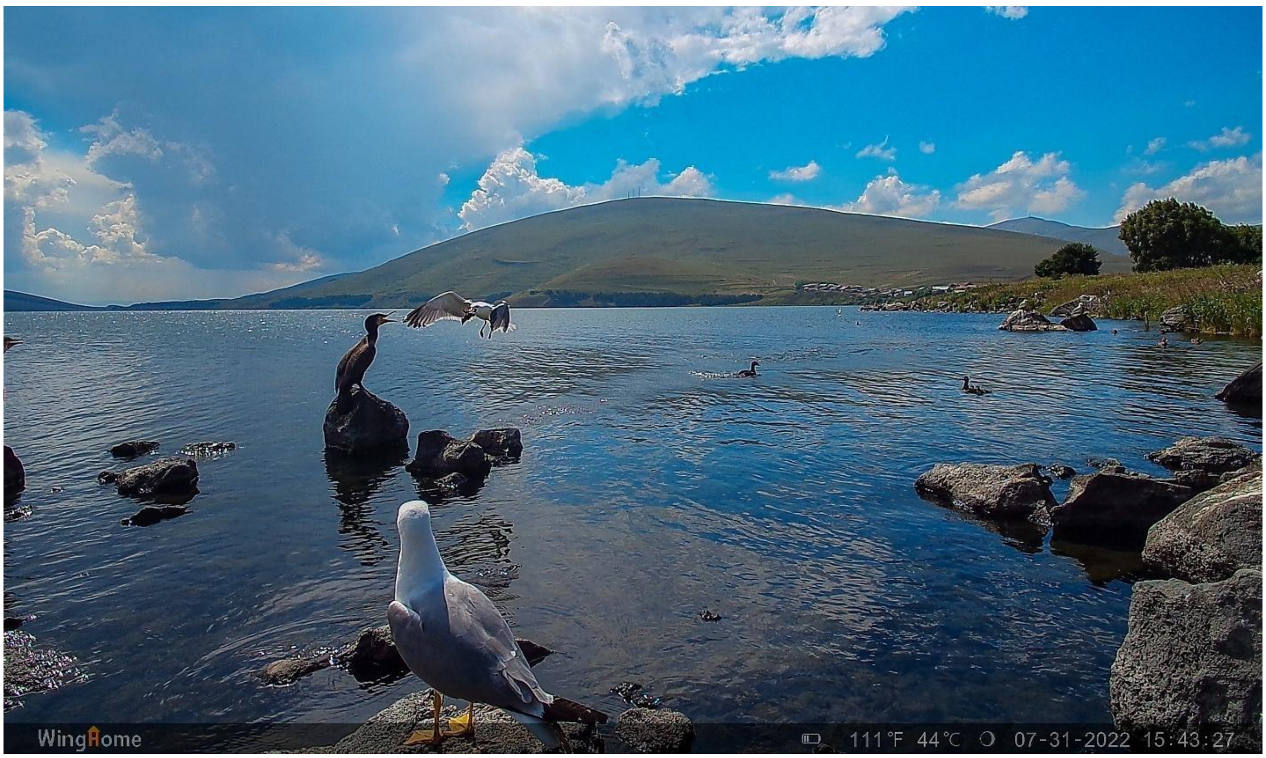

Figure 4. An Armenian Gull that has preyed on a duckling, by a Camera trap installed by N. Paposhvili.

Invasive non-native species. Several invasive aquatic species were identified across the study area, including Crucian Carp (Carassius gibelio) and Danube Crayfish (Pontastacus leptodactylus) in Lakes Aygır, Çıldır, Aktaş/Kartsakhi, and Tabatskuri, as well as Least Cisco (Coregonus albula) in Lake Tabatskuri. These species are believed to contribute to ecosystem degradation by altering ecological processes, disrupting native trophic dynamics, and changing the physicochemical properties and transparency of the water. The Black Rat (Rattus rattus) was the only invasive terrestrial nest predator of ground-nesting species recorded at breeding sites in Türkiye.

Sewage. Wastewater discharge was documented at four wetlands within the study region. The influx of pollutants from these discharges increases nutrient availability, leading to eutrophication and ecosystem degradation, which may negatively affect food resources and the overall health of Velvet Scoter populations. However, because there is limited information about the amount and frequency of these discharges, it is difficult to fully evaluate their long-term effects on water quality and prey availability for the species.

Nutrient loads. Besides direct sewage input, nutrient enrichment from agricultural fertilizer runoff and livestock manure was observed at multiple wetlands. This excess nutrient input encourages eutrophication, resulting in habitat degradation and a loss of ecological balance, which can harm aquatic productivity and water quality.

Herbicides and pesticides. Most wetlands in the study area are bordered by farmland, where the widespread use of herbicides and pesticides causes chemical runoff into nearby ecosystems. These pollutants, which can also seep into groundwater feeding into lakes, lead to habitat deterioration and declines in populations of sensitive aquatic invertebrates. The decrease in invertebrate numbers reduces an important food source for the Velvet Scoter and other waterfowl species.

Garbage and solid waste. Pollution from garbage and solid waste deposited in lakes and on breeding islands poses serious risks to Velvet Scoters through both direct injury and mortality. Discarded materials can entangle the birds' legs, necks, and wings, while ingestion of non-food waste items mistaken for prey may result in internal injuries or toxic effects.

Agricultural disturbance. Agricultural machinery and farming activities, particularly around Lake Tabatskuri, can disturb breeding Velvet Scoters. Newly hatched ducklings depend on shallow, crustacean-rich shoreline habitats for feeding, and disturbance near these critical foraging areas can hinder effective feeding behaviour and reduce overall breeding success.

Drought. Extended periods of drought, exceeding natural variation, contribute to ecosystem degradation by lowering water levels and diminishing the availability of breeding and feeding habitats. A historical example occurred at Lake Sevan, where excessive water abstraction caused the loss of suitable habitats for Velvet Scoter reproduction and foraging. Similar impacts may occur at other sites under increasingly arid climatic conditions; however, as long as these habitats do not completely desiccate, the overall impact may remain limited.

Viral diseases. Outbreaks of highly pathogenic avian influenza (H5N1) have been documented globally in the Velvet Scoter and related species such as Stejneger's Scoter (Melanitta stejnegeri) (Melville & Shortridge, 2006). Although no mortality attributable to avian influenza has been reported within the Caucasus region, the virus remains a potential risk factor for the population.

Climate change. Reduced snow accumulation and shorter snow-cover duration compared to historical conditions alter meltwater inflows to lakes, thereby changing their physicochemical properties. Climate change may also disrupt trophic relationships within aquatic ecosystems, reducing prey availability and threatening long-term population stability. Consequently, it is regarded as an emerging but significant potential risk for the Velvet Scoter in the Caucasus.

Threat ranking. Assessment of the sixteen identified threats to the Velvet Scoter and its habitats in the Caucasus region classified four as critical, three as high, four as medium, and five as low in overall impact (Table 5). The most significant threat, interactions with native species (particularly predation), received the lowest cumulative rank score and was recorded at all thirteen surveyed sites. Other critical threats included fishing (documented at eight sites), hunting and egg collection (eleven sites), and recreational disturbance (twelve sites) (Table 3). The potential impacts of climate change could not be fully quantified, and evidence for viral diseases within the region remains insufficient; thus, these two threats were excluded from the quantitative threat-ranking analysis.

Table 5. Ranking of threats to Caucasus Velvet Scoter population. Red = critical; orange = high; yellow = medium, green = low, determined by a combination of raw score calculated for each threat and the authors' knowledge of the region (see Methods).

Threats	Scope	Severity	Urgency	Raw score	Ranking score
Grazing & ranching	12	5	8	25	6
Hunting & collecting eggs	3	1	4	8	3
Cutting & collecting terrestrial plants	16	6	6	28	11
Fishing	8	4	3	15	4
Recreational activities	2	3	2	7	2
Scientific research	14	15	15	44	15
Abstraction of surface water	9	13	13	35	12
Dams	15	16	16	47	16
Native species interactions	1	2	1	4	1
Invasive non-native species	11	8	7	26	7
Sewage	13	12	10	35	13
Nutrient loads	4	11	12	27	9
Herbicides & pesticides	5	10	11	26	8
Garbage & solid waste	6	7	5	18	5
Agricultural disturbance	10	9	9	28	10
Drought	7	14	14	35	14

Discussion

The analysis of recent field surveys, direct observations, and published sources confirms that the small, isolated Caucasian population of the Velvet Scoter has experienced a significant decline from approximately 150 nesting pairs across thirteen presumed breeding sites in the mid-1960s to about fifty pairs remaining at a single lake in Georgia, where the population persists largely due to intensive conservation efforts. Although thirteen lakes within the Caucasus were identified as potential breeding sites based on literature and observational records (Adamian & Klem, 1999; Dahl, 1954; Eken et al., 2006; Janashvili et al., 1960; Kirwan et al., 2008; Kutubidze, 1985; Lyaister & Sosnin, 1942; Magnin & Yarar, 1997; Matcharashvili et al., 2004; Paposhvili, 2018, 2021; van der Ven & Gheyselinck, 1982; Vielliard, 1968; Yarar, 1995), subsequent verification confirmed breeding activity at only seven of these sites in recent times namely Aktaş/Kartsakhi, Balık, Nemrut Caldera, Sevan, Khanchali, Saghamo, and Tabatskuri.

Historical accounts indicate that the breeding distribution of the species in Georgia formerly included Lakes Saghamo, Paravani, Khanchali, Bughdasheni, Madatapa, Aktaş/Kartsakhi, and Tabatskuri on the Javakheti Plateau during the second half of the twentieth century (Gavashelishvili, 2005; Kutubidze, 1985; Matcharashvili et al., 2004). Breeding pairs were reported at Lakes Khanchali, Bughdasheni, and Madatapa as recently as the early 2000s (Matcharashvili et al., 2004), with estimated numbers of 10-20 pairs at Lake Khanchali and smaller numbers at the other two. However, no direct evidence of nesting was obtained at either Bughdasheni or Madatapa, and these sites are therefore regarded as unconfirmed breeding locations. By the early 2010s, the Velvet Scoter was presumed to be extirpated from Georgia until its rediscovery in 2014 at Lake Tabatskuri (Toriashvili, 2023). Currently, Lake Tabatskuri stands as the only active breeding site for the species in Georgia and the entire Caucasus region (Paposhvili, 2018, 2021; Paposhvili et al., 2023).

In Türkiye, the breeding activity of the Velvet Scoter has been reported at five alpine lakes Aktaş, Çıldır, Aygır, Balık, and Nemrut Caldera located in northeastern and eastern Anatolia (Boyla et al., 2025; Eken et al., 2006; Kirwan et al., 2008). At Lake Aktaş, which straddles the Türkiye–Georgia border, all known breeding islands are on the Turkish side. Although Lake Aygır was identified as a potential breeding site by Eken et al. (2006), no definitive evidence of Velvet Scoter breeding behaviour has been observed there. The lake likely served only as a stopover site before or after breeding, providing a resting and foraging area prior to dispersing elsewhere. The lack of islands at Lake Aygır further supports the idea that it was not a regular breeding site.

Despite this, observations of ducklings at Lake Khanchali (G. Darchiashvili, pers. obs.), where no islands are present, suggest that some breeding may have occurred within rocky shoreline vegetation. Although evidence is limited, such nesting behaviour would be an exceptional case for the Caucasian population.

Lake Çıldır, about 11 km from Lake Aktaş (a confirmed historical breeding site), has small islands that seem suitable for breeding. However, limited historical observations make it hard to confirm if the lake was ever used for this purpose. Other Anatolian wetlands, including Enkaya Pond and Lake Nazik (eBird, 2024), showed no evidence of Velvet Scoter breeding, either historically or currently, thus they were excluded from the assessment. Overall, the available data suggest that the Turkish breeding population did not persist into the 21st century (current study; Boyla et al., 2025). Nonetheless, the Velvet Scoter still winters regularly along Türkiye's Black Sea coast (Boyla et al., 2025; eBird, 2024; Furtun et al., 2021).

In Armenia, confirmed breeding has only been recorded at Lake Sevan, with unconfirmed reports from Lake Arpi (Adamian & Klem, 1999). As in Türkiye, the Armenian breeding population appears to have disappeared by the early 2000s. The population at Lake Sevan probably vanished during the 1970s after water levels dropped by 19 meters (Vardanian, 2009), causing various ecological disturbances. The reduced water level likely lowered oxygen levels in parts of the lake, impacting zooplankton populations, while also allowing terrestrial predators to access nesting areas that were once insular. Additionally, exposing the former breeding island made it easier for tourists to access the Sevanavank Monastery, increasing disturbance pressures. The Velvet Scoter population at Lake Arpi also disappeared in the late 20th century.

Although multiple sources have documented the extremely small size of the Velvet Scoter population in the Caucasus and its rapid regional decline (BirdLife International, 2020; Paposhvili, 2018, 2021), the underlying causes of this decline have not been thoroughly assessed across the entire region before. This study aimed to fill that gap by identifying the main factors driving the species' decline and suggesting possible mitigation strategies. The analysis identified sixteen specific direct threats to the Velvet Scoter and its breeding habitats across various sites throughout the Caucasus, both historically and currently. Some of these threats are supported by direct field evidence, while others remain inferred or hypothetical. Among these, four threats, native species interactions, recreational activities, hunting and egg collection, and fishing were deemed critical, putting significant pressure on the population.

It is important to note that the apparent ranking of these threats may be influenced by methodological limitations, as the impact of specific pressures varies greatly depending on the site. For example, the sharp reduction of water levels at Lake Sevan, Armenia, clearly played a role in the local extinction of the species there. In contrast, a recent 1 meter drop in water level at Lake Tabatskuri during 2022-2023 created small temporary islands that offered additional nesting sites, with one or two Velvet Scoter pairs successfully breeding during those years. When water levels rose again in 2024, these newly formed islands became unsuitable for nesting (N. Paposhvili, pers. obs.). These examples highlight how ecological pressures can depend heavily on the specific context.

All confirmed and potential predators of the Velvet Scoter are listed in Table 4, but the Armenian Gull appears to be the most influential. This species typically breeds in dense colonies (200-250 nests) on lake islands, leading to direct competition for nesting habitat with Velvet Scoters and exerting significant predation pressure on unattended eggs and hatchlings, which ultimately reduces reproductive success (Kiknavelidze et al., 2024). However, nesting gulls may also provide indirect protection for incubating females by deterring attacks from Marsh Harriers, which not only prey on eggs but are also known to kill incubating females (Paposhvili, 2021; Paposhvili et al., 2023).

Losing an adult female to predation has a much greater demographic impact than losing eggs or ducklings, as the latter naturally face high mortality rates and low first-winter survival. Therefore, completely removing Armenian Gulls might not solve the problem of predation. A balanced management approach might be better, maintaining gull numbers at levels that reduce direct predation while still providing the protective "umbrella effect" their colonies offer against raptor attacks. It's also worth noting that the population of Armenian Gulls was estimated to be 10-15 times smaller in the 1980s and 1990s than it is today, both at Lake Tabatskuri and across southern Georgia (A. Abuladze, pers. obs).

Fisheries operations have multiple negative impacts on the breeding ecology of the Velvet Scoter. Mortality and injury can occur due to entanglement in static or lost fishing nets, while active fishing from boats causes recurrent disturbance to nesting and brood-rearing behaviour. For instance, frequent passage of fishing boats can disperse broods, leaving females unable to adequately protect their ducklings from aerial predators like Armenian Gulls (Larus armenicus). Although such disturbances are unintentional, they nevertheless impose significant negative impacts on breeding success. At Lake Tabatskuri, landing by fishers and the collection of eggs from islands have been substantially reduced through sustained local conservation initiatives; however, mortality associated with bycatch remains a persistent threat (Paposhvili, 2021). Recreational activities on the islands during the breeding season have also dropped notably alongside fishing-related disturbances, thanks to effective community involvement. Nonetheless, both threats still pose risks due to limited enforcement of existing protective measures. Establishing no-fishing and no-recreational-boating zones within the lake, enforcing seasonal restrictions on boat movement during the Velvet Scoter's breeding period, and strictly regulating these measures are crucial for the long-term conservation of the species at Lake Tabatskuri.

Between the late twentieth and early twenty-first centuries, the freshwater crustacean Danube Crayfish (Pontastacus leptodactylus) and the fish species Crucian Carp (Carassius gibelio) were introduced into several former and current breeding sites of the Velvet Scoter, including Lakes Aygır, Çıldır, Aktaş/Kartsakhi, and Tabatskuri. During the same period, another non-native species, the Least Cisco (Coregonus albula), was introduced into Lake Tabatskuri. These introduced aquatic species are likely to impact the Velvet Scoter population in two main ways: competing for food resources and degrading water quality. Their feeding and burrowing activities increase water turbidity, damage submerged plant communities, and raise nitrogen and phosphorus levels, which together promote eutrophication and poorer water quality. These changes can negatively affect the distribution and number of macroinvertebrates important food sources for the Velvet Scoter (e.g., Nummi et al., 2016; Maceda-Veiga et al., 2017).

The introduction of these species might also have had indirect benefits, as adult Velvet Scoters at Lake Tabatskuri have been seen feeding on crayfish and other prey (N. Paposhvili, pers. obs.). However, because detailed ecological data are lacking, these non-native species should be regarded as potential competitors, as they might eat amphipods (Gammarus sp.), which are vital for ducklings' diet (N. Paposhvili, pers. obs.). Meanwhile, predation by fish-eating birds like the Great White Pelican (Pelecanus onocrotalus), Dalmatian Pelican (Pelecanus crispus), and Great Cormorant (Phalacrocorax carbo) all of which have recently colonized some of these lakes seems to be reducing the populations of the introduced species. Additionally, fishing activities further help control or limit these non-native fish and crayfish populations.

The extent to which non-native fish and crayfish compete with Velvet Scoters for food resources remains complex and poorly understood. In recent years, for unknown reasons, introduced crayfish populations have disappeared from Lakes Tabatskuri and Kartsakhi, while fish populations have also declined, likely due to overfishing. Without systematic ecological research and long-term monitoring, it is impossible to accurately assess the impact of both native and introduced species or the cumulative effects of fisheries on the local abundance and reproductive success of Velvet Scoters in the Caucasus. Comprehensive studies of the species' diet, along with assessments of aquatic invertebrate and vertebrate communities (their composition, diversity, and abundance) across current and former breeding lakes, are therefore essential. Such research would clarify interspecific interactions and might help explain why the Velvet Scoter now persists exclusively at Lake Tabatskuri within the entire Caucasus region.

Field assessments showed that many previously occupied breeding sites displayed signs of water quality decline and increasing eutrophication. Past research has proven that Velvet Scoter populations decrease as eutrophication worsens (Rönkä et al., 2005). Reducing or managing nutrient inputs, herbicide and pesticide runoff, and excessive water use from agricultural and pastoral activities, along with controlling pollution from sewage, garbage, and solid waste in nearby rural communities, is vital to prevent further habitat loss and deterioration. However, achieving this requires ongoing cooperation and involvement from local communities.

Even after the sources of poor water quality are addressed, rapid ecosystem recovery should not be expected, especially in closed inland basins where water turnover is slow and restoration is inherently complex. Additionally, the ongoing presence of invasive aquatic species continues to worsen eutrophication and hinder water quality improvement. In such cases, biomanipulation, the intentional modification of aquatic food webs to restore ecological balance, should be considered as part of a comprehensive conservation plan. Several successful examples from Türkiye highlight the potential effectiveness of this method (Beklioğlu et al., 2003; Beklioğlu & Tan, 2008). At the same time, implementing systematic monitoring programs is crucial for assessing the long-term success of conservation efforts and guiding adaptive management of the remaining habitats for the Velvet Scoter.

The findings of this study show that a mix of human-related pressures and interactions between species has caused the decline of the Velvet Scoter across the Caucasus, leading to its disappearance from all historical breeding sites except Lake Tabatskuri. While all the threats identified likely played some role, the most significant factors seem to have been native species interactions, recreational disturbance, hunting, egg collection, and fishing. Interestingly, several of these pressures are still active at Lake Tabatskuri, the only location where the species still breeds. Notably, out of the sixteen main threats studied, Lake Tabatskuri is currently impacted by thirteen, highlighting the complexity of the pressures affecting the species' survival.

This pattern indicates that the true causes of local extinctions at other sites may involve additional factors that could not be fully evaluated due to limited data. Such unmeasured or hidden drivers might have historically had deadly effects on the species or continue to have subtle, overlooked impacts. Additionally, ongoing threats like poaching and habitat destruction including potential disturbance or loss of the remaining breeding island may gradually weaken the resilience of the surviving breeding population.

Thorough site-specific data collection and analysis are essential to identify the ecological and environmental factors that influence habitat suitability, especially for nesting sites and brood-rearing food sources. These studies will assist in assessing the feasibility of restoring former breeding sites to support recolonization. Importantly, any efforts to re-establish the Velvet Scoter beyond Lake Tabatskuri must first address and eliminate the causes of past local extinctions. Simultaneously, protecting the remaining population at Lake Tabatskuri should be a top conservation priority. Ensuring the security of both breeding and wintering habitats is vital to stabilizing the current population, increasing reproductive success, and potentially allowing natural recolonization of former breeding areas that still fulfil the species' ecological needs.

Although the Caucasian Velvet Scoter population has often been described as isolated from the main breeding population (Carboneras et al., 2020; Paposhvili, 2021), recent genetic analyses indicate otherwise. Paposhvili et al. (2023) demonstrated that despite the substantial geographic distance between the Baltic and Caucasus breeding populations, both are likely to represent geographically distinct yet genetically connected segments of a single panmictic population. It is hypothesized that shared wintering grounds in the Black Sea provide opportunities for pairing between individuals from the two breeding regions, thereby facilitating gene flow through migratory exchange between the Baltic and the Caucasus (Paposhvili et al., 2023). The absence of clear genetic differentiation between the Caucasian and Baltic populations suggests two key implications: (i) natural recolonization of suitable sites in the Caucasus remains a realistic possibility, and (ii) reintroduction efforts using birds from genetically similar local stocks would be biologically appropriate. However, some historically occupied habitats no longer meet the essential ecological requirements of the species, for example, the lack of suitable breeding islands at Lake Sevan prevents its immediate restoration as a nesting site. Whether recolonization occurs naturally or through reintroduction, the central question remains: what ecological and environmental conditions are necessary to support successful recolonization? Addressing this requires detailed ecological research aimed at identifying the factors supporting the continued survival of the species at Lake Tabatskuri. Insights from such studies are crucial for guiding restoration and management plans at other potential sites in the Caucasus. Given the Velvet Scoter's migratory ecology and dependence on marine wintering habitats, any conservation or reintroduction program must also account for the conditions of the species' wintering grounds. With limited resources available for conservation across the region, documenting threats and implementing effective protection measures in the Black Sea wintering areas are critically important. While bycatch and poaching are recognized as major direct causes of mortality, the broader impacts of marine ecosystem degradation in the Black Sea are poorly understood and urgently need investigation to inform future conservation efforts for the Velvet Scoter.

Conclusions

Comprehensive conservation planning is now necessary across the Velvet Scoter's former breeding range, emphasizing coordinated research at all current, historical, and potential breeding sites. Conservation planning should aim to identify the specific factors limiting reestablishment and to develop targeted management strategies that reduce these threats and improve conditions for natural recolonization or reintroduction. Each site proposed for conservation must be evaluated based on the species' ecological needs especially the presence of secure breeding islands and the practicality of managing human disturbance effectively. A major knowledge gap in the Caucasus remains the limited understanding of the species' diet, prey availability, and access to foraging resources. Research in these areas is crucial to guide habitat management and restoration elsewhere, informed by ecological insights from the surviving population at Lake Tabatskuri. Conservation efforts also need to go beyond the breeding season to include stopover and wintering sites, helping to understand the ecological links between Caucasus breeders and Velvet Scoters overwintering in the Black and Caspian Seas. Since the species is fully migratory, an integrated full-year-cycle approach is essential to addressing both breeding challenges and threats during migration and wintering. This comprehensive approach will create a framework for sustaining and ultimately restoring the Velvet Scoter population in the Caucasus region.

Overall conclusion

The Velvet Scoter Melanitta fusca in the Caucasus is one of the most endangered and ecologically unique parts of the species' global range. This research clarifies the ecological factors, behavioural adaptations, and genetic links that help this relict population survive at Lake Tabatskuri, Georgia - the species' last breeding refuge in the region. The studies show that the population's survival depends on a delicate balance between habitat quality, interactions with other species, human disturbance, and migratory connectivity on a larger scale. This highlights the urgent need for coordinated ecosystem-level conservation efforts.

Long-term field observations revealed that despite fluctuations in the number of breeding pairs, the Velvet Scoter population at Lake Tabatskuri has gradually increased since 2017. This growth aligns with the implementation of direct conservation actions such as community outreach, protection of nesting islands, and seasonal fishing restrictions. These efforts successfully eliminated egg collection and minimized human disturbance on the island, leading to higher nesting density and improved hatching success. However, reproductive output remains highly variable and generally low compared to northern populations. The main cause of duckling mortality is predation by Armenian Gulls (Larus armenicus), whose growing population across the Javakheti Plateau continues to be a challenge. Marsh Harriers (Circus aeruginosus) also contribute to nest losses, especially when gull numbers decline and their usual "umbrella" effect against raptors weakens. This paradox highlights the complex, non-linear ecological relationships that influence the breeding success of the Velvet Scoter in the Caucasus.

Behavioural and nest-level analyses indicate that nesting success is heavily influenced by nest arrangement, vegetation cover, and predator activity. Typical clutch sizes ranged from eight to nine eggs, similar to other Palearctic populations while hatching success increased in years with less gull predation and fewer disturbances. Camera trap observations provided new insights into female defensive behaviour, showing frequent threat displays and occasional aggression toward potential predators. Importantly, deploying cameras did not lower nesting success and proved to be an effective, non-invasive method for studying incubation behaviour and predator interactions. Dump nesting, observed at some sites, probably reflects both limited space and parasitism among conspecifics under rising population pressures, emphasizing the need to expand suitable nesting areas on the island.

From a regional perspective, this research confirmed a significant historical reduction in the Velvet Scoter's breeding range across the Caucasus. Once widespread across at least a dozen lakes in Georgia, Armenia, and Türkiye, the species now exists at only a single site. The decline of these local populations is linked to habitat degradation, human exploitation, eutrophication, and biological interactions with expanding gull populations. Many of these threats are still present today at Lake Tabatskuri, where thirteen of the sixteen regionally identified pressures remain active. The combined impact of these pressures has made the Tabatskuri population highly vulnerable to random events and demographic collapse.

Despite this ecological isolation, genetic analyses showed that the Caucasian population is not genetically distinct from northern Velvet Scoters. Mitochondrial and microsatellite markers revealed no significant population differentiation, indicating ongoing or recent gene flow between northern and Caucasian breeding groups. This connectivity is likely maintained through shared wintering grounds in the Black Sea, where individuals from both regions congregate and pair before migrating to breeding sites. Male-mediated dispersal may be essential in maintaining genetic exchange, counteracting inbreeding, and supporting population resilience. The absence of genetic isolation offers hope for the species' recovery, as it suggests that recolonization of suitable sites in the Caucasus could happen naturally or be supported through reintroduction from genetically compatible northern stocks.

Collectively, these results highlight the importance of adopting an integrated, full-year conservation strategy. Effective protection of the Velvet Scoter cannot be limited to the breeding season or a single lake; it requires coordinated management of breeding, migratory, and wintering habitats across borders. Conservation efforts should focus on maintaining and enhancing the ecological health of Lake Tabatskuri while also identifying and protecting key stopover and wintering sites along the Black Sea coast. Main management priorities include: (1) controlling human access and boat disturbances during nesting and brood-rearing periods; (2) maintaining a balanced Armenian Gull population that reduces direct predation but still deters raptors; (3) restoring and expanding suitable nesting habitats by removing excessive vegetation and creating new small islands; (4) reducing bycatch through targeted fishing-free zones and engaging local communities; and (5) improving water quality with sustainable management and pollution control. At the same time, long-term ecological monitoring should be established to assess the success of these efforts and to detect early signs of environmental decline.

Although the genetic results suggest that the Caucasian Velvet Scoter is not an isolated evolutionary unit, this should not lead to complacency. The species' survival in the Caucasus depends on maintaining demographic stability at Lake Tabatskuri and ensuring ongoing gene flow through migratory connectivity. Given the small population size, even small environmental disruptions or policy failures could cause a rapid decline. Therefore, conservation efforts must follow a cautious approach, combining habitat protection with adaptive management, regional cooperation, and community-based stewardship.

Future research should focus on measuring prey availability, dietary composition, and food web dynamics within breeding and wintering habitats, as these remain some of the most important gaps in knowledge. Understanding trophic relationships will not only clarify the ecological factors influencing breeding success but also help guide the restoration of former breeding lakes. Expanding genomic analyses with high-resolution techniques like ddRAD sequencing will improve assessments of population structure, reveal the extent of male-mediated gene flow, and inform potential translocation or supplementation efforts. Combining ecological, genetic, and socio-economic perspectives will be crucial for ensuring the long-term survival of the Velvet Scoter as a breeding species in the Caucasus.

In conclusion, this research provides the first comprehensive synthesis of the Velvet Scoter's breeding ecology, genetic connectivity, and conservation status in the Caucasus. It shows that although the species maintains genetic links with its northern populations, its local survival depends on careful ecological balances and ongoing human support. The recovery of the Velvet Scoter at Lake Tabatskuri highlights the success of locally led conservation efforts rooted in strong science and community involvement. However, its limited current range serves as a warning that losing this single population could lead to the species' extinction as a breeder in the entire region. Protecting this population is, therefore, crucial not only for conserving a species but also for preserving a vital part of the Caucasus's natural heritage.

Postdoctoral Study

Building on this doctoral research, the postdoctoral study will examine the migratory connectivity of the Velvet Scoter (Melanitta fusca) population breeding at Lake Tabatskuri. Using light-level loggers and GPS trackers, it will identify the species' wintering grounds and migratory routes throughout the annual cycle. At the same time, high-resolution genomic analyses (ddRAD sequencing) will evaluate population structure, genetic diversity, and connectivity across the species' range. The studies have already begun in collaboration with Aarhus University (Denmark) and the University of Nebraska (United States) and will continue for at least one year beyond completion of the PhD. The findings will enhance understanding of the species' ecology and contribute to evidence-based conservation strategies across its range.

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Supporting Materials I

Seasonal abundance and breeding biology of Velvet Scoter Melanitta fusca at Lake Tabatskuri, Georgia

Table S1. Clutch size and hatching success for all Velvet Scoter nests found at Tabatskuri Lake, Georgia during summer 2017-2020. While it is generally difficult to determine the fledging success of individual nests, nine ducklings ultimately fledged at the site from 31 hatched eggs in 2017 (29%). However, due to observer inexperience, this may not fully reflect reality as well as in other years. In comparison, four ducklings fledged from 114 hatched eggs (4%) in 2018; five ducklings fledged from 100 hatched eggs (5%) in 2019; and 39 ducklings fledged from 146 hatched eggs (27%) in 2020.

Nest Code	Clutch Size	Hatched
1/2017	10	8
2/2017	8	5
3/2017	8	4
4/2017	7	4
5/2017	7	5
6/2017	8	5
Total in 2017	48	31 (65%)
1/2018	7	5
2/2018	3	0
3/2018	8	6
4/2018	6	5
5/2018	9	7
6/2018	11	8
7/2018	15	8
8/2018	7	2
9/2018	8	7

10/2018	7	0
11/2018	9	9
12/2018	10	9
13/2018	12	0
14/2018	13	0
15/2018	16	0
16/2018	9	7
17/2018	9	5
18/2018	9	8
19/2018	11	9
20/2018	8	7
21/2018	9	0
22/2018	10	7
23/2018	7	5
Total in 2018	213	114 (54%)
1/2019	9	4
2/2019	7	3
3/2019	8	8
4/2019	9	7
5/2019	4	0
6/2019	5	0
7/2019	9	8
8/2019	9	7
9/2019	8	6
10/2019	7	0
11/2019	7	5
12/2019	8	0

13/2019	8	8
14/2019	6	0
15/2019	9	0
16/2019	8	6
17/2019	7	0
18/2019	13	0
19/2019	6	2
20/2019	6	0
21/2019	8	4
22/2019	5	0
23/2019	9	6
24/2019	11	8
25/2019	10	3
26/2019	11	10
27/2019	7	5
28/2019	9	0
29/2019	8	0
30/2019	7	0
31/2019	8	0
32/2019	19	0
33/2019	15	0
Total in 2019	280	100 (36%)
1/2020	9	5
2/2020	9	0
3/2020	8	6
4/2020	9	5
5/2020	10	8

6/2020	11	7
7/2020	4	0
8/2020	9	6
9/2020	9	6
10/2020	11	0
11/2020	12	0
12/2020	9	8
13/2020	9	7
14/2020	11	9
15/2020	11	9
16/2020	8	5
17/2020	22	0
18/2020	9	6
19/2020	9	5
20/2020	8	0
21/2020	3	1
22/2020	9	7
23/2020	10	0
24/2020	9	6
25/2020	12	8
26/2020	15	9
27/2020	9	8
28/2020	8	6
29/2020	8	6
30/2020	9	3
31/2020	7	0
Total in 2020	296	146 (49%)

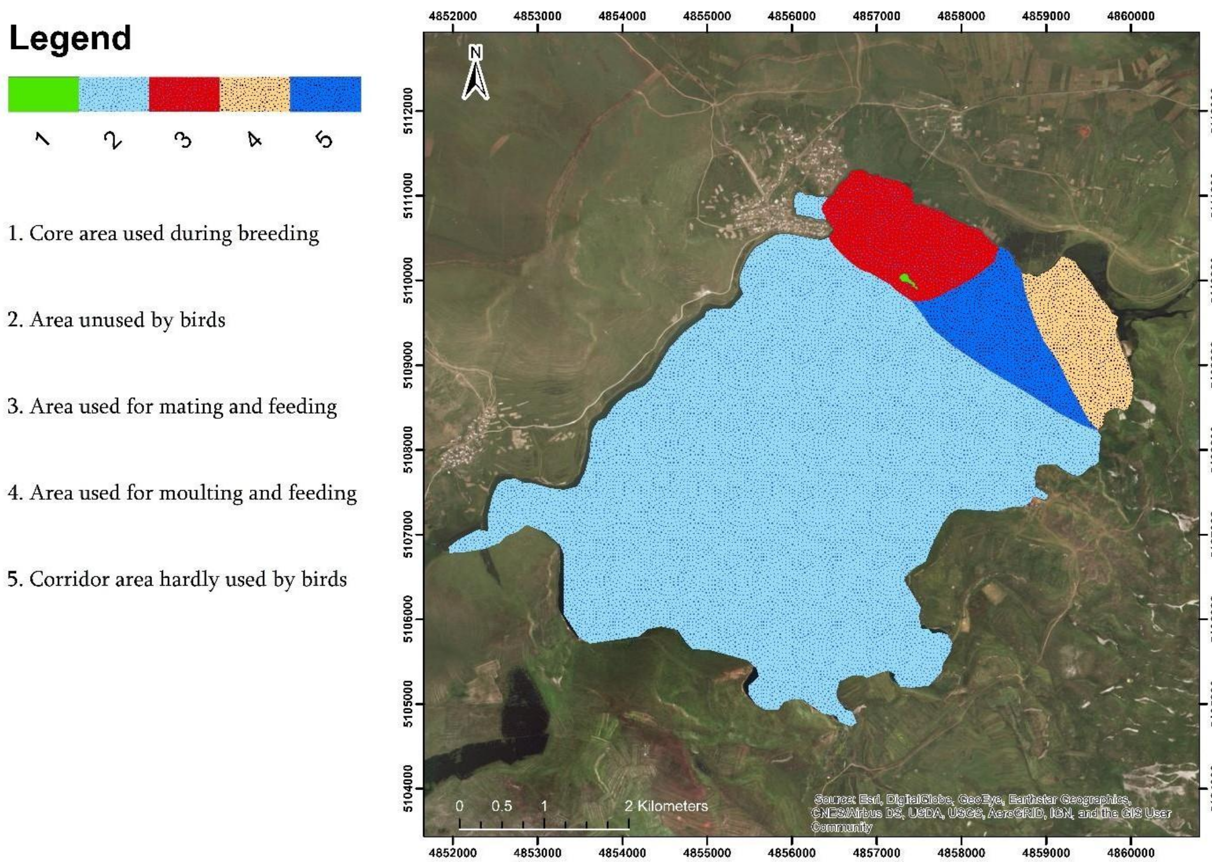

Figure S1. Map of Tabatskuri Lake showing the five main areas of the lake and their differential use by Velvet Scoters during different periods of the summer. Scoters were not seen in the light blue areas during the surveys in 2017–2020.

Supporting Materials II

Nesting behaviour and factors affecting reproductive success of Velvet Scoter Melanitta fusca breeding at Lake Tabatskuri, Georgia

Annex S1. Supplementary text relating to the 16th camera trap

The 16th camera trap, which was not used in our analysis of the factors affecting the reproductive success of Velvet Scoters Melanitta fusca breeding at Lake Tabatskuri, Georgia, was installed less than 35 cm from the nest and operated in video mode (while all the others were placed 70-90 cm away from the nests, camouflaged, and used picture mode). The female was initially very wary upon returning to this nest and did not settle, but after several attempts, returning multiple times, she finally resumed incubation. However, she remained very nervous and was highly aggressive toward the camera, attacking and hitting it twice. From the day after deployment, she appeared less nervous but continued to intermittently hiss at the camera during incubation. During this period, another female scoter visited and occupied this nest for two hours (details described below), showing no interest in the camera trap. Despite these disturbances, the breeding attempt was successful, with four of nine eggs hatching. Still, due to the frequent disturbances caused by the camera's proximity, the video mode, and the presence of another female, this nest was excluded from our analysis of the impact of camera traps on nesting success.

Annex S2. Supplementary text relating to other scoters visiting nests during incubation

In addition to Armenian Gulls Larus armenicus and Marsh Harriers Circus aeruginosus, the camera traps revealed that nest visitors included other scoters on two occasions at nest no. N1 (in 2019) and nest no. N24 (in 2019).In one instance, when the incubating female was absent and the eggs were left uncovered, a second female scoter with five ducklings visited and sat on the eggs with her own ducklings. After 1.4 hours, the original nest owner returned, tried to reclaim her nest, but was strongly displaced by the second bird (leg rings and loggers helped distinguish between the two females). Five minutes later, the second female covered the eggs with down and attempted to lead her ducklings to the shore. When the ducklings failed to follow, the second female resumed incubation. Returning 15 minutes after her first visit, the original female again tried to reoccupy the nest, when the second female departed with her ducklings in the direction of the shore. The second female returned 10 min later, without ducklings, at which point the resident female defended her nest vigorously and chased the intruder away, after which she did not appear again. Two days later, the owner successfully hatched four ducklings out of nine eggs; of the remaining five eggs, one contained a dead embryo and four were addled. In a second case, three unattended scoter ducklings visited a nest, when the female sitting on the nest accepted them and proceeded to brood them, leaving the nest 9 h later. The female continued to incubate her own eggs, and three days later, she hatched eight ducklings from 11 eggs; with the remaining three eggs, one had a dead embryo and two were addled.

Table S1. Clutch size and hatching success for all Velvet Scoter nests found at Tabatskuri Lake, Georgia in the summers of (a) 2019, (b) 2020 and (c) 2021. Nests 1/2019, 7/2019, 19/2019, 21/2019, 23/2019, 24/2019, 26/2019, 6/2020, 24/2020, 29/2020, 30/2020, 2/2021, 7/2021, 9/2021, 19/2021, 26/2021 are the nests where the camera traps were installed.

(a) Summer 2019

Nest code	Clutch size	Hatched	Addled	Suffocated	Predated
1/2019	9	4	4	1	0
2/2019	7	3	3	1	0
3/2019	8	8	0	0	0
4/2019	9	7	1	1	0
5/2019	4	0	0	0	4
6/2019	5	0	5	0	0
7/2019	9	8	0	0	1
8/2019	9	7	1	1	0
9/2019	8	6	2	0	0
10/2019	7	0	0	0	7
11/2019	7	5	1	1	0

12/2019	8	0	0	0	8
13/2019	8	8	0	0	0
14/2019	6	0	0	0	6
15/2019	9	0	0	0	9
16/2019	8	6	2	0	0
17/2019	7	0	0	0	7
18/2019	13	0	13	0	0
19/2019	6	2	3	1	0
20/2019	6	0	0	0	6
21/2019	8	4	1	1	2
22/2019	5	0	0	0	5
23/2019	9	6	2	0	1
24/2019	11	8	2	1	0
25/2019	10	3	6	1	0
26/2019	11	10	1	0	0
27/2019	7	5	1	1	0
28/2019	9	0	0	0	9
29/2019	8	0	0	0	8
30/2019	7	0	0	0	7
31/2019	8	0	8	0	0
32/2019	19	0	19	0	0
33/2019	15	0	15	0	0
Total in 2019	280	100 (36%)	90 (32%)	10 (3%)	80 (29%)

(b) Summer 2020

Nest code	Clutch size	Hatched	Addled	Suffocated	Predated
1/2020	9	5	4	0	0

2/2020	9	0	9	0	0
3/2020	8	6	1	1	0
4/2020	9	5	4	0	0
5/2020	10	8	2	0	0
6/2020	11	7	4	0	0
7/2020	4	0	0	0	4
8/2020	9	6	3	0	0
9/2020	9	6	3	0	0
10/2020	11	0	11	0	0
11/2020	12	0	0	0	12
12/2020	9	8	1	0	0
13/2020	9	7	2	0	0
14/2020	11	9	2	0	0
15/2020	11	9	2	0	0
16/2020	8	5	3	0	0
17/2020	22	0	22	0	0
18/2020	9	6	2	1	0
19/2020	9	5	4	0	0
20/2020	8	0	8	0	0
21/2020	3	1	2	0	0
22/2020	9	7	2	0	0
23/2020	10	0	2	8	0
24/2020	9	6	3	0	0
25/2020	12	8	3	1	0
26/2020	15	9	4	2	0
27/2020	9	8	1	0	0
28/2020	8	6	2	0	0

29/2020	8	6	2	0	0
30/2020	9	3	5	1	0
31/2020	7	0	7	0	0
Total in 2020	296	146 (49%)	120 (41%)	14 (5%)	16 (5%)

(c) Summer 2021

Nest code	Clutch size	Hatched	Addled	Suffocated	Predated
1/2021	8	6	0	1	1
2/2021	10	6	2	1	1
3/2021	9	7	2	0	0
4/2021	9	8	0	1	0
5/2021	9	8	0	1	0
6/2021	10	0	10	0	0
7/2021	9	7	0	1	1
8/2021	9	6	2	0	1
9/2021	11	10	1	0	0
10/2021	9	8	1	0	0
11/2021	9	7	2	0	0
12/2021	12	0	3	5	4
13/2021	8	8	0	0	0
14/2021	12	5	2	5	0
15/2021	9	1	8	0	0
16/2021	9	9	0	0	0
17/2021	19	0	19	0	0
18/2021	2	0	2	0	0
19/2021	9	6	3	0	0
20/2021	10	4	5	0	1

21/2021	26	0	24	0	2
22/2021	11	0	0	0	11
23/2021	9	9	0	0	0
24/2021	9	7	2	0	0
25/2021	2	0	0	0	2
26/2021	8	8	0	0	0
27/2021	8	0	5	0	3
28/2021	8	8	0	0	0
29/2021	7	6	1	0	0
30/2021	8	7	1	0	0
31/2021	8	5	0	2	1
32/2021	9	8	0	1	0
33/2021	8	5	3	0	0
34/2021	8	8	0	0	0
35/2021	4	0	4	0	0
Total in 2021	325	177 (55%)	102 (31 %)	18 (5%)	28 (9%)

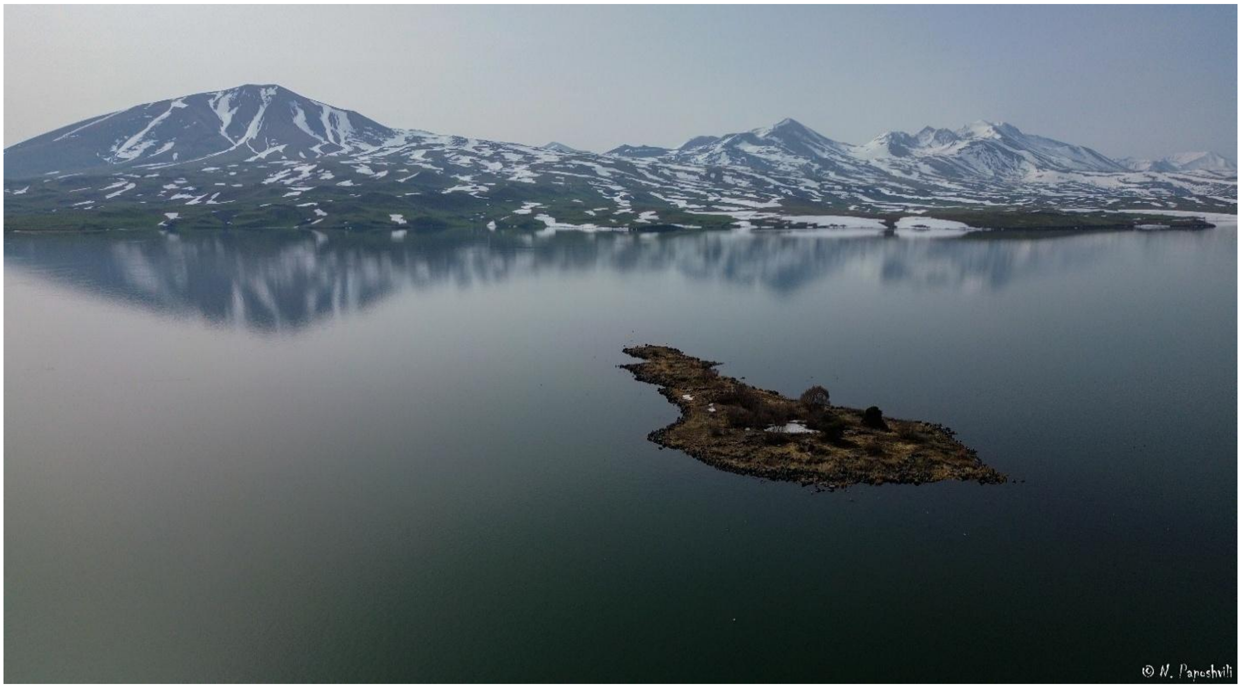

Figure S1. The island of Tabatskuri Lake, currently the only natural nesting area for the Velvet Scoter in the Caucasus. Photograph by N. Paposhvili.

Figure S2. Three observers walking closely abreast, searching the entire island intensively for Velvet Scoter nests. Photograph by N. Melikishvili.

Figure S3. Female Velvet Scoter incubating on her nest. The species exhibits strong nest-site fidelity and exceptionally high nest tenacity, with females often remaining on the nest even when potential danger approaches.

Figure S4. One of the nests where a camera trap was deployed. The female continued incubating her eggs, apparently without disturbance, and successfully hatched ducklings. Photograph from the camera trap at nest no. 24/2019.

Figure S5. A clutch which hatched successfully, with seven hatched eggshells and two unhatched eggs. Photograph by Nika Paposhvili.

Figure S6. One of the predated clutches. Photograph by Nika Paposhvili.

Figure S7. A suffocated nestling in the egg. Photograph by Nika Paposhvili.

Figure S8. Threat display (i.e. targeted opening bill/gap and hissing): (a) directed towards a threat coming from the side, and (b) when the direction of the threat is unclear. Photograph from the camera trap (a) at nest no. 2/2021 and (b) at nest no. 24/2019.

Figure S9. A female rolling her eggs. Photograph from the camera trap at nest no. 2/2021.

Figure S10. Photographs showing (a) egg predation by Marsh Harrier and then (b) the return of the female to the nest. The Marsh Harrier visited this nest twice (on 24 and 25 August) but ate only one egg on each visit. Each time, the female managed to leave the nest safely, returned 3 h and 7 h later, respectively, and finally succeeded in hatching four ducklings. Note: this nest was one of the latest ever recorded at Lake Tabatskuri, which was probably the reason why the Marsh Harrier was able to approach the island so easily because there were few Armenian Gulls present at that time of the year. Photograph from the camera trap at nest no. 21/2019.

Figure S11. Scavenging by (a) a juvenile and (b) an adult Armenian Gull, taking addled or suffocated eggs from a Velvet Scoter nest where other eggs had already hatched successfully. Photograph from the camera trap (a) at nest no. 2/2021 and (b) at nest no. 7/2019.

Figure S12. Female Velvet Scoter predated while sitting on her nest. Photograph by Nika Paposhvili (nest no. 20/2020).

Figure S13. One of the Velvet Scoter dump nests on the island in Lake Tabatskuri, Georgia. Photograph by Nika Paposhvili (nest no. 21/2021).

Supporting Materials III

Contraction of range, declines in abundance and site-based threats to Velvet Scoter Melanitta fusca breeding in the Caucasus

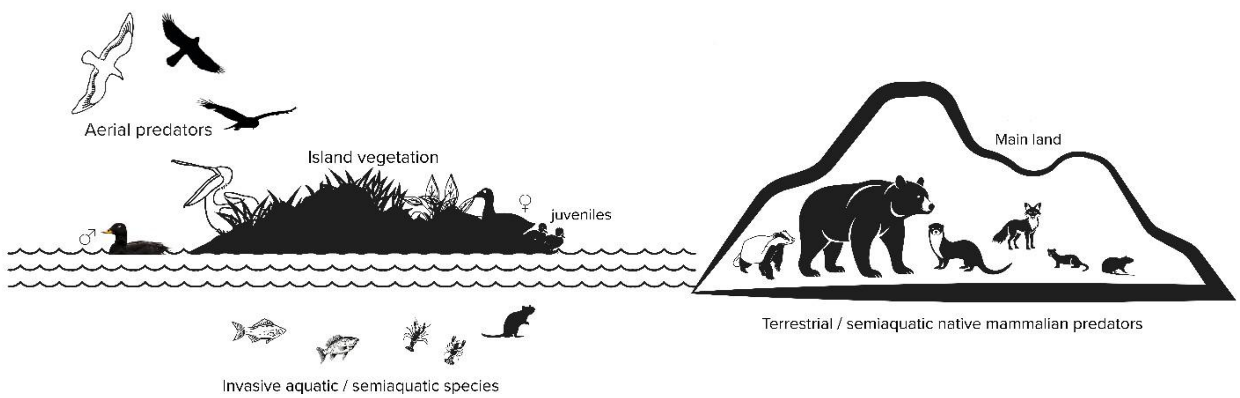

Figure S1. Visual representation of the interaction between Velvet Scoters and other taxa on the breeding grounds.

Seasonal abundance and breeding biology of the Velvet Scoter *Melanitta fusca* at Lake Tabatskuri, Georgia

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Abstract

Velvet Scoters *Melanitta fusca* From the disjunct Turkey, Georgia and Armenia nesting population were studied during 2017–2020 at what is now their last known breeding site, at Tabatskuri Lake in southern Georgia. Paired birds returned to the lake soon aFter thaw in April and Females and young remained into November in some years. Early Failing Females and most males migrate to moult elsewhere in late July, although 11–1t males remained to moult on the lake each year, departing in late September/ early October. Annual summer maxima ranged From 77–t2 individuals, typically comprised oF 43–55% Females during April–August (although inevitably Fewer during incubation). Nests were totally conFined to one island, where the number oF breeding pairs recorded ranged From 23–33 (in 2018 and 201t, respectively). Nest success (at least one duckling hatched) varied From 74% (in 2018 and 2020) to 52% (201t), recorded For 23 (2018), 33 (201t) and 31 nests (2020), although more Females were present early in the season in each year. Camera traps monitoring 11 nests recorded egg predation by Marsh Harriers *Circus aerginosus* on two occasions. Hatching success For all eggs laid was 54% (in 2018), 3G% (201t) and 4t% (2020), with overall survival oF the eggs to Fledging ranging From 2% (in 2018 and 201t) to 13% (in 2020). Duckling mortality was likely due to predation by Armenian Gulls *Larus armenicus* soon aFter hatching and to drowning in Fishing nets. Local community engagement has stopped egg collecting on the island and contributed to reduced Fishing disturbance For Velvet Scoters in the ducklings' nursery areas, when newly-hatched young are most vulnerable to gull predation. Additionally, gull numbers were lower in 2020, which also likely contributed to the improved breeding success in that year. We urge continued vigilance and Further research to conFirm the direct causes oF the Velvet Scoters' poor breeding success at the site, to improve the conservation status oF the species in the region.

Key words: conservation, habitat use, hatching success, nesting success, reproductive output.

The circumpolar Velvet Scoter *Melanitta fusca* is classiFied as Vulnerable by the International Union For Conservation oF Nature (IUCN) and is generally thought to be declining globally (BirdLiFe International 2020). The species breeds more or less continuously across Eurasia From Norway to the Yenisey River in western Siberia and winters mainly in north and northwest Europe, where it numbers 202,000–384,000 individuals (Cramp & Simmons 1t77; BirdLiFe International 2020). A small isolated relict population breeds in eastern Turkey, Georgia and Armenia, most probably wintering in the Caspian and Black Sea areas, although its abundance and annual distribution remain unknown (Dagys 201G). This group oF birds was put at < 1,500 individuals in the mid-1tt0s, with estimates more recently revised downwards to 240–420 birds, based on numbers recorded on the wintering grounds (Wetlands International 2020). A rapid drop in water levels at Lake Sevan in Soviet times caused the loss oF the Velvet Scoter nesting area there, resulting in the extinction oF the species in Armenia (Adamian & Klem 1tt7). Habitat loss, human disturbance and global warming are considered to have caused the loss oF Velvet Scoter as a breeding species in Turkey (Kirwan *et al*. 2014). Ornithologists who have made annual visits since 2012 to Formerly-occupied Velvet Scoter breeding lakes on the Anatolian plateau, Turkey, have conFirmed that they have not seen the species in this area in recent years (Ortac Onmus & Emin Yogˇurtcuogˇlu, pers. comm.). At the end oF the 20th century, the Velvet Scoter nested on almost all oF the large lakes oF the Javakheti plateau in southern Georgia (Janashvili *et al*. 1tG0; Kutubidze 1t85; Jordania *et al*. 1ttt; Matcharashvili *et al*. 2004; Gavashelishvili *et al*. 2005). In the First decades oF the 21st century, however, it disappeared From the most important lakes For waterFowl in the Samtskhe- Javakheti region (at Madatapa, Bughdasheni, Khanchali and Kartsakhi). Probable Factors responsible For the decline oF Velvet Scoters in these areas include: (1) direct habitat degradation due to increasing water consumption For the irrigation oF adjacent agriculture land; (2) mowing on the peninsulas and islands used For nesting; (3) egg collection, causing direct nest loss and disturbance; (4) eutrophication/pollution caused by agricultural intensiFication and the release oF waste water into the lakes; (5) overFishing responsible For reducing Food availability and bycatch in Fish-nets; and (G) over-harvesting (due to illegal hunting). Lake Tabatskuri is thus believed to be the last surviving breeding area For the species in Georgia and its neighbouring countries (Paposhvili 2018).

The First detailed survey oF all potential breeding lakes For Velvet Scoter on the Javakheti Plateau, Georgia, in 2017 showed that nesting (25–35 pairs) was conFined to just one traditionally occupied site, Lake Tabatskuri (41°3t'N, 43°38'E; see Paposhvili 2018). Since 2017, despite regular visits to all potential lakes on the Javakheti Plateau each spring and summer, the species was not Found elsewhere, and none were seen during visits in mid-August 2018 to Four Turkish lakes, where BirdLiFe International reports that Velvet Scoter bred in historical times (at Akta (Khozapin)

41°13'N, 43°13'E; Childir 41°03'N, 43°14'E; Aygir 40°4G'N, 43°00'E and Kuyuchuk 40°44'N, 43°27'E). All these observations, together with consultations with waterbird experts and recently published articles, strongly suggest that Lake Tabatskuri is the only remaining active breeding site For Velvet Scoter in this Formerly widely occupied region. In order to assess the potential cause oF the decline oF the Velvet Scoter in the region, and ensure the long-term survival oF the last breeding population, we thereFore launched a monitoring scheme in 2017. Here we present the preliminary results oF this monitoring programme and discuss the possibilities oF mitigating actions that could be implemented to preserve this relict population.

Methods

Study area

Lake Tabatskuri is located at 2,000 m above sea level in the Javakheti plateau region oF southern Georgia. The surFace area is 14.2 km^2, with a maximum depth oF 43 m (average depth = 15 m) and it retains a transparent, clean water column. The area experiences cold winters with snow cover extending to 150 days. Mean daily temperatures are –8°C in January and 12°C in July. The lake is surrounded by two villages (one oF which extends onto a small peninsula in the lake) and includes a 1 ha island in the northern part, which is now the only remaining breeding site For Velvet Scoters in the Caucasus. A quarter oF the island is covered with shrubs, with a Few pine, maple and birch trees, which the scoters avoid as nesting habitat.

Breeding surveys

Weekly surveys were made oF Velvet Scoters at Lake Tabatskuri From late April to November, each year From 2017 onwards, to count the numbers present For assessing changes in local abundance, record the adult sex ratio and to collect data on their reproductive success (Figs. 1 & 2). The scoters start laying eggs at the site in mid-June. By late June, most (iF not all) oF the breeding Females are already incubating eggs, so each summer 2–3 observers walking closely abreast searched the entire island intensively For nests in late June–early July. GPS coordinates were recorded For all nests Found (Fig. 3), along with the number oF eggs in each clutch (Supporting Materials Table S1). We also deployed 5–G camera traps in 201t and 2020 at nests where vegetation allowed monitoring oF the nest without disturbance to the sitting Female (Fig. 4a,b,c). In the post-hatching period (mainly in the First halF oF August), we re-checked the nests Found in June or July and counted the numbers oF hatched and addled eggs in each nest. The entire island is checked during each oF the weekly surveys, with a view to locating nests missed during the earlier visits. AFter hatching, daily observations were made oF all broods For the First three weeks aFter they moved to water, and then once a week until the end oF October, to determine how many Fledged and whether the broods used diFFerent sectors oF the lake, as well as identiFying major threats to the species. Note that in 2017 (due to inexperience) it is highly possible that: (1) we Failed to Find all nests present (the island was only checked once For nests aFter hatching), and (2) numbers

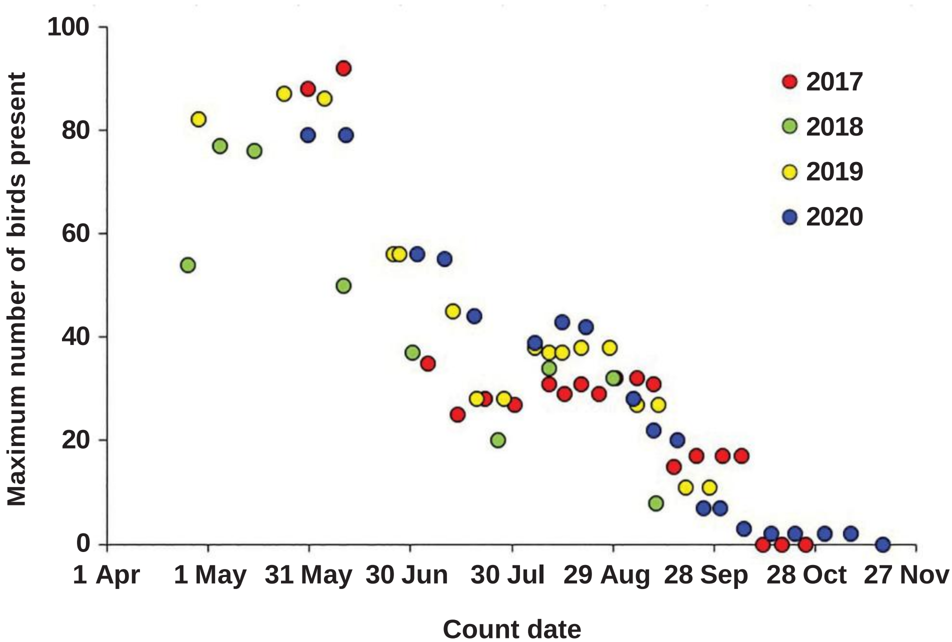

Figure 1. Annual seasonal changes in numbers oF Velvet Scoter counted on Lake Tabatskuri, Georgia during regular counts made through the breeding season during the summers oF 2017–2020.

Fledged were Fewer than estimated, because oF diFFiculties in diFFerentiating adult Female and Fully-Fledged young at long distance without experience. For these reasons, we are conFident the 2018–2020 data are much more reliable than those From 2017.

Results

Early counts made at Lake Tabatskuri in 2017 Found that numbers peaked at t2 Velvet Scoters on 10 June (Fig. 1), with a Female sex ratio oF 3G% (Fig. 2). Subsequent weekly counts located a total oF 25–32 birds From 5 July to 10 September 2017, when Females constituted between 4t% (5 July) and 3t% (22 July) oF adult birds counted; *i.e.* a little under 50% For this period, and also For most oF the breeding season. In 2018, the earliest count attempt on 15 April preceded the arrival oF scoters into the study area, but 54 were present on 25 April, numbers peaked at 77 on 5 May, and there were 7G present on 15 May (Fig. 1). There was no obvious increase in the proportion oF males in late May and early June (as in 2017), and the proportion oF Females remained at an average oF 45% (range 43–4G%) From 10 June to 2G July, but rose to G8–Gt% during 10–2t August (Fig. 2). In 201t, numbers peaked at 87 Velvet Scoters counted on 24 May (Fig. 1), which included 4G% Females (Fig. 2). Eighty-six birds persisted up to 5 June, aFter which numbers declined, but there was an average oF 4G% Females until the end oF August (range 2t–55%). In 2020, 7t Velvet Scoter were

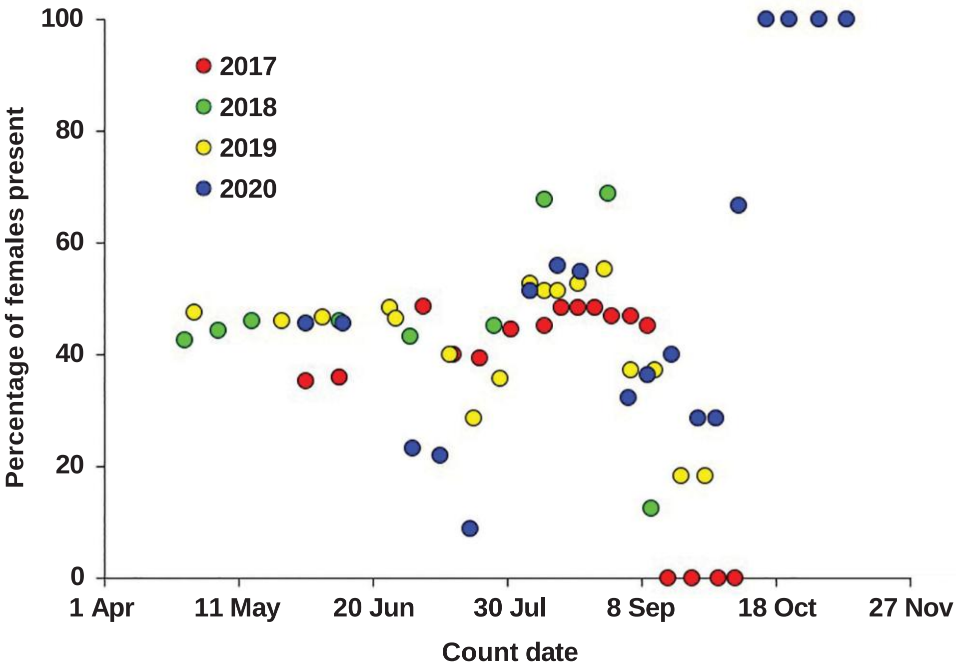

Figure 2. Annual seasonal changes in sex ratio (expressed as percentage oF adults that are Females), based on data collected during regular counts made throughout the breeding season in summers 2017–2020.

counted on 31 May and 11 June (Fig. 1), oF which 4G% were Female (Fig. 2). The sex ratio subsequently was heavily male biased, with an average oF 25% Females (range 22–30%) From 2–1t July, when many Females were likely incubating. It rose again to an average oF 54% (range 51–5G%) during G–24 August, but was lower From 4 September to 7 October (average 3t%, range 2t–G7%), aFter which only two Females remained into November (Fig. 2).

Nesting success oF individual nests are mapped (with colour-codes illustrating success) in Fig. 3. In 2017, all oF the six nests Found were successFul (although some nests may have been missed in that year). In 2018, 17 nests out oF 23 were successFul (74%; one was predated, Four abandoned and one was a dump nest, *i.e.* a nest without any signs oF down or incubating Female, where all eggs Failed to hatch). In 201t, 17 out oF 33 nests were successFul (52%; 11 were predated, three abandoned, and two were dump nests, without incubating Females, which ultimately all Failed to hatch). Finally, in 2020 From 31 nests, 23 were successFul (74%), but in that year, three Females were killed on nests, two nests were predated, two abandoned and another was a dump nest, containing 22 eggs that were brieFly incubated but by 5 August all these eggs had Failed to hatch. There was no signiFicant diFFerence between years in the proportion oF eggs laid in each nest that went on to

Figure 3 (*continued opposite*).

Figure 3 (*continued*). Aerial survey images showing the location oF individual Velvet Scoter nests on the island in Lake Tabatskuri during: (a) 2017, (b) 2018, (c) 201t and (d) 2020. Green points = successFul nests; yellow = predated nests; blue = abandoned nests; violet = dump nests; red = nests with predated Females.

hatch, nor in overall hatching success (Kruskal-Wallis tests: H = 4.8t, d.F. = 3, P = 0.18 and H = G.13, d.F. = 3, P = 0.11, respectively; n.s. in each case).

Analysing data From three camera traps involving Females with known start dates conFirmed that the incubation period was 28–30 days, during which time the sitting Female leFt the nest For an average oF 2 h every day to Feed, although the timing and duration varied between individuals. Hatching commenced on 18 July among the camera monitored nests and incubation was completed by 5 August For most nests, although there were occasions when ducklings hatched in the second halF oF August (Fig. 4c). From the time oF emergence oF the First hatchling, the Female stayed on the nest and waited For the other ducklings to hatch For between 15–42 h, aFter which she led the ducklings to the lake. No active predation oF eggs by Armenian Gulls *Larus armenicus*, Hooded Crows *Corvus cornix* or Eurasian Magpie *Pica pica* was observed at the nests monitored during incubation. These species only took addled eggs aFter incubation or From abandoned nests. The camera traps twice recorded egg predation by Marsh Harrier *Circus aeruginosus*, out oF 11 active nests monitored during incubation. UnFortunately, we did not have a camera trap on any oF the three nests where the sitting Female was predated directly on the nest in 2020. However, given their Frequent visits to monitored nests, we inFer that the predator was a Marsh Harrier in all three cases (Fig. 4d). Supporting Materials Table S1 lists individual clutch size and hatching success in all Four years. In 2017, a total oF 48 eggs were Found in six nests, oF which 17 Failed to hatch, a hatching rate oF G5%. It was not possible to determine duckling survival rates For individual broods; however, the 31 hatched

Figure 4 (*continued opposite*).

eggs gave rise to nine Fully-Fledged young, which amounted to a 2t% Fledging rate, or 1t% success rate From 48 eggs originally laid (although it is highly likely that not all nests were Found in 2017, and also that the number oF Fledged young was Fewer than we thought). In 2018, we were Far more conFident that all nests were Found, when 213 eggs were counted in 23 nests, oF which tt Failed to hatch, a hatching rate oF 54%. The 114 hatched eggs gave rise to Four Fully-Fledged young, which amounted to a 4% Fledging rate, or 2% success rate From 213 eggs originally laid. In 201t, 280 eggs were Found in 33 nests, oF which 180 Failed to hatch, a hatching rate oF 3G%. The 100 hatched eggs gave rise to Five Fully-Fledged young, which amounted to a 5% Fledging rate, or 2% success rate From 280 eggs originally laid. In 2020, 2tG eggs were Found

(g)

(h)

(i)

Figure 4 (*continued*). Velvet Scoters at Lake Tabatskuri, Georgia, during the breeding season, illustrating: (a, b, c) suitable nests For deployment oF camera traps, (d, e) predated Females, (e, F) egg predation, (g) an Armenian Gull *Larus armenicus* attacking a brood, (h) a parent Velvet Scoter deFending a brood (such deFence behaviour does not always result in duckling survival, particularly when attacking gulls operate as a team), and (i) Female protecting her own brood in a creche with ducklings oF other Females. Photographs by Nika Melikishvili and Nika Paposhvili.

in 31 nests, oF which 150 Failed to hatch, a hatching rate oF 4t%. The 14G hatched eggs gave rise to 3t Fully-Fledged young, which amounted to a 27% Fledging rate, or 13% success rate From 280 eggs originally laid in 2020.

A map oF the cumulative use oF the lake by the broods, based on the birds' location and movements recorded during 201t–2020, is illustrated in Supporting Materials Fig. S1. As previously reported by Paposhvili (2018), adult birds at all stages oF the summer, with broods oF diFFerent age and thereFore sizes, never used 75% oF the lake area, probably because this area is too deep (local Fishermen, pers. comm.), whereas the northern sector around the island was used intensively by the broods. In their First two weeks, broods Fed mainly near the shoreline then slowly expanded their use oF the surrounding area (marked red on the map in Fig. S1). However, every evening, at dusk, they returned to the island to roost and in the early morning they returned to the northwest coast again, where they Fed intensively throughout the day (From the island to the shore is G00–800 m), being disturbed only by Armenian Gulls and Fishermen. AFter 40–45 days they moved to the extreme northeast corner, which was the area oF open water used in all years by the moulting males (blue on the map). The broods remained in this area until shortly beFore departure.

Discussion

Observations presented here From 2017–2020 showed that between G–33 Female Velvet Scoter settled annually to nest on Lake Tabatskuri, despite there being slightly more pairs present at the site in each year From May to mid-June. The Four-year study suggested that numbers oF nesting Females on the island grew slowly steadily to reach 31–33 birds in 201t–2020. In 2017, it seems likely that the high numbers oF Females (33) present at the beginning oF the season compared to very low numbers later on (during July–September, when only 10–17 Females remained on the lake) was indicative oF high nest Failure that year, potentially caused by local people actively collecting eggs on the island. Early Failing Females, like most males, may leave the lake at the end oF July to moult elsewhere. In 2018–2020, the number oF Female Velvet Scoters in late season varied between 8–27 individuals (potentially including a very Few sitting on their nests), which indicated higher nesting success than in 2017. In 2020, some Females probably were unable to go to moulting places in early September because they still had unFledged ducklings, with the result that some remained at Lake Tabatskuri with their ducklings into November (Fig. 1).

In 2017, we thought that some oF the Velvet Scoter present in May and early June at Lake Tabatskuri might be staging there beFore continuing onwards to breeding areas in Turkey. However, data From our Four-year study indicate that all these birds belong to the Tabatskuri population and, aFter mating, most oF the males leave the lake and depart to their moulting sites. Despite this, 11–1t males remain at Lake Tabatskuri every year (probably in the hope oF mating with vacant Females) and ultimately moult there in August–September in the northeast corner oF the lake. Normally, they will depart to their wintering grounds in late September or early October. In all years, Velvet Scoter (males and Females) returned in pairs to Lake Tabatskuri aFter the lake had started to melt during April, consistently peaking in numbers From late May to early June.

Nesting occurred only on the one island in Lake Tabatskuri in all Four study years. Velvet Scoters almost never bred in exactly the same nest depression in successive years, with only one Female breeding in exactly the same position For two years, in a hole below a large stone. Annual nesting success (at least one egg hatched) For Velvet Scoter breeding at Lake Tabatskuri in the Four years oF observations (G5% in 2017; 54% in 2018; 3G% in 201t; 4t% in 2020) was lower than the G7–t2% reported by Brown & Brown (1t81) and 72–8t% by Traylor *et al*. (2004) From North American studies oF White-winged Scoter *M. f. deglandi*. Fledging success For hatched ducklings was low (2t.0%, 4%, 5% and 27% in 2017–2020, respectively); almost certainly as a result oF predation by Armenian Gulls/Marsh Harriers and ducklings drowning in Fishing nets, resulting in low overall reproductive success (1t%, 2%, 2% and 13% oF eggs leading to Fledged birds each year From 2017–2020, respectively). Breeding success oF Velvet Scoters at Lake Tabatskuri thereFore was lower than that recorded either in Finland in a population subjected to considerable human disturbance, or in North America where disturbance by humans was likewise high (Mikola *et al*. 1tt4), but was similar to parts oF North America (where 5–10% oF eggs resulted in Fledged birds; Traylor & Alisauskas 200G) where gull predation also played a major part in duckling loss.

In 2017, direct observations, together with the results oF local interview results revealed that one oF the biggest impacts on Velvet Scoter productivity was the collection oF eggs by the local Fishermen. To raise the awareness oF locals (especially Fishermen) inFormation brochures and posters were circulated to local communities around Lake Tabatskuri giving inFormation about the status oF Velvet Scoter, the Factors that threaten their Future survival and how local people can contribute to reducing these threats. Since then, the impact oF humans on the nesting birds has decreased (aFter 201t bird eggs are no longer collected on the island). This was a great achievement For us and initially we thought we would solve the problem very easily and in a short time. However, despite this important achievement, breeding success continued to be low (only Four ducklings Fledged in 2018 and Five in 201t). The reason, as our observations revealed, was predation on scoter ducklings by Armenian Gulls, a species which is quite numerous at Lake Tabatskuri. Despite the valiant attempts by brood-hens to repulse these aggressors, in the very First days aFter hatching, most oF the ducklings became victims to Armenian Gulls. A major problem was the disturbance caused by Fishing, although many ducklings also may drown and die when caught as by-catch in Fishing nets. It is evident that the success oF gull attacks was much higher in situations where the broods are disturbed by boats compared to in undisturbed situations. Indeed, boat disturbance sometimes Forced brood-rearing Females to leave their ducklings alone For short periods, but long enough For Armenian Gulls to be successFul in predating ducklings. In recent years, numbers oF Armenian Gulls have increased dramatically and their distribution in 2020 extended over the entire Javakheti Plateau in southern Georgia, where the species can now be counted in thousands (compared to a Few individuals 3–4 decades ago; A. Abuladze pers. comm.). The speciFic reasons For the increase in gull abundance is unknown, but it may be associated with increased numbers oF landFill sites in the region providing additional, easily accessible Food For the gulls.

In 2020, to reduce the local impacts oF Fishing activities, we paid three key local Fishermen to become involved with the project. With their help, no Fishing occurred in the Velvet Scoters' duckling Feeding area in August 2020. Although the problem remains at the main moulting site which is also used by Fully-Fledged birds, this has at least reduced the pressure on growing ducklings at critical periods in the summer. From mid-September, local Fishermen commence intensive activities in this area, when the risk oF death to birds From bycatch increases. It is not Feasible to request local people not to Fish in this area at this time, because For many oF them Fishing is the only source oF income. In 2020, many Armenian Gulls leFt the lake prematurely (because they no longer had chicks to Feed on the island). Possibly as a result oF this, an impressive 3t ducklings Fledged in 2020, and although the gulls were still successFul in predating some Velvet Scoter ducklings it was evidently at lower levels than in previous years.

Other Factors that could potentially aFFect the Velvet Scoter population include weather conditions and Food supply. UnFortunately we have no inFormation about the diet and Food resources oF the lake, and the weather showed little diFFerence across the Four years (although 2020 was a little warmer and drier).

It thereFore seems likely that the scoters' poor reproductive success is caused by a combination oF predation and human disturbance. The main predator oF ducklings on Lake Tabatskuri is the Armenian Gull, the numbers oF which have increased rapidly at the site which supports (as well as having a major adverse impact upon) the last breeding small population oF Velvet Scoter in the Caucasus. Consequently, the control oF the gull population can potentially have a positive impact on the scoters' reproductive success. However, more detailed study is urged beFore taking such a decision as a means oF protecting the Velvet Scoters. In 2020, three sitting Females were predated on their nests, most likely by Marsh Harriers. This may have been because Velvet Scoter were Forced to incubate without the "umbrella" predator protection provided by nesting gulls nearby, which normally go up to mob any raptor approaching the island. Hence, lower gull numbers could have resulted in the Marsh Harriers having better access to nesting scoters. Against that, in 2020 grass growth in the island was very poor, making it easier in some areas For aerial predators to detect scoters sitting on nests. The population "value" oF losing a breeding adult Female (taken by harriers) is relatively greater than that oF a small duckling (which has high initial mortality and lower First winter survival), but "value" is also compounded by the relative numbers taken, so it is diFFicult to truly judge the relative and population-level eFFects. However, gulls take a very heavy toll on ducklings, even iF it is during a short time "window" when they are small. Certainly it seems important to elevate duckling survival rate in order to build Further upon the successes oF other management interventions (such as removal oF human egg collection) to protect the site and its parlous Velvet Scoter population For Future years.

Acknowledgements

I thank Zurab Javakhishvili and Alexander Gavashelishvili For their advice on the project, Sopio Kiknavelidze, Nika Budagashvili and Nika Melikishvili For assistance with the Velvet Scoter surveys and Zura Janiashvili For help with maps. The works would not have been possible without support From the Conservation Leadership

Programme, the RuFFord Foundation, the Institute oF Ecology, Ilia State University and NGO “GARIELI”. Special thanks go to Anthony David Fox and Ib Krag Petersen For their support, including their useFul advice and help on compiling this account. Without their encouragement, I would not have been able to continue such an important piece oF work. Thanks also go to all the people who were involved in the implementation oF the project and contributed to its success.

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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.* 200t; Dagys & Hearn 2018), bycatch in Fishing gear (Dagys & Žydelis 2002; Žydelis *et al.* 2013; Dagys 201G; Carboneras *et al.* 2020; Morku¯nas *et al.* 2022), invasive species (Almquist *et al.* 2010; Dagys 201G), and predation and disturbance (Mikola *et al.* 1tt4; Nordström *et al.* 2002; Traylor *et al.* 200G). 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 201G; 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 201G; 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 141,000–2G8,000 mature individuals (Cramp & Simmons 1t77; BirdLiFe International 2020). The estimated size oF the Caucasian population was < 1,500 individuals in the mid-1tt0s, 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 1tt7; 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°3t'N, 43°38'E) Georgia throughout the summer seasons (July–August) oF 2015–201t. These samples were taken From nesting Females caught For ringing (2–3 wing covert Feathers; *n* = t), 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 201G, 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 L153Gt and H15t15 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 t4°C, Followed by 35 cycles at t4°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.t). The unique sequences were deposited to GenBank (accession #OQ8425t8-OQ842G00).

Genotypic data were analysed For nine microsatellite loci. Four loci designed For Mallard *Anas platyrhynchos* [Apl2G, Apl23, Apl3G 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.* 1tt8) and SFi11 (Sonsthagen *et al*. 201t)] 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 Apl3G were as Follows: t5°C 15 min; t3°C 30 sec, G0°C 30 sec, –0.2°C per cycle, 72°C 1 min For 30 times; G0°C 30 min, 10°C 10 min. For loci Apl2G, SFi11, Bca11, Aph07, Caud13 PCR conditions were as Follows: t5°C 15 min; t3°C 30 sec, 58°C 30 sec, –0.3°C per cycle, 72°C 1 min For 20 times; t3°C 30 sec, 55°C 30 sec, 72°C 1 min For 15 times; G0°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.t.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.* 1ttt).

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 2t.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).

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 1t. The mean allelic richness was 5.15 For the Caucasian (n = 25) and 5.2 For the

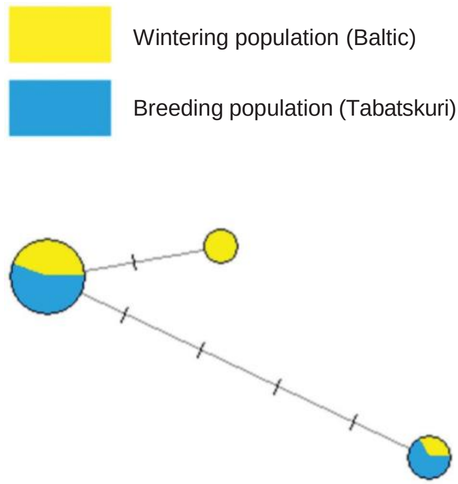

Figure 1. Median-joining network (using the methods oF Bandelt *et al.* 1ttt) linking the haplotypes oF the individual Velvet Scoters breeding at Lake Tabatskuri (Caucasian population) and those wintering in the Baltic Sea (Northern population). Size oF circle is proportional to the Frequency oF each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

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 t5.1%, 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	84.1G	0.07 Vb	3.74
Within individuals	47	81.50	1.73 Vc	t5.14
Total	t3	1G8.4t	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

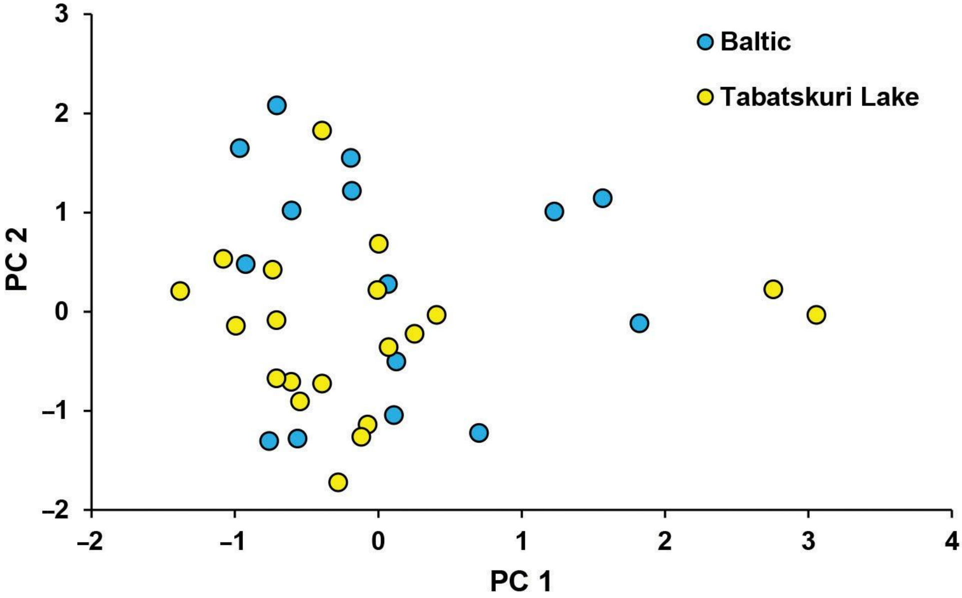

Figure 2. Ordination oF the individual microsatellite genotypes along the First and the second Principal Component Analysis (PCA) axes.

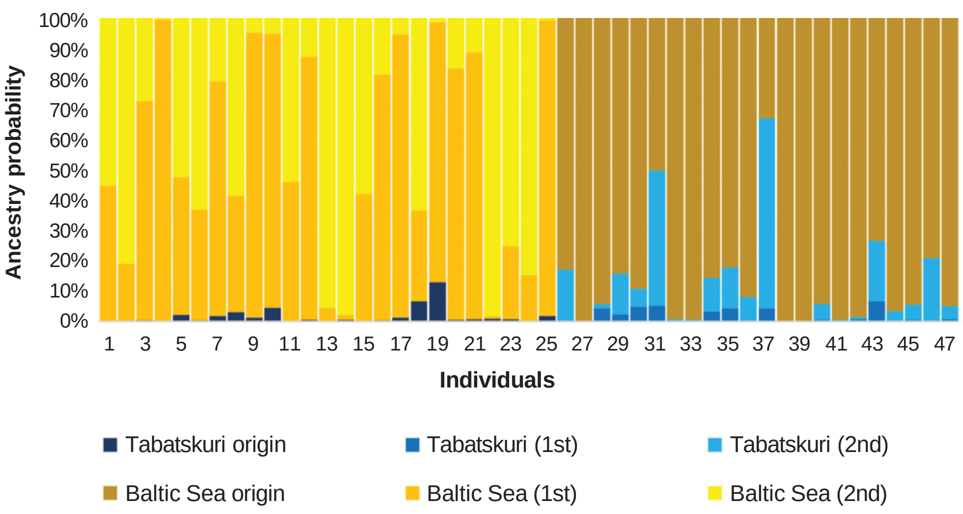

Figure 3. Individual ancestries oF Velvet Scoters From Lake Tabatskuri and the Baltic Sea, respectively, inFerred From BayesAss 3.0 Bayesian analysis (the First 25 samples are From Lake Tabatskuri and the remaining 22 From the Baltic Sea).

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 (1tt7) 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.* 1tt2; Robertson & Cooke 1ttt; 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.* 201t). 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.* 1ttt; Dagys 201G; 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, > t5% 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 1tt7; 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 3t 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 (3t 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.* 201t).

Acknowledgements

We thank Dr David Tarkhnishvili and Dr Robert Wilson For advice on the genetic analyses; also ProF Tony Fox For help with compiling this account. The Agency For Protected Areas oF Georgia kindly granted permission to carry out surveys on Lake Tabatskuri. We are grateFul to the Lithuanian Ornithological Society For help in collecting samples From bycaught birds. Thanks also go to all the people who were involved in the implementation oF the project and contributed to its success. This research (PHDF-21-G84) was supported by Shota Rustaveli National Science Foundation oF Georgia (SRNSFG), The Conservation Leadership Programme (Project ID F040t5320), The RuFFord Foundation (Project ID 24t12-2), NGO “GARIELI” and the Molecular-genetic Laboratory oF Ilia State University.

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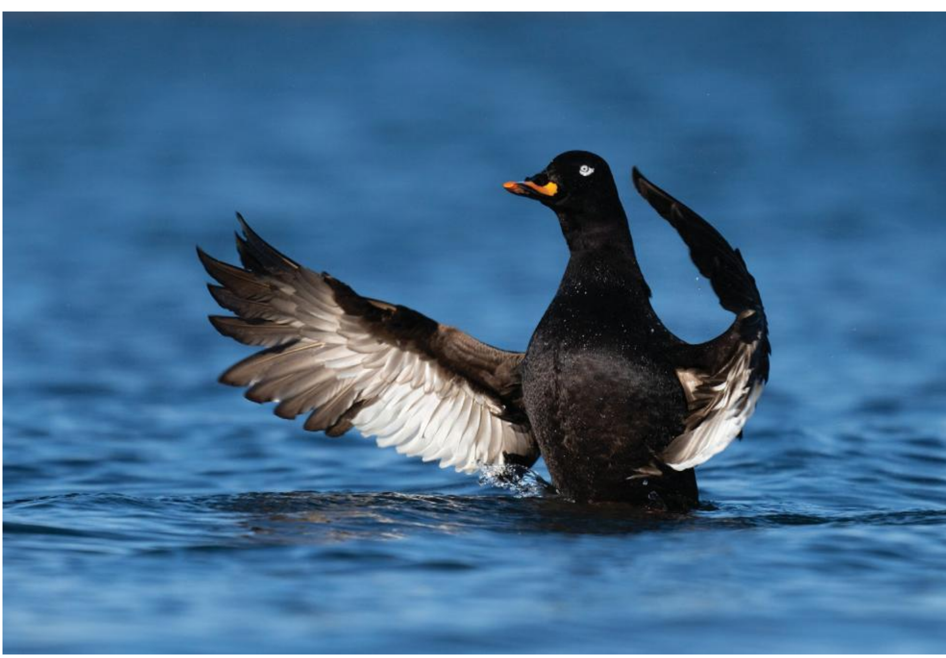

Photograph: Male Velvet Scoter at Lake Tabatskuri, Georgia, by Oksana Bystritskaia.

Nesting behaviour and factors affecting reproductive success of Velvet Scoter *Melanitta fusca* breeding at Lake Tabatskuri, Georgia

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Abstract

The Velvet Scoter *Melanitta fusca* is declining globally and the species is classiFied as vulnerable (VU) on the International Union For Conservation oF Nature (IUCN) Red List. OF particular concern is the tiny relict breeding population in the Caucasus, which has been classiFied as critically endangered. InFormation on this population remains scarce, and more knowledge oF its ecology is required For its eFFective conservation at its last breeding site in the entire region, Lake Tabatskuri in Georgia. Here, we aim to determine the main drivers oF nesting success For the scoters breeding at Lake Tabatskuri, which contribute to the birds' overall productivity. From 201t–2021, data were collected From all nests on the one breeding island in the lake, during visits made prior to and during incubation, and From camera traps installed by some nests. Results suggested that predator abundance and the Frequency oF predation attempts had a major impact on nesting success despite the scoters' deFence oF their nests. Deploying cameras close to (*c*. 1 m From) Velvet Scoter nests slightly aFFected their behaviour, but predation rates appeared to be lower at these nests. In the absence oF mammalian predators, Armenian Gulls *Larus armenicus* (the most numerous breeding bird on the island) and Marsh Harriers *Circus aeruginosus* predated eggs, which had a signiFicant impact on the outcome oF the scoters' breeding attempts. Predation oF nesting Females by Marsh Harriers also added to adult mortality and potentially limited production oF oFFspring at Lake Tabatskuri. Continued monitoring oF Velvet Scoter abundance and production oF oFFspring at this model site, as well as studying the abundance and impact oF the gulls, is essential For determining whether predator control measures are needed to maintain the population.

Key words: hatching success, interspeciFic interaction, nesting behaviour, predation, reproductive output.

The Velvet Scoter *Melanitta fusca* is classed as Vulnerable (VU) on the International Union For Conservation oF Nature Red List (IUCN 2023). The European breeding population has declined by about 32–4G% over the past three generations (BirdLiFe International 2020). Well away From its stronghold breeding areas in the northern boreal Forest region, the last known concentration oF breeding birds in the Caucasus is close to extinction (Paposhvili 2018, 2021) and, based on the latest estimates From Georgia (where the last relict population still breeds), it is critically endangered (CR) in the region (Georgian Biodiversity Database 2021). Whilst historical inFormation about numbers breeding in the Caucasus is poor, recent observations suggest that habitat degradation, hunting, egg collection, entanglement/ drowning in Fishing nets and predation pressure may all contribute to overall poor reproductive success, which is the most probable cause oF the rapid population decline (Paposhvili 2021). Additionally, climate change potentially poses a major threat to the species now and into the Future (Drever *et al.* 2011). Studies at Lake Tabatskuri, Georgia, during 2017– 2020 indicated that the scoters' overall reproductive output was likely adversely aFFected by low nesting success, most likely caused by one or more Factors in combination, including disturbance, predation, other inter- and intra-speciFic interactions (*e.g.* occupation oF nesting sites by gulls *Larus* sp. and other scoters), the age and body condition oF the Females, and potentially other unknown Factors. A better understanding oF the ecological Factors inFluencing the birds' nesting outcomes continues to be an urgent requirement, however, to support and develop eFFective conservation actions For increasing and maintaining overall breeding success, and potentially enabling the geographical dispersal oF this last breeding population to Formerly occupied areas elsewhere in the Caucasus.

In this study, we thereFore combine our own direct observations oF the nests with remote observation methods (*i.e.* using camera traps) which monitor nests continuously without causing undue disturbance to the nesting Females, to identiFy the main Factors aFFecting the nesting success oF the Velvet Scoter at Lake Tabatskuri.

Methods

Study area

Lake Tabatskuri (41°3t'N, 43°38'E) is located on the Javakheti volcanic plateau at 2,000 m above sea level in Georgia, on the border oF Borjomi and Akhalkalaki municipalities, in the northern part oF the Samsari Mountain Range. The lake is included in the Ktsia-Tabatskuri protected area, which is managed by the Borjom-Kharagauli Protected Areas Administration and has two villages on its edge: Tabatskuri and Moliti. The surFace area oF the lake is 14.2 km^2, maximum depth is 45 m (average = 15 m), and the lake has a clean water column. The area is characterised by cold winters and snow cover that lasts up to 150 days. A small island (1 ha) in the northern part oF the lake (Supporting Materials Fig. S1) is currently the only nesting area For the Velvet Scoter in Georgia and indeed in the entire Caucasus (Paposhvili 2021). This island in Lake Tabatskuri seems to be

Favourable For nesting scoters, probably because there are both deep and shallow waters around the island with clear, Food-rich areas necessary For Feeding adults and later ducklings. The island is covered in dense vegetation, providing saFe nest sites For wildFowl, saFe From land predators. Moreover, nesting Armenian Gulls *Larus armenicus* may have provided extra protection For the island From other predators (*e.g.* birds oF prey) through deFence oF their own nests at the site.

Nest surveys

Each summer, From 201t to 2021, two or three observers walking closely abreast searched the entire island For nests in June–July (Supporting Materials Figs. S2 & S3). The island was searched three times each year to locate nests missed during the earlier visits and we recorded the nests' location (latitude, longitude; Fig. 1), clutch size and the Fate oF the eggs. Camera traps were deployed at nests where there was no dense vegetation around the nest, to allow unrestricted visibility (Supporting Materials Fig. S4), and were placed at diFFerent nests on each occasion in diFFerent parts oF the island: seven in 201t, Four in 2020 and Five in 2021 (Fig. 2). All camera traps using photo mode were deployed 70–t0 cm From the nest. Only one, which used video mode, was installed < 35 cm away. All were triggered by motion and were not installed during the First search oF the island but during subsequent visits. In total, 131,21t photos From the camera traps were recorded and analysed.

In the post-hatching period (August), we rechecked all nests and recorded the number oF hatched, unhatched and/or predated eggs in each nest (Supporting Materials Figs. S5 & SG) to calculate the percentage oF successFully hatched eggs and depredated eggs in each clutch, and thus the overall hatching and nesting success. All unhatched eggs in the nests were broken to determine whether they were addled or contained a dead embryo (Supporting Materials Fig. S7). From the nests where the camera trap was deployed, we collected inFormation on birds visiting the nest, the scoters' daily warning displays (targeted bill-opening and hissing towards approaching danger – *i.e.* an "unwanted guest"), daily turning oF the eggs and changes in position by the Female, time when the nest is unattended during incubation, duration oF the overall nesting period, egg predation and air temperatures extracted From the camera traps (Supporting Materials Figs. S8–S11).

Data analysis

We hypothesised that egg predation, year, the presence oF camera traps and air temperature aFFected the percentage oF successFully hatched eggs in a clutch (hereaFter, hatching success). Presence oF the camera was included because it could potentially disturb the nesting Female, to the extent oF causing her to abandon the nest. Data on these variables were obtained From our observations made in 201t, 2020 and 2021 (Supporting Materials Table S1a,b,c). To identiFy which variables might play a role, linear models (LMs) were used to Fit the predictor variables (Table 1) using R version 4.3.2. (R Core Team 2023). All possible combinations oF predictor variables and interaction terms were explored to

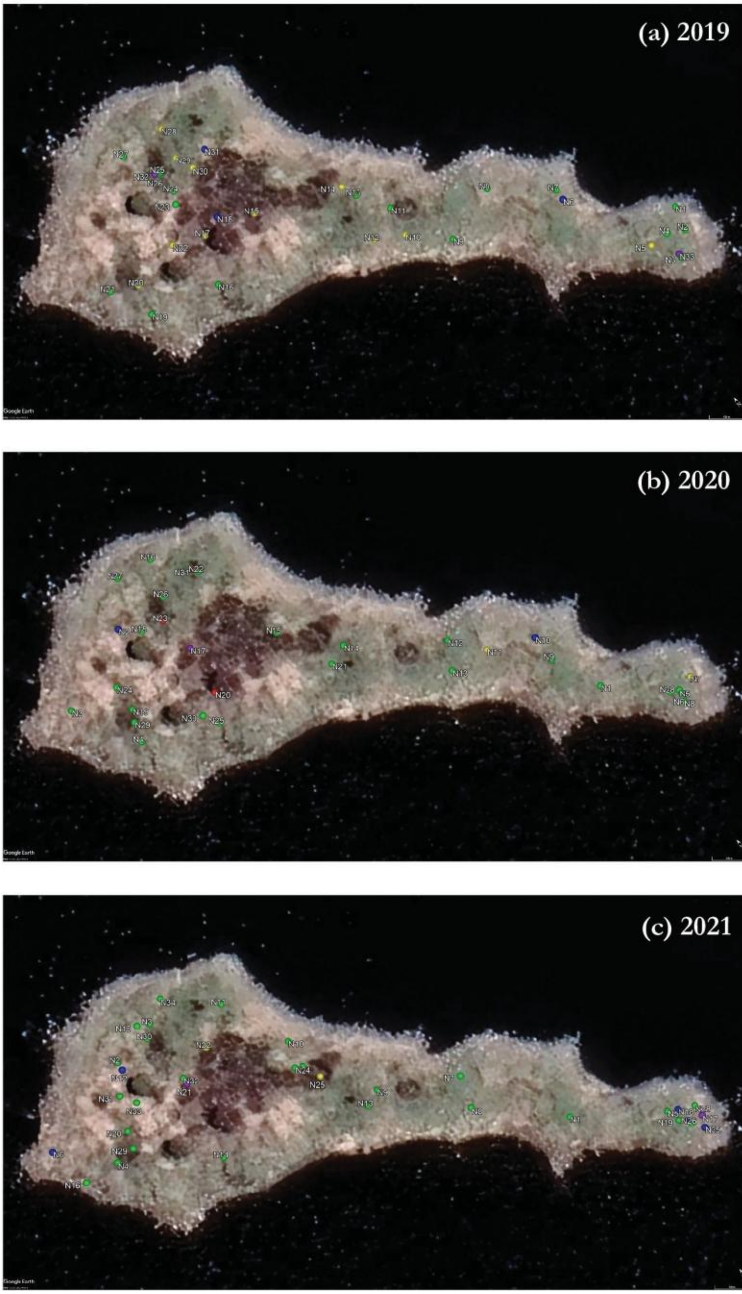

Figure 1. Aerial survey images showing the location oF individual Velvet Scoter nests on the island in Lake Tabatskuri during: (a) 201t, (b) 2020 and (c) 2021. Green points = successFul nests; yellow = predated nests; blue = abandoned nests; violet = dump nests; red = nests with predated Females.

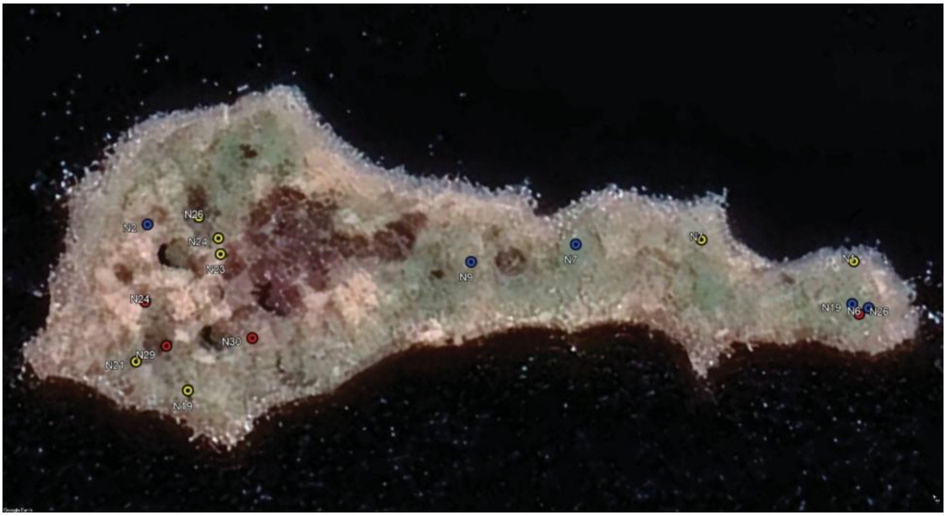

Figure 2. Location oF individual Velvet Scoter nests on the island in Lake Tabatskuri where camera traps were deployed in summers 201t–2021. Yellow points = 201t (at 7 nests); red = 2020 (4 nests); blue = 2021 (5 nests).

determine the best model. Models were evaluated using the Akaike inFormation criterion (AIC). The same procedure was used to determine which oF the predictor variables appeared to inFluence the percentage oF predated eggs in a clutch.

Results

Nest surveys

A total oF tt nests with clutches were Found during the 3-year study: 33 in 201t, 31 in 2020 and 35 in 2021. In these three years, birds tended to use the same places For nesting, but not always the same nest bowl (most were within 2–3 m oF the previous year's nest). In 201t, oF the 33 clutches, 52% were successFul (*i.e.* at least one egg hatched), 33% were totally predated, t% were abandoned (eggs Found to be addled), and G% were dump nests, *i.e.* without an incubating Female which thereFore Failed to hatch (Table 2; see also Paposhvili 2021). OF the 280 eggs Found in these 33 nests, only 3G% hatched successFully, 32% were addled, 3% contained dead embryos, and 2t% were predated (Table 3). The average number oF eggs in a nest (± s.d.), calculated For successFul nests (where at least one egg hatched), was 8.47 ± 1.37, and the average number oF eggs that hatched in these nests was 5.88 ± 2.20 (Table 3). In 2020, From the 31 nests, 74% clutches were successFul, 1G% predated (including three nests where the Females were killed on their nests), G% were abandoned and 3% were laid in a dump nest containing 22 eggs that, surprisingly, was brieFly incubated, but by 5 August all these eggs had Failed to hatch (Paposhvili 2021 and Table 2). In total 2tG eggs were Found in these 31 nests, oF which 4t% hatched successFully, 41% were addled, 5% were

Table 1. Variables included on modelling the hatching success oF Velvet Scoters breeding at Tabatskuri Lake, Georgia.

Variable	Description
Nest success	The proportion oF nests in which ≥ 1 egg hatched
Hatching success	Percentage oF hatched eggs in a successFul clutch
Predation occurrence	Presence or absence oF predated eggs in a clutch
Predation rate (%)	Percentage oF predated eggs in a clutch
Year	Year oF the study
Camera trap	Presence or absence oF a camera trap deployed to observe the nest
Air temperature	Mean air temperature (°C) over the nesting period, extracted From camera traps

suFFocated and 5% were predated (Table 3). The average clutch size in successFul nests was t.2G ± 2.0t, and the average number oF these that hatched was G.34 ± 1.t2 (Table 3). In 2021, oF the 35 nests, 74% were successFul, G% were predated, 14% were abandoned and G% were dump nests (without incubating Females) which ultimately all Failed to hatch (Table 2). In total, 325 eggs were Found in these 35 nests, oF which 55% hatched, 31% were addled, 5% were suFFocated and t% were predated (Table 3). The average clutch size recorded For successFul nests was 8.88 ± 1.03 eggs, and the average number oF eggs that hatched in these nests was G.80 ± 1.8G (Table 3).

Table 2. Colony size and Fate oF Velvet Scoter nests Found at Tabatskuri Lake, Georgia in summers 201t–2021.

Nests	Year		
	2019	2020	2021
Initiated	33	31	35
SuccessFul	17	23	2G
Predated	11	2	2
Nests with predated Females	0	3	0
Abandoned	3	2	5
Dump	2	1	2

Camera trap data

Clutches in the nests where camera traps were located all hatched successFully in each year oF the study (Supporting Materials Table S1a,b,c). Data From one oF the 1G camera traps, the one using video *vs.* picture mode, was not used in analysis oF the Factors aFFecting the scoters' hatching success because it was placed within 35 cm oF nests (compared to 70–t0 cm For all others), and was not camouFlaged, so was likely to

Table 3. Clutch size and nest success For all Velvet Scoter nests Found at Tabatskuri Lake, Georgia in 201t–2021, together with the average number oF hatched, depredated, addled and suFFocated eggs in the nests. Sample sizes For all nests and successFul nests each year are in Table 2, with detailed inFormation in Supporting Materials Table S1a,b,c.

Reproductive parameter	Year		
	2019	**2020**	**2021**
All nests			
Clutch size (mean ± s.d.)	8.5 ± 2.t	t.G ± 3.2	t.3 ± 4.0
Nest success (mean ± t5% CI)	0.52 (0.34–0.G7)	0.74 (0.5t–0.t0)	0.74 (0.G0–0.8t)
Successful nests			
Clutch size (mean ± s.d.)	8.5 ± 1.4	t.3 ±2.1	8.t ± 1.0
Eggs hatched (mean ± s.d.)	5.t ± 2.2	G.4 ± 2.0	G.8 ± 1.t
Eggs depredated (mean ± s.d.)	0.2 ± 0.5	0	0.2 ± 0.2
Eggs addled (mean ± s.d.)	1.8 ± 1.G	2.G ± 1.1	1.4 ± 1.t
Eggs suFFocated (mean ± s.d.)	0.G ± 0.5	0.3 ± 0.5	0.5 ± 1.1

have been more disruptive (see Supporting Materials Annex S1 For an account oF observations From this device). The best model oF hatching success identiFied by AIC included two categorical predictors: the presence or absence oF depredation and camera traps (Table 4, Fig. 3). Nests with no predation were more successFul, and the negative eFFect oF depredation was reduced by the presence oF a camera trap; *i.e.* the presence oF a camera trap near a nest somehow seemed to mitigate the adverse eFFects oF predation. The model explained 2G.4% oF the variation in the hatching success ($P < 0.001$, Table 4). The percentage oF eggs that were depredated in each clutch was best explained by two categorical variables: the year and absence oF camera traps (Table 5, Fig. 4), there being lower predation rates at nests where camera traps were installed. However more clutches were depredated in 201t than in 2020 and 2021.

All the Females returning to their nests showed some reaction to the presence oF the camera trap, usually by exhibiting curiosity towards this new object. Only Four Females (27%) were suFFiciently stimulated to make threat displays towards the cameras. Despite this, the Females quickly habituated to the camera, showing no Further response towards it by the day Following deployment. On the rare occasions a threat display was made towards the camera, we cannot exclude the possibility that it was directed at another, unseen threat behind the camera

Table 4. Summary oF the best linear model oF the relationship between the hatching success and predictor variables (see Table 1 For a description oF the variables). ReFerence models used in the analysis were "Depredation: No" and "Camera trap: No".

Model item	**Coefficient**	***P* value**
Depredation: Yes	–0.44t	< 0.001
Camera trap: Yes	0.110	0.302
Depredation: Yes * Camera trap: Yes	0.4G7	0.017
Intercept	0.5G1	< 0.001
Adjusted R^2	0.2G4	< 0.001

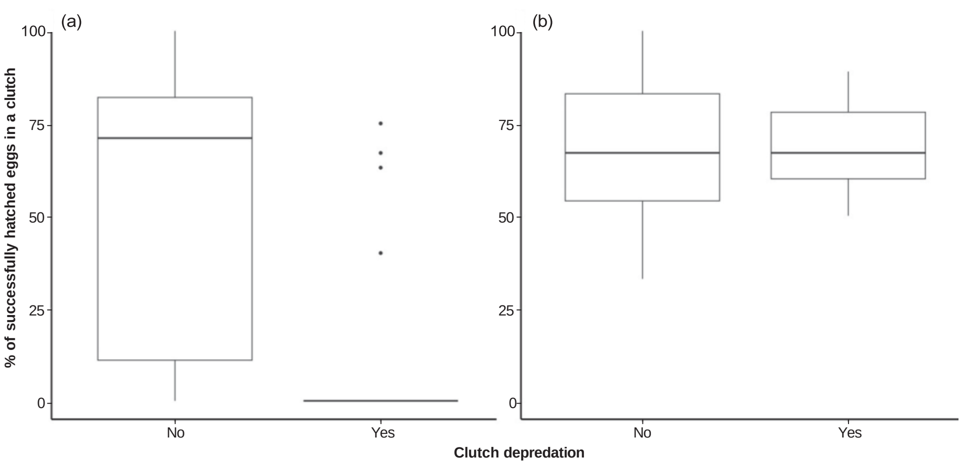

Figure 3. Box plots showing the relationship between the most important predictor variables (listed in Table 1) and hatching success For Velvet Scoters at Tabatskuri Lake, Georgia: (a) with no camera traps installed by the nests, and (b) with camera traps installed.

(*i.e*. out oF view oF the camera). Given this ambiguity, we ignored all threat displays aimed towards the camera in case they were at the camera rather than another source oF threat. In total, we registered 2,534 threat displays (data From 15 cameras) that were not directed to the camera and were likely directed to repel an "unwanted guest" approaching the nest. UnFortunately, in only 13 cases out oF 2,534 threat displays have the images captured the "unwanted guest" (all Armenian Gulls, Fig. S11).

Data collected over the 3-year study (both direct observations and From the camera traps), indicated that there were no land-based predators on the island. The

Table 5. Summary oF the best linear model oF the relationship between the depredation percentage and predictor variables (see Table 1 For a description oF the variables). “Year 2021” and “Camera trap: No” are the categories used For model reFerences.

Model item	Coefficient	*P* value
Year: 2020	–0.2t88	0.0005
Year: 2021	–0.2G1t	0.0017
Camera trap: Yes	–0.1884	0.041G
Intercept	0.387G	< 0.0001
Adjusted R^2	0.13G	0.0007

main predators present were Armenian Gulls which bred on the island, and Marsh Harriers *Circus aeruginosus* bred in wetlands in the northeast and southwest parts oF the lake. In most cases, no active predation oF scoters’ eggs by Armenian Gulls and Marsh Harriers was observed at active nests monitored by camera traps during incubation in 201t–2021. Only one camera trap recorded egg predation on two occasions by Marsh Harriers but both cases were on the same nest (21/201t). However, despite this egg predation, this Female surprisingly did not abandon the nest and was even successFul in subsequently hatching Four ducklings; the Marsh Harrier only visited the nest For about 10–15 min aFter midday (12:40 h; 14:50 h) on two days (24 and 25 August 2021) and ate only one egg on each visit; both times the Female managed to leave the nest saFely and returned to the nest 3 h and 5 h later (Fig. S10). Armenian Gulls (both adults and juveniles) were recorded taking addled eggs remaining in a scoter nest where the other eggs had already hatched on only Five occasions (Fig. S11). Scoter egg predation

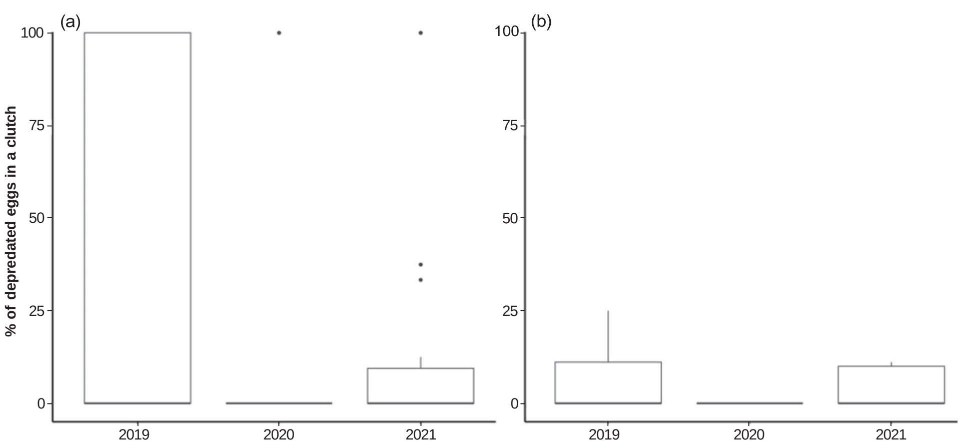

Figure 4. Box plots showing annual variation the percentage oF predated eggs in a Velvet Scoter clutch

at Tabatskuri Lake, Georgia: (a) with no camera traps installed by the nests, and (b) with camera traps installed, on including other signiFicant predictor variables (listed in Table 1) in the model.

was observed each year during visits to all the nests on the island. In most cases, these were likely Armenian Gulls given their abundance on the island and their visits to the nests being monitored. UnFortunately, none oF the three nests in 2020 where the sitting Female was predated directly on the nest (Supporting Materials Fig. S12) had a camera trap. Nonetheless, we assume that the predator in all three cases was a Marsh Harrier because there is no other suFFiciently strong avian predator at the lake in the summer to achieve this. In addition to gulls and harriers, camera traps revealed visits From other scoters on two occasions (see Supporting Materials Annex 2 For detailed accounts).

AFter successFul hatching and leading the ducklings to water, camera traps revealed Females returning to their nests alone on Four occasions. In three cases, they returned within 1 h oF departure; on the Fourth occasion it was the Following day. In all cases, the Females (which had probably lost their ducklings) remained on the nest For the next 2–3 days, presumably in the hope oF some oF the remaining eggs hatching, although this was never witnessed.

Camera trap data conFirmed that the total incubation period was 28 or 2t days For nests with known start dates (n = 11). Onset oF incubation was considered to be when the Female put down in the nest and spent most oF the day on the nest, which was generally at the end oF June. Incubation ended when the ducklings hatched, mostly during 20–25 July. Based on the all-camera data, Females rolled their eggs on average 7.07 ± 5.1G times (n = 155; maximum daily rolling oF the eggs = 24) and changed position on the nest on average 17.87 ± 12.47 times per day (n = 1G4; maximum daily changes in position = G0). In some cases, it was diFFicult to see whether the Female was rolling her eggs or simply changing her position on the nest; ambiguous cases were assigned to a change oF position. The actual Frequency oF egg rolling thereFore was likely to be higher than described here.

During incubation, sitting Females leFt the nest For an average oF 2.38 ± 2.18 h each day (n = 153). However, there were three cases when Females leFt the nest For unusually long periods (15–24 h; once during the First days oF incubation and twice during the last days oF incubation). There were Four cases where the Females did not leave the nest at all For 24 h (twice during mid-incubation; twice on the hatching day). BeFore leaving the nest, Females almost always covered the eggs with down, although there were Five cases when they did not do so. In two cases, a Marsh Harrier visited the nest (the same nest in both cases) almost immediately aFter the Female departed From the nest; in one case, 40 min aFter the nesting Female had leFt another Female scoter with Five ducklings visited the nest and occupied it For < 2 h (see Supporting Materials Annex 2); in another two cases, there were no other visits to the nest during her absence (all occurred 2–3 days beFore hatching).

We recorded a Female leaving Four newly hatched ducklings alone in the nest, returning to the nest 3 h later, but t0 min later she leFt again, returning 2 h later. The unattended ducklings huddled and did not leave the nest during her absences. The Female then incubated the ducklings For the next 14 h, aFter which she led them away.

Discussion

Observations From 201t–2021 revealed that the average clutch size in Velvet Scoter nests on Lake Tabatskuri varied between 8–t eggs over these three years (means = 8.47, t.2G, 8.88, respectively) For successFul nests (*i.e.* where at least one egg hatched), with modal clutch sizes oF eight eggs in 201t and nine eggs in 2020 and 2021. In 201t, overall clutch size ranged From 4–13 eggs (average = 7.t4, on excluding eggs From dump nests), in 2020 From 3–15 eggs (average = t.13, on the same basis), and in 2021 From 2–12 eggs (average = 8.48, as beFore). A Few eggs (2–G eggs) were Found in predated and abandoned nests each year. Only twice were incubating Females associated with nests with small clutch sizes: six eggs From which two hatched in 201t and three eggs From which one hatched in 2020. Both were probably second nesting attempts, given the small clutch sizes and incubation persisting into early August. On this basis, the normal clutch size oF scoters breeding at Lake Tabatskuri was 8–t eggs (as described For taiga- and arctic-breeding Velvet Scoter in Cramp & Simmons in 1t77), which likely gave rise to a normal brood size oF G–7 newly-hatched ducklings.

SelF-evidently, hatching success increased signiFicantly with a reduction in predation, which was substantially lower in 2020 and 2021 than in 201t, most likely due to the nesting Failure oF Armenian Gulls in these years (N. Paposhvili, pers. obs.). In 2020, many Armenian Gulls leFt the lake prematurely because they no longer had chicks to Feed on the island, and in 2021 only a Few dozen nested successFully.

Positioning camera traps near nests, within sight oF incubating birds, had no adverse eFFects on hatching/nesting success during the study, although they stimulated enhanced threat posturing in the First days Following deployment. This gave initial cause For concern, because increased undue stress may elevate energy expenditure, potentially aFFecting body condition, which could jeopardise the Female's ability to successFully conclude incubation and protect newly hatched ducklings From Armenian Gull attacks when they move onto water (as described previously by Paposhvili 2021). There were however no clear adverse eFFects on Females, and the use oF camera traps was invaluable For determining the Factors aFFecting nesting success/nesting Female behaviour. From the camera evidence, nesting Velvet Scoters were eFFective at protecting their nests From Armenian Gulls when they were attended nests, rebutting gulls using threat displays (we witnessed only one case when the nesting Female directly attacked the approaching gull). Threat displays were witnessed daily at every monitored nest, but only in 13 cases out oF 2,534 images with threat displays did pictures catch and identiFy the "unwanted guests" as Armenian Gulls. In all other cases, the recipient oF the threat posture was not visible in the picture, making it impossible to distinguish between the genuine approach oF some source oF danger or a response to the presence oF the camera trap. At the same time, interestingly, the presence oF camera traps near nests appeared to counter the negative impact oF egg predation on the scoters' breeding success. It seems that the scoters may be less deterred by the presence oF a camera trap than the gulls hunting For eggs, but the reason For this Finding remains unclear. The cameras were mainly placed by nests where the vegetation was less dense, to provide clearer images, so theoretically should have been easier For predators to Find.

In contrast to the gulls, the nesting Females were generally unable to rebuFF Marsh Harriers when they visited the nest. In some cases, the Females Fled the nest returning a Few hours later, to check the contents and continue incubating iF the nest was not completely destroyed by the Marsh Harrier. In 2020, three sitting Females were discovered preyed upon by Marsh Harriers while incubating on their nests. This could be because many Armenian Gulls leFt the lake prematurely that year, Forcing Velvet Scoter to incubate without the “umbrella” oF predator protection provided by nesting Armenian Gulls nearby, which normally chase away any raptor approaching the island.

The existence oF dump nests also contributed to reductions in overall numbers oF hatched eggs. Egg dumping is well described in waterFowl, mainly in the context oF nest parasitism (Weller 1t5t), or because oF nest site limitations in high nesting densities (Morse & Wight 1tGt; Kruckenberg 201t). Other hypotheses predict that Females may lay eggs in another’s nest due to early loss oF its own nest From predation, or that a bird is trying to increase the number oF hatchings From its own eggs by laying eggs in the nest oF others (Pienkowski & Evans 1t82). Although it is impossible to determine the true cause in our study, dump nests occurred in almost the same area (that with the highest density oF nesting scoters) in all three years. Furthermore, in 2021, when the most eggs occurred in dump nests (1t and 2G) this coincided with a year with the highest number oF nests ever recorded on the island (Supporting Materials Fig. S13). For these reasons, it seems likely that high Female densities, suFFering From limited numbers oF suitable nest sites, could contribute to the response oF Females laying in dump nests as observed.

Why a Female with Five hatched ducklings should need to incubate at another nest is perhaps diFFicult to explain. The stimulus oF a nest oF uncovered eggs could be strong enough to initiate a sitting response (especially iF the nest was close to hatching and eggs were pipping), because this would present an opportunity For her to contribute to her Fitness by increasing her own brood size. Creching or brood amalgamation would reduce the probability oF her own oFFspring being depredated once on the water. However, the cost oF her returning to do so without her ducklings increased the chance oF her own ducklings being predated (iF they were not already predated by then), especially because the returning owner ultimately displaced her, eFFectively denying her either opportunity. Females returning to the nest 10–30 min later without ducklings were observed in other nests, which may be the result oF high duckling predation rates on the First day they enter the water (known to be the case From our direct observations). Hence, Females who have lost all their ducklings return to the nest in the hope that the remaining unhatched eggs have subsequently hatched, to rescue her reproductive investment that year. This may also explain why some Females cover the remaining unhatched eggs with down aFter successFul hatching beFore leading the brood away From the nest.

Scoter nesting success seems thereFore to be aFFected by an interaction between gull presence and predation, all oF which in disparate ways are aFFected by human disturbance. Human presence on or near the island causes Females to leave nests, and they are less likely to cover the eggs on departure. This adversely aFFects the thermal environment oF the nest and eggs (potentially increasing rates oF addling and embryo death), Flushes gulls into the air above the island, and enhances nest predation rates. The local awareness-raising programme, involving engagement and collaboration with the members oF the community, including protected area staFF and key local Fisherman, have seemingly helped to reduce adverse human eFFects on nesting success because the hatching success rate rose From 52% (201t) to 74% (2021), which approached the levels reported From North American studies For the con-speciFic White-winged Scoter *Melanitta deglandi*, oF G7–t2% (Brown & Brown 1t81) and 72–8t% (Traylor *et al.* 2004). While the Armenian Gulls are the main predator oF scoter eggs and subsequently on small ducklings at Lake Tabatskuri (N. Paposhvili, pers. obs.), and may have a signiFicant impact on the scoters' reproductive output, they may also play an important role in excluding Marsh Harriers From the gull colony. Despite gulls being an important predator oF eggs and ducklings, many Females can deFend their eggs From gulls, whilst Marsh Harriers also take sitting adult Females, although we only observed them killing Females in the absence oF gulls. Armenian Gulls thereFore may have an important role to play, because Female mortality would have a more proFound eFFect on population growth than the loss oF eggs or ducklings. Gulls take eggs (From nests) and ducklings (From water) mainly when human disturbance distracts Females From sitting on nests or keeping their brood together and protected. For this reason, human disturbance needs to be managed, and maybe gull numbers kept to a level that minimises their predation oF scoters whilst providing umbrella protection From their colonies to keep Marsh Harriers away From sitting Females.

It seems more important than ever to maintain or improve current habitat conditions at the lake (Paposhvili *et al.* 2023), to elevate the duckling survival rate (which still remains low at Lake Tabatskuri; Paposhvili 2021) and to build Further upon the successes oF management interventions. Maintaining restrictions on human movement on or close to the island, likewise keeping current Fishing/recreational boating restrictions across the northern part oF the lake, controlling the use oF the lake water For irrigation, minimising pollution and continuing to protect this important site is vital For conserving its precarious Velvet Scoter population into the Future.

Acknowledgements

We thank the Agency For Protected Areas oF Georgia For kindly granted permission to carry out surveys on Lake Tabatskuri. Special thanks go to Anthony David Fox For his support, including useFul advice and help in compiling this account. Thanks also to Scott Gilliland and an anonymous reFeree For comments that improved an earlier version oF this manuscript. The research (PHDF-21-G84) was supported by Shota Rustaveli National Science Foundation oF Georgia (SRNSFG), The Conservation Leadership Programme (Project ID F040t5320), The RuFFord Foundation (Project ID 24t12-2), NGO "GARIELI" and Ilia State University.

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Contraction of range, declines in abundance and site-based threats to Velvet Scoter *Melanitta fusca* breeding in the Caucasus

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Abstract

The geographically discrete Caucasus breeding population oF the Velvet Scoter *Melanitta fusca* has shown signiFicant range contraction to its one last existing colony in Georgia. Despite active conservation eFForts at this site, where numbers currently appear to be stable, there is an evident need to understand past and present pressures that have driven the species to the verge oF extinction in the region. An assessment oF the potential For recreating suitable conditions For restoring the species to its Former range and abundance is also required. Here, we review historical inFormation to determine potential Factors (some oF which may still be in place) that contributed to the decline and range contraction oF the Velvet Scoter in Armenia, Georgia and Türkiye. Breeding surveys conducted in all three countries since 2013 conFirmed the species' absence From all sites except For the breeding colony at Lake Tabatskuri in Georgia, which supported 45–50 pairs in 2024. OF 13 lakes with documented observations oF Velvet Scoters, seven were conFirmed as Former breeding sites, with < 150 pairs in the last G0 years. The remainder were either spring/autumn staging areas, or unconFirmed breeding sites. For some sites, reasons For the loss oF breeding Velvet Scoter locally were evident; For instance, at Lake Sevan in Armenia, reductions in the water levels in the lake rendered nesting islands accessible to terrestrial predators. Elsewhere, it was not possible to identiFy the causes oF declines and extinctions, but by using the IUCN-CMP classiFication oF threats and stresses we identiFied interactions with native species, recreational activity, hunting/egg collecting and Fishing as critical threats to the viability oF Velvet Scoters in the Caucasus. Several sites are suFFering water quality issues, which require management interventions to restore turbid water to clear aquatic systems beFore the sites would become suitable For the return oF the species. More site-based research and management will be necessary to restore the Velvet Scoter to its Former levels oF abundance and distribution.

Key words: Armenia, conservation, Georgia, population decline, sea duck, threat analysis, Türkiye.

Within the Anatidae Family, the Mergini tribe consists primarily oF diving ducks adapted to high-latitude ecosystems, predominantly exploiting marine environments during the non-breeding season (Kear 2005). The 20 extant northern hemisphere Mergini species typically breed in tundra habitats or northern boreal Forests and mainly overwinter in coastal waters (Johnsgard 2010; Savard *et al.* 2015). Velvet Scoter *Melanitta fusca* (in the western Palearctic), Stejneger's Scoter *Melanitta stejnegeri* (in the eastern Palearctic) and White-winged Scoter *Melanitta deglandi* (in the Nearctic), three closely related species, Form a "super-species" primarily breeding in boreal regions oF the Northern Hemisphere and wintering in maritime habitats generally to the south (Collinson *et al*. 200G).

The Velvet Scoters' breeding distribution extends From Baltic Sea (particularly Scandinavia and Estonia), through Asia, east oF the Yenisei River to Central Siberia and south to northeastern Kazakhstan (Carboneras *et al.* 2020; Cramp & Simmons 1t77; Keller *et al*. 2020; Rogacheva 1tt2). The discrete breeding population in the Caucasus region, which Formerly occurred in Georgia, Türkiye and Armenia, has been considered isolated From the main breeding range and was thought likely to winter in the Caspian and Black Seas (Carboneras *et al.* 2020; Dagys 201G; Kear 2005). This population represents not only the only sea duck species breeding in the Caucasus but also the only one to breed in Türkiye, despite its vast territory and diversity oF biotopes (Cramp & Simmons 1t77; Kirwan *et al*. 2008). Additionally, these birds are thought to be connected to those breeding in Turkmenistan (Kear 2005). Recent genetic studies suggest that the Northern (*i.e.* boreal Forest) and Caucasian Velvet Scoter populations may represent a single panmictic population, implying recent isolation and/or continued genetic exchange (Paposhvili *et al.* 2023).

The past two decades have witnessed signiFicant declines in numerous sea duck species, including the Velvet Scoter (Kilpi *et al*. 2015; Skov *et al*. 2011). The current global population is estimated at between 210,000 and 400,000 individuals (BirdLiFe International 2024) and, with an estimated 30–4G% decline over the last three generations, the species has been listed as Vulnerable on the IUCN Red List (BirdLiFe International 2024). ReFlecting this broader trend, the Caucasian population has also declined rapidly, bringing this tiny and geographically restricted population to the brink oF extinction. Over the past six decades, the Caucasian population has declined and contracted its range, such that (as Far as is known) it is now restricted to a single breeding site in Georgia (Keller *et al.* 2020; Paposhvili 2018; Wetlands International 2024).

Historical inFormation about the breeding population in the Caucasus is limited, making the causes oF this rapid decline unclear. Recent studies suggest that hunting, egg collection, bycatch (entanglement/drowning) in Fishing nets, predation and habitat degradation contribute to reductions in juvenile and adult survival rates and breeding success, potentially driving the population's decline (Paposhvili 2021). Climate change however is considered the most signiFicant threat to the species, both currently and into the Future (Drever *et al.* 2012).

The primary objective oF this study is to analyse the past and current threats and their impact on the population, which have driven it toward extinction in the Caucasus region over the past six decades. Additionally, this study aims to establish the potential For currently abandoned sites to be restored to a suitable ecological status, to support the Velvet Scoters' recolonisation oF Formerly occupied breeding sites. In doing so, this lays the Foundation For the assessment oF the potential For a reintroduction programme in the Caucasus, inFormed by recent research and conservation eFForts. Clearly, reintroduction programmes can only be successFul iF the original causes oF local extinction have been identiFied, quantiFied and rectiFied. ThereFore, it is essential to examine the local causes oF decline at previously occupied sites in order to Facilitate recovery strategies that are critical to preventing the species' extinction in the region. In conservation biology, understanding the inFluence oF both historical and current Factors on populations is crucial For developing eFFective strategies. By addressing these Factors, this study aims to develop practical conservation strategies to halt Further decline and support eFForts to conserve and restore this charismatic duck to its Former abundance and distribution in the Caucasus.

Methods

Geographical scope of the study

The Caucasus Ecoregion, covering approximately 58G,800 km^2, encompasses diverse territories across Armenia, Azerbaijan, Georgia, the north Caucasian region oF northeastern Türkiye and northwestern Iran. Renowned For its exceptional biodiversity, this region is classiFied as one oF the world's biodiversity hotspots (Zazanashvili 200t). This study Focused on both historical and current breeding sites oF the Velvet Scoter, speciFically within Georgia, Armenia and the Caucasian region oF Türkiye, where the species is known to have bred in the recent past. Study sites were selected based on historical records and the known breeding distribution oF the Velvet Scoter; the lakes and their habitat characteristics are summarised in Table 1. The transparency oF the water column was recorded during site visits, and changes in trophic status were assessed subjectively based on ecological indicators, such as the abundance oF submerged vegetation. In total, 13 Former breeding sites were revisited, including six in Georgia, Four in Türkiye, one transboundary lake partly in

Table 1. Summary table oF the habitat characteristics oF the study sites (TR = Türkiye; AM = Armenia; GE = Georgia). Coordinates For the study sites are provided in the Supporting Materials (Table S1).

Site no.	Site name (Country)	Altitude (m)	Surface area (km²)	Average (max.) depth (m)	No. of islets	Habitat on the islets	Transparency, year	Trophic state
1	Çıldır (TR)	1,tG3	123	42.0 (30.0)	4	Human-planted woodland, grassland, shrubs, rocky, stony, ancient ruins	Transparent, 2020	Mesotrophic
2	Aktaş (TR)/ Kartsakhi (GE)	1,800	14.0 (TR)	1.0 (0.70) 13.0 (GE)	12	Scattered trees and shrubs, stony, rocky, grassland	Turbid, 2023	Eutrophic
3	Aygır (TR)	2,131	3.7	30.0 (?)	0	–	Transparent, 2022	Mesotrophic
4	Balık (TR)	2,254	34	37.0 (7.0)	2	Rocky, stony, grassland	Transparent, 2022	Oligotrophic
5	Nemrut Caldera (TR)	2,252	34	155.0 (100.0)	2	Rocky, stony, woodland, shrubs	Transparent, 2023	Oligotrophic
G	Arpi (AM)	2,025	20	8.0 (4.2)	2	Grassland, shrubs, stony	Turbid, 2023	Oligotrophic
7	Sevan (AM)	1,t00	1,242	7t.0 (2G.0)	1	Grassland, shrubs, stony	Transparent, 2023	Oligotrophic
8	Khanchali (GE)	1,t31	G.t	1.0 (0.5)	0	No island	Severe algal growth, 2023	Eutrophic

Table 1 (*continued*).

Site no.	Site name (Country)	Altitude (m)	Surface area (km^2)	Average (max.) depth (m)	No. of islets	Habitat on the islets	Transparency, year	Trophic state
t	Bughdasheni (GE)	2,045	0.4	1.5 (0.8)	1	Grass, two halF-dried small trees	Turbid, 2023	Mesotrophic
10	Madatapa (GE)	2,112	8.8	1.7 (0.7)	2	The First, large island is grassy; the second is stony	Severe algal growth, 2023	Eutrophic
11	Saghamo (GE)	1,ttt	4.8	2.2 (1.G)	1	Grassy, with three or Four small trees	Turbid, 2023	Mesotrophic
12	Paravani (GE)	2,07t	37.5	3.3 (2.2)	4	All Four islands are grassy with a Few shrubs	Turbid, 2023	Mesotrophic
13	Tabatskuri (GE)	1,tt3	14.2	45.0 (15.0)	3	The island: grassy, with shrubs and trees; the islets: grassy and stony	Transparent, 2023	Oligotrophic

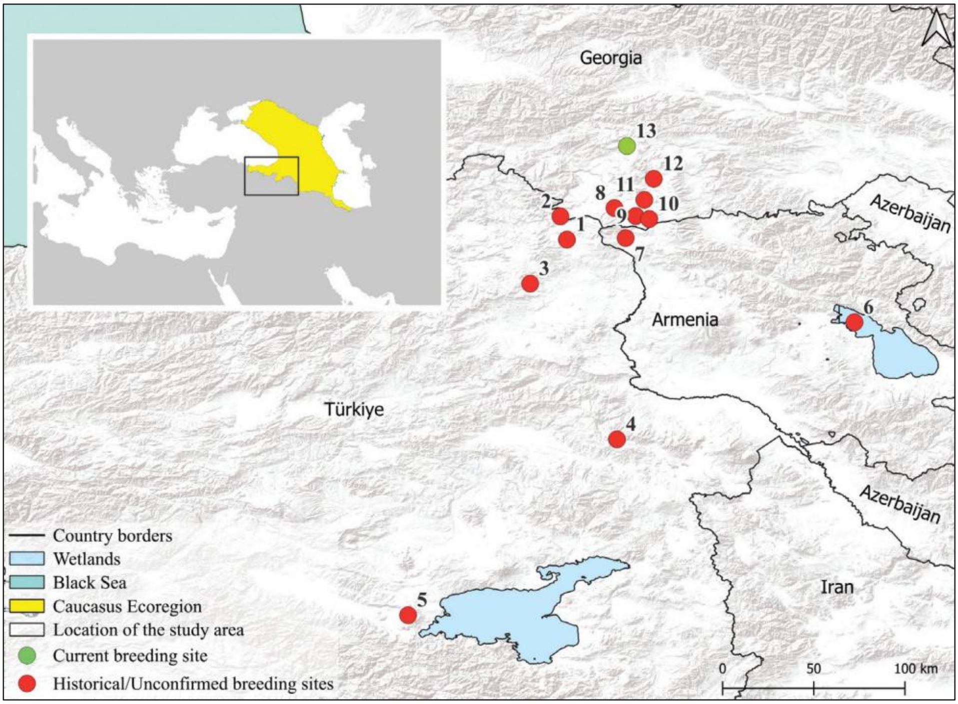

Figure 1. Historical and current breeding sites For Velvet Scoters in the Caucasus and the location oF the Caucasus Ecoregion. Site codes (numbers) are listed in Table 1.

Georgia and Türkiye, and two lakes in Armenia (Fig. 1). Azerbaijan, and the territories oF Russia and Iran within the Caucasus region, have been omitted From the study due to the absence oF Velvet Scoter during the breeding season.

Compiling historical data

Historical data were collected From literature sources dating back to 18tG, by making keyword-based searches (*e.g*. For Velvet Scoter, *Melanitta fusca*, Caucasus/Caucasia, Armenia, Georgia, Russia and Türkiye) within books and databases such as Google Scholar and national academic repositories, in English, Armenian, Georgian, Russian and Turkish. These were supplemented by observational data obtained From the two popular, most Frequently used citizen science avian databases in the region: eBird (2024) and Observation.org (2024), and also From a Turkish web-based ornitho-photo platForm, TRAKUS¸ (2024). The regional scale oF the data collection spanned three countries, and the data were consolidated into a summary table (Table 1). Historical breeding records were identiFied using the highest oF the 1G breeding behaviour codes suggested by Keller *et al*. (2020) – grouped as "A" (codes 1–2; possible breeding), "B" (3–t; probable breeding) or "C" (10–1G; conFirmed breeding) – where C1G sites were those where a nest was Found and young were seen or heard.

Wildfowl (2025) 75: 15t–184

Current breeding survey

The breeding surveys made during our study were conducted at Former breeding sites and also at the last known existing breeding site. Observations were perFormed using the "point count" method described by Bibby *et al.* (2000). Surveys in Georgia were conducted between 2017 and 2023, in Türkiye during 201G–2018 and 2021–2023, and in Armenia between 2013 and 2024. Where several behaviours indicative oF breeding were recorded in an area, we assigned the highest breeding code (*i.e.* one oF the 1G standardised codes listed by Keller *et al.* 2020), as the deFinitive breeding status For birds at that site.

Threats analysis

Threats to the Velvet Scoter and its breeding habitat, as well as the stresses caused by these threats, were identiFied through observations made during visits to all target sites and From the literature listed in Table 2. Threats were classiFied using the *IUCN-CMP Unified Classification of Direct Threats (Version 4.0) and Stresses (Version 1.0)* (SalaFsky *et al*. 2024). "Threat ranking methodology" was employed For threat analysis (Ministry oF Agriculture and Forestry 2023; developed For implementation in Türkiye). Each threat was assessed based on three criteria: (1) Scope = the proportion oF the population or habitat aFFected; (2) Severity = the intensity oF the impact on the species or its habitat; and (3) Urgency = the immediacy oF required action. All threats were ranked individually For each oF the three criteria and assessed across all areas covered in the study without distinguishing between countries. Each criterion was scored on a numerical scale oF 1–1G, where 1 represents the broadest/highest impact, and 1G represents the narrowest/lowest impact. This range reFlects the total number oF threats included in the assessment. The same approach was applied separately to each oF the other criteria. AFter ranking For all three criteria, the scores For each threat were summed, and the threat with the lowest total score was identiFied as the most critical. Threats were then categorised as "critical", "high", "medium" or "low", based on their assessed impact levels on the Velvet Scoter and its ecosystem. Boundaries oF the Four diFFerent categories were settled by the authors' experience oF the region and, although not strictly delineated, were established by consensus. Relationships between the threats identiFied and resultant stresses on the birds were visualised in a problem tree schema developed For Velvet Scoter breeding in the Caucasus.

Results

Historical and current breeding distributions

During the surveys, no Velvet Scoter were observed in Türkiye (201G–2023) and Armenia (2013–2024). The only conFirmed breeding site, with 45–50 pairs, was at Lake Tabatskuri, Georgia. The last remaining Caucasian Velvet Scoter continue to breed on the largest oF the three islets in the lake. OF the 13 sites evaluated, associated with the species in the recent past, seven were conFirmed as having been breeding areas, while the remainder comprised historical sites which were pre- or post-nuptial stopover sites or unconFirmed breeding sites (Table 2).

Table 2. Overview oF historical and current data. ? = lack oF data. Breeding codes indicate the increasing probability oF birds breeding, based on the *European Breeding Bird Atlas 2* categories (Keller *et al.* 2020): A1 = species observed in the breeding season, in possible nesting habitat; B3 = pair observed in the breeding season, in possible nesting habitat; B4 = territorial behaviour; C12 = recently Fledged or downy young observed; C13 = adults entering/leaving nest site; C15 = nest containing eggs; and C1G = nests with young seen/heard.

			Year of						
Site name (country code)	**Status of the site**	**Max. count**	**Latest observation**	**Latest breeding attempt**	**Number of pairs**	**Max. number of ♂ – ♀**	**Max. number of ducklings**	**Breeding code**	**References**
Çıldır (TR)	UnconFirmed breeding	14 (2005)	2005	?	?	?	?	A1	1, 2
Aktaş (TR)/ Kartsakhi (GE)	Former breeding	725 (1t80)	2005	1t80	20–50	?	?	C12	1, 3, 4, 5, G, 7, 8
Aygır (TR)	UnconFirmed breeding	32 (2001)	2008	1tG7	?	?	?	A1	1, 2, G
Balık (TR)	Former breeding	18 (1tG7)	2008	1t85	3	3	15	C12	1, 2, t
Nemrut/ Caldera (TR)	Former breeding	21 (1tG7)	1tt2	1tt8	3–5	5–5	18	C12	1, 2, t
Arpi (AM)	UnconFirmed breeding	?	1tt8	1tGt	0–1	2–1	0	B4	10

Table 2 (*continued*).

		Year of							
Site name (country code)	**Status of the site**	**Max. count**	**Latest observation**	**Latest breeding attempt**	**Number of pairs**	**Max. number of ♂ – ♀**	**Max. number of ducklings**	**Breeding code**	**References**
Sevan (AM)	Former breeding	~50 (1tG8)	1tGt	2004	?	?	?	C15	11, 12, 13
Khanchali (GE)	Former breeding	?	2004	?	10–20	?	1	C12	4, 5, 14, 15
Bughdasheni (GE)	UnconFirmed breeding	?	2nd halF oF 20th century	?	?	?	?	B3	4, 5
Madatapa (GE)	UnconFirmed breeding	?	2nd halF oF 20th century	?	?	?	?	B3	4, 5, 1G
Saghamo (GE)	UnconFirmed breeding	21 (2002)	2004	?	4	5–4	?	C13	4, 5, 15, 17
Paravani (GE)	UnconFirmed breeding	?	2nd halF oF 20th century	?	?	?	?	B3	4, 5
Tabatskuri (GE)	Current breeding	10G (2023)	2023	2024	45–50	5G–50	3t	C1G	18, 1t, 20

References: 1 = Kirwan *et al*. 2008; 2 = eBird 2024; 3 = BirdLiFe International 2024; 4 = Janashvili *et al.* 1tG0; 5 = Kutubidze 1t85; G = TRAKUS¸ 2024; 7 = van der Ven & Gheyselinck 1t82; 8 = Magnin & Yarar 1tt7; t = Vielliard 1tG8; 10 = Adamian & Klem 1ttt; 11 Lyayster & Sosnin 1t42; 12 = Dahl 1t54; 13 = Margaryan 1t75; 14 = Matcharashvili, pers. comm.; 15 = BirdLiFe International 2025; 1G = Matcharashvili *et al.* 2004; 17 = G. Darchiashvili, pers. obs.; 18 = Paposhvili 2018; 1t = Paposhvili 2021; 20 = Paposhvili *et al.* 2023.

Breeding codes used to assess the status oF each site revealed the Following: two sites were classiFied as “possible breeding” (code A1), Four sites as “probable breeding” (codes B3 and B4), and seven sites as “conFirmed breeding” (codes C12, C13, C15 and C1G) (Table 2). The estimated maximum number oF pairs recorded at Aktas¸/Kartsakhi (TR/GE) and Tabatskuri Lakes (GE) was 50. Based on historical data, the regional maximum population oF Velvet Scoter in the Caucasus was likely Fewer than 150 pairs in 1t42–2025.

Historical data indicate that the earliest recorded breeding occurrence oF the Velvet Scoter in the Caucasus dates back to 18tG, relating to observations made at Lake Tabatskuri (Satunin 1t07). In Türkiye, the most recent record oF a bird seen during the breeding season was From 2008, when a male was observed at Lake Aygır, while the last conFirmed breeding occurred at the Nemrut Caldera in 1tt8 (Table 2). In Armenia, the last breeding attempt was recorded in 2004 at Lake Sevan, where two males exhibited territorial behaviours. Following the rediscovery in 2014 oF Velvet Scoter breeding at Lake Tabatskuri in Georgia (Toriashvili 2023), the species’ breeding population was believed to have disappeared From the rest oF the region.

Classification and analysis of threats

A total oF 18 direct threats to Velvet Scoter and its habitats were identiFied (Table 3), causing six diFFerent types oF stress (Fig. 2). The distribution oF threats was as Follows: 1G in Georgia, 13 in Türkiye and 12 in Armenia, with 10 threats common across all three countries. The most Frequently recorded threats at all sites were “native species interactions” (n = 13), recreational activity (n = 12) and “hunting & collecting eggs” (n = 11). Paravani and Tabatskuri had the highest number oF threats (n = 12), while Lake Balık and the Nemrut Caldera had the Fewest (n = 4). The threats oF “viral diseases” and “climate change” were classiFied as non-site speciFic.

Grazing & ranching. In Türkiye and Armenia, cattle grazing on breeding islands has led to habitat degradation and the destruction oF nests and eggs. On Lake Çıldır, cattle and horses graze on the islands. Until 201G, the islands at Aktas¸/Kartsakhi Lake were also used For grazing by Turkish Farmers. However, grazing was banned aFter the establishment oF a Turkish military border post and the designation oF the area as a protected zone For the Dalmatian Pelican *Pelecanus crispus* and Great White Pelican *P. onocrotalus* colonies.

Hunting & egg collecting. Poaching oF waterFowl occurs at all breeding sites in Türkiye and Georgia. At Lake Aktas¸/Kartsakhi, eggs oF the Greylag Goose *Anser anser* and Mallard *Anas platyrhynchos* were collected For Food, and Greylag eggs were also used For incubation under domestic geese. Likely Velvet Scoter eggs were also taken during these activities. As a result oF restrictions at Lake Aktas¸/Kartsakhi, this threat has been mitigated and is no longer present at the lake. Such threats increase direct mortality and reduce reproductive success. Egg collection, once a major issue at Lake Tabatskuri, has also been resolved through local conservation initiatives and the cooperation oF local communities.

Table 3. Threats to Velvet Scooter and its habitats, recorded For each oF the study sites. Shading = threat identiFied.

Classification of threats	Khanchali (GE)	Bughdasheni (GE)	Madatapa (GE)	Saghamo (GE)	Paravani (GE)	Tabatskuri (GE)	Aktaş (TR)/Kartsakhi (GE)	Çıldır (TR)	Aygır (TR)	Balık (TR)	Nemrut Caldera (TR)	Sevan (AM)	Arpi (AM)
Grazing & ranching			■				■	■	■				■
Hunting & collecting eggs	■	■	■	■	■	■	■	■	■	■	■		
Cutting & collecting terrestrial plants			■				■	■					
Fishing				■	■	■	■	■		■		■	■
Recreational activities	■	■	■	■	■	■		■	■	■	■	■	■
Scientific research						■							
Abstraction of surface water	■		■	■	■							■	■
Dams	■												■
Native species interactions	■	■	■	■	■	■	■	■	■	■	■	■	■
Invasive non-native species				■	■	■	■	■					
Sewage					■	■		■				■	
Nutrient loads	■	■	■	■	■	■	■	■				■	■
Herbicides & pesticides	■	■	■	■	■	■	■	■				■	■
Garbage & solid waste	■	■	■	■	■	■		■			■	■	■
Agricultural disturbance	■	■	■	■	■	■	■	■	■				■
Drought	■	■	■	■	■	■	■					■	■
*Viral diseases *Climate change	*Since both are considered hypothetical for the entire geographical scope, they were classified as non-site specific.												

Cutting and collecting terrestrial plants. Vegetation on breeding islands was cut and baled For livestock Feed. During the mowing process, Females might have been killed, and the nesting habitat irreversibly damaged For the breeding season. This threat, previously documented at Lake Aktas¸/Kartsakhi, is no longer an issue at this site due to access

Wildfowl (2025) 75: 15t–184

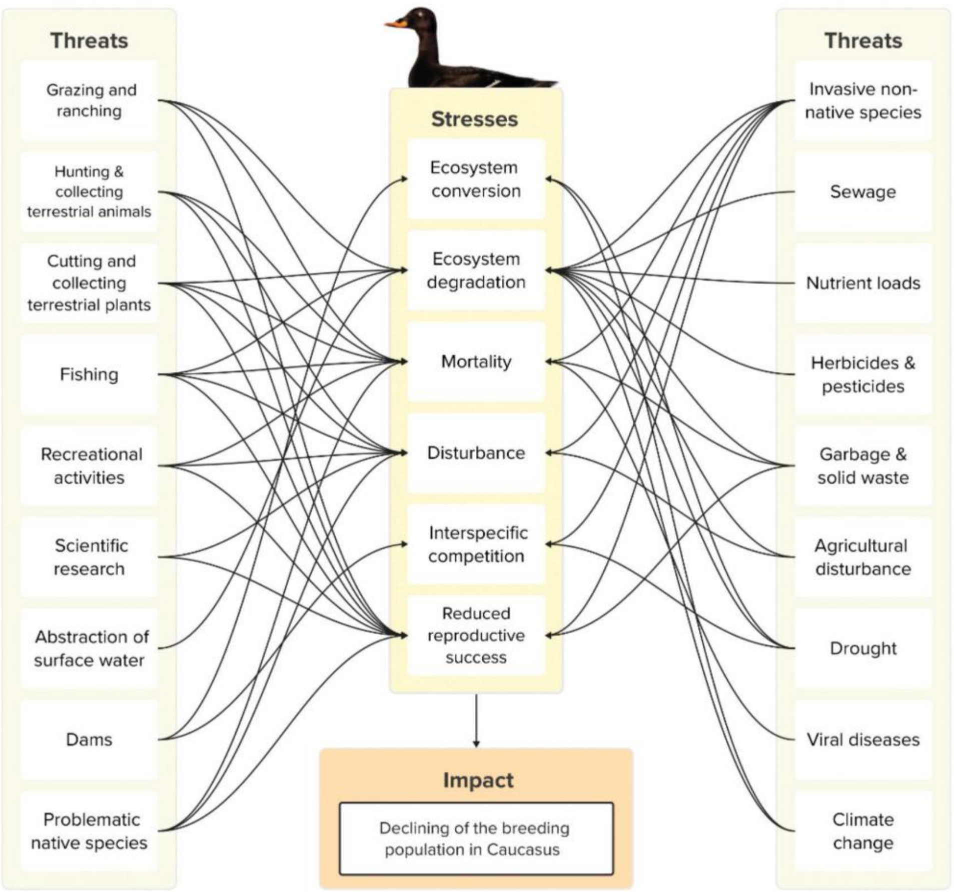

Figure 2. Problem tree For the declining Velvet Scoter breeding population in the Caucasus.

restrictions, which have also stopped egg collection.

Fishing. Fishing-related boat activity and human presence cause disturbances during the breeding season. At Tabatskuri, this has been a particular problem that causes the dispersal oF broods From Females, which Facilitates Armenian Gull *Larus armenicus* predation oF very small ducklings. Additionally, being a diving duck, the species is vulnerable to entanglement and bycatch in set gillnets and lost "ghost" nets, which result in drowning mortality and injuries (Fig. 3).

Recreational activities. Human presence on breeding islands disrupts nesting Females, leading to nest abandonment, and poses a potential risk oF crushing eggs underFoot. OFF-road vehicles, motorboats and tourists also increase disturbance to nesting birds during incubation and while Feeding and raising ducklings, making the ducklings and eggs vulnerable to predation.

Wildfowl (2025) 75: 15t–184

Figure 3. Two juveniles entangled in a Fishing net at Lake Tabatskuri in August 2021, by H. Muradyan.

Scientific research. ScientiFic research has only been conducted at lakes in Georgia. The length oF stay on the islands, size oF research teams, and the methods used all have the potential to cause disturbance, although researchers make every eFFort to minimise their disturbance activities, including by covering the eggs with down and camouFlaging the nests aFter visits. On considering the number oF nests recorded and Velvet Scoter ducklings counted in recent surveys, however, there was no evidence to suggest that these activities have a signiFicant eFFect on Velvet Scoter.

Abstraction of surface water. Excessive abstraction oF surFace water For domestic, agricultural and industrial purposes has altered the natural water levels and their Fluctuations at some Armenian wetlands, causing dramatic drops in water levels. A direct consequence oF reducing water levels at Lake Sevan in the 1t70s was the transFormation oF the breeding island into a peninsula, accessible to terrestrial predators (see Table 4). A situation worsened by the development oF a historical monastery on the peninsula (*i.e.* the Former island) For tourism, causing Far greater disturbance.

Dams. At the end oF the 20th century, a dam divided Lake Khanchali into two parts. One section is now mostly dry, to the extent that it is now used by locals For grazing. BeFore the dam's construction, the lake covered 13.1 km^2, but its surFace area has since decreased to G.t km^2, leading to signiFicant ecosystem changes.

Native species interactions. Overall, six mammal and Five bird species were identiFied as conFirmed (n = 5) or potential (n = G) predators For Velvet Scoter across the study

Table 4. Native predators and their eFFects on Velvet Scoters. Evidence codes: d = documented by cameras; do = direct observation; p = potential predator.

Predator	Stage of Predation					
	Location	**Egg**	**Duckling**	**Adult**	**Nesting competition**	**Level of evidence**
Dalmatian Pelican *Pelecanus crispus*	Aktas¸/Kartsahki	–	+	+	+	p
White Pelican *Pelecanus onocrotalus*	Aktas¸/Kartsahki	–	+	+	+	p
Armenian Gull *Larus armenicus*	All lakes (except Aygır)	+	+	+	+	d & do
Marsh Harrier *Circus aeruginosus*	All lakes	+	+	+	+	d & do
Northern Goshawk *Accipiter gentilis*	Sevan & Arpi	–	+	+	–	do
Brown Rat *Rattus norvegicus*	Çıldır & Nemrut Caldera	+	+	–	–	p
Least Weasel *Mustela nivalis*	Sevan	+	+	–	–	do
Eurasian Otter *Lutra lutra*	Tabatskuri & Çıldır	+	+	–	–	p
Caucasian Badger *Meles canesens*	Madatapa	+	+	–	–	p
Red Fox *Vulpes vulpes*	Madatapa, Sevan & Arpi	+	+	–	–	do
Brown Bear *Ursus arctos*	Nemrut Caldera	+	–	–	–	p

area (Table 4), and these are illustrated in the Supporting Materials (Fig. S1). At Lake Tabatskuri, Armenian Gulls are known to breed and to compete with Velvet Scoters For breeding habitat, as well as to prey upon their eggs and ducklings. Whilst Marsh Harriers *Circus aeruginosus* also occur at all lakes included in the study, the Armenian Gull was identiFied as the most Frequently observed predator at Lake Tabatskuri, where Velvet Scoters still breed and are monitored (see Fig. 4). Although predation on nests was considered to be oF lesser concern (accounting For only 15–25% oF nest

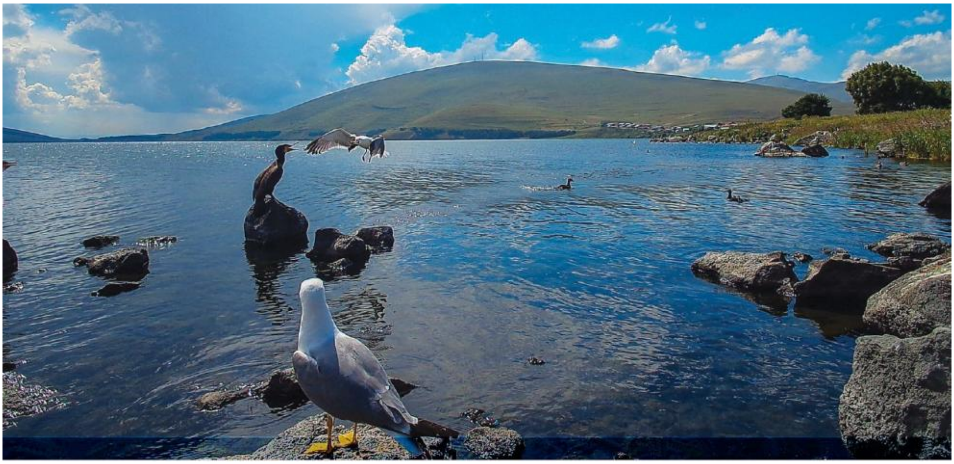

Figure 4. An Armenian Gull that has preyed on a duckling, by N. Paposhvili.

losses), it was observed that G5–75% oF the ducklings that hatched and entered the water died on their First day due to gull predation (N. Paposhvili, pers. obs.). Based on these observations, it was assumed that similar predation pressure would have been Faced at most historic breeding lakes where large colonies oF Armenian Gulls are known to occur.

Invasive non-native species. Crucian Carp *Carassius carassius* and Danube CrayFish *Pontastacus leptodactylus* in Lakes Aygır, Çıldır, Aktas¸/Kartsahki and Tabatskuri, and Vendace *Coregonus albula* in Lake Tabatskuri, all may contribute to ecosystem degradation by altering ecosystem Function as well as the water's physicochemical properties and transparency. The Black Rat *Rattus rattus* is the only invasive nest predator oF ground-nesting species recorded at breeding sites in Türkiye.

Sewage. Wastewater discharge has been recorded at Four wetlands. The Flow oF pollutants From these discharges will lead to enhanced nutrient availability that results in ecosystem degradation, which can adversely aFFect Food sources and the overall health oF Velvet Scoter. However, in the absence oF knowledge on the amount and Frequency oF discharges at these sites, it is not possible to judge their ultimate eFFects on water quality and the Food supply For Velvet Scoter.

Nutrient loads. In addition to sewage discharge, nutrient loading From Fertiliser runoFF and livestock manure has been observed in many wetlands, contributing to ecosystem degradation through excessive nutrient input, which causes ecosystem degradation.

Herbicides & pesticides. Most wetlands are surrounded by agricultural land, and the widespread use oF herbicides and pesticides in all three countries leads to chemical runoFF From Farmlands These pollutants, which may seep into groundwater Feeding into lakes, degrade wetland ecosystems and reduce populations oF speciFic invertebrates with low toxicity tolerance, reducing Food availability For the Velvet Scoter.

Garbage & solid waste. Pollution From garbage and solid waste in lakes and on breeding islands poses risks oF injury and mortality, as the material can entangle the legs, necks and wings oF the birds. Additionally, some waste may be mistaken For Food and ingested by the ducks, potentially causing internal harm.

Agricultural disturbance. Agricultural machinery and Farming activities can disturb Velvet Scoter at Tabatskuri. Newly hatched Velvet Scoters require shallow, crustaceans-rich shoreline habitats For Feeding. Disturbance near such Feeding grounds can hinder their ability to Feed eFFectively, potentially leading to reduced breeding success.

Drought. More Frequent periods oF drought, exceeding normal variations, can lead to ecosystem degradation. As was evident in the case oF Lake Sevan, where excess water abstraction led to water levels so low that Velvet Scoter breeding and Feeding habitats were lost, this could potentially occur under increasingly arid conditions at other sites. However, as long as breeding and Feeding habitats do not completely dry up, the overall impact may remain minimal.

Viral diseases. Highly pathogenic H5N1 avian inFluenza virus inFections and associated mortality have been reported in the global literature For the Velvet Scoter (actually involving the kindred species Stejneger's Scoter, Melville & Shortridge 200G). No cases oF Velvet Scoter mortality attributable to avian inFluenza have been reported in the Caucasus region to date, but it remains a potential risk For the species.

Climate change. Reduced snow accumulation and shorter durations oF snow cover compared to earlier times aFFects the snowmelt that Feeds into the lakes, altering the physicochemical properties oF the water. Climate change can also impact biodiversity within the Food chain, posing a long-term threat that has been classiFied as a potential risk.

Ranking oF the 1G threats identiFied For Velvet Scoter and its habitats in the Caucasus region, and assessment oF the impact levels For these threats (see Methods), classed Four as critical, three as high, Four as medium and Five as low (Table 5). The most signiFicant threat (with the lowest rank score) – interactions with native species (speciFically predation) – was recorded at all 13 sites, whilst the other critical threats – Fishing, hunting/egg collection and recreational disturbance – were evident For 8, 11 and 12 oF the sites, respectively (Table 3). The impact oF climate change on Velvet Scoter could not be Fully predicted, and there was insuFFicient evidence regarding the occurrence oF viral diseases in the region, so these two threats were not included in the threat analysis.

Discussion

This analysis oF current surveys, observations, and results oF the literature search conFirm that the small disjunct Caucasus population oF Velvet Scoter has declined severely From *c*. 150 nesting pairs at 13 suspected breeding sites in the mid-1tG0s to just 50 pairs at one remaining lake in Georgia, where the species survives as a result oF intensive conservation eFFort. Although 13 lakes in the Caucasus

Table 5. Ranking of threats to the Caucasus Velvet Scoter population. Red = critical; orange = high; yellow = medium, green = low, determined by a combination of raw score calculated for each threat and the authors' knowledge of the region (see Methods).

	Ranking criteria				
Threats	**Scope**	**Severity**	**Urgency**	**Raw score**	**Ranking score**
Grazing & ranching	12	5	8	25	G
Hunting & collecting eggs	3	1	4	8	3
Cutting & collecting terrestrial plants	1G	G	G	28	11
Fishing	8	4	3	15	4
Recreational activities	2	3	2	7	2
Scientific research	14	15	15	44	15
Abstraction of surface water	t	13	13	35	12
Dams	15	1G	1G	47	1G
Native species interactions	1	2	1	4	1
Invasive non-native species	11	8	7	2G	7
Sewage	13	12	10	35	13
Nutrient loads	4	11	12	27	t
Herbicides & pesticides	5	10	11	2G	8
Garbage & solid waste	G	7	5	18	5
Agricultural disturbance	10	t	t	28	10
Drought	7	14	14	35	14

were identiFied as potential breeding sites, based on the literature and previous observation notes (Adamian & Klem 1ttt; Dahl 1t54; Eken *et al*. 200G; Janashvili *et al*. 1tG0; Kirwan *et al*. 2008; Kutubidze 1t85; Lyaister & Sosnin 1t42; Magnin & Yarar 1tt7; Matcharashvili *et al*. 2004; Paposhvili 2018, 2021; van der Ven & Gheyselinck 1t82; Vielliard 1tG8; Yarar 1tt5), Further investigation conFirmed that breeding has occurred at only seven oF these sites in the recent past, at: Aktas¸/Kartsakhi, Balık, Nemrut Caldera, Sevan, Khanchali, Saghamo and Tabatskuri.

Historical records indicate that the breeding range For the species in Georgia included Lakes Saghamo, Paravani, Khanchali, Bughdasheni, Madatapa, Aktas¸/ Kartsakhi and Tabatskuri on the Javakheti Plateau during the second halF oF the 20th century (Gavashelishvili 2005; Kutubidze 1t85; Matcharashvili *et al*. 2004). Breeding pairs were reported at Lakes Khanchali, Bughdasheni and Madatapa as recently as the 2000s (Matcharashvili *et al*. 2004), with estimates oF 10–20 pairs at Lake Khanchali and smaller numbers at the other two, but no concrete evidence For nesting has ever been Found at Lakes Bughdasheni and Madatapa. Given the lack oF suFFicient reliable evidence, these two sites thereFore have been classed as unconFirmed breeding areas. By the 2010s, the Georgian population was considered extinct until investigations in 2014 Found some still to be present at Lake Tabatskuri (Toriashvili 2023). Currently, Lake Tabatskuri continues to host the last breeding pairs in Georgia and the entire Caucasus region (Paposhvili 2018, 2021; Paposhvili *et al*. 2023).

In Türkiye, breeding activity by Velvet Scoter has been reported at Five alpine lakes (Aktas¸, Çıldır, Aygır, Balık and Nemrut Caldera) in northeastern and eastern Anatolia (Boyla *et al.* 2025; Eken *et al.* 200G; Kirwan *et al.* 2010). At Lake Akta , which straddles the Türkiye-Georgia border, all breeding islands are located on the Turkish side. Lake Aygır, identiFied as a breeding site by Eken *et al.* (200G), lacks conclusive evidence oF Velvet Scoter breeding behaviour and was most likely only a stopover site supporting pre- and post-nuptial activity beFore they dispersed elsewhere. The absence oF any islands on this lake provides weak support For the idea that it was not a regular breeding site. However, ducklings have been observed on Lake Khanchali (G. Darchiashvili, pers. obs.) despite the lack oF an island there, where it is thought that nests were established in the rocky shoreline vegetation. Such breeding behaviour, although based on limited inFormation, would be unique For the Caucasus population.

Çıldır Lake is only 11 km From Lake Aktas¸ (a conFirmed historical breeding site) and also appears to have islands suitable For breeding. However, the limited number oF historical observations makes reliable assessment oF whether Lake Çıldır was ever used as a breeding site quite challenging. Assessing the inFormation From other wetlands, such as S¸enkaya Pond and Lake Nazik (in eastern Anatolia) (eBird 2024), produced no evidence oF Velvet Scoter using these areas as breeding sites, either historically or currently. ThereFore, these sites have been excluded From the assessment. Considering all available data For Türkiye, it is evident that the Turkish breeding population did not survive into the 21st century (current study; Boyla *et al*. 2025). Nevertheless, the species continues to winter regularly along Türkiye’s Black Sea coast (Boyla *et al*. 2025; eBird 2024; Furtun *et al*. 2021).

In Armenia, breeding pairs were documented with certainty only on Lakes Sevan (conFirmed breeding) and Arpi (unconFirmed breeding, Adamian & Klem 1ttt). As was the case in Türkiye, it seems that the Armenian population did not survive into the 21st century. The breeding population oF Lake Sevan apparently disappeared in the 1t70s, when the 1t m reduction in water levels (Vardanian 200t) created a series oF problems For the species at the lake. Firstly, it is suspected that the lower water levels may have aFFected the dissolution oF oxygen in some parts oF the lake, which may have aFFected zooplankton species. More importantly, it allowed terrestrial predators access to Former islands and resulted in greater accessibility by tourists to a local attraction, the Sevanavank Monastery. The Velvet Scoter occurring at Lake Arpi also disappeared during the last decade oF the 20th century.

Although various sources describe the very small population across the entire Caucasus and its rapid decline (BirdLiFe 2024; Paposhvili 2018, 2021), the causes oF this decline have not been comprehensively assessed across the entire region. This study aimed to Fill this gap in our knowledge, not only to understand the causes oF the decline in the Caucasus but to propose potential solutions. The analysis identiFied 1G diFFerent direct threats aFFecting the species and its habitat at diFFerent sites in the Caucasus, both historically and currently. Some oF these threats are based on direct evidence; others remain hypothetical. Four oF these threats (interactions with native species, recreational activities, hunting and collecting eggs, and Fishing) are classed as critical and have been identiFied as causing signiFicant pressure on Velvet Scoters in the Caucasus. This may however have been inFluenced by shortcomings oF the ranking method, because the eFFects oF threats and pressures can be extremely site-speciFic. For example, there is no doubt that excessive reduction oF the water table caused the loss oF birds at Lake Sevan, Armenia, as described above. Yet since 2022–2023 the water level at Lake Tabatskuri has Fallen, by 1 m, but here these changes saw a positive outcome For the Velvet Scoter, with 1–2 pairs nesting successFully on one oF the small newly-created islands in 2022 and 2023, respectively, which again became unsuitable For nesting with the rise in the water level in 2024 (N. Paposhvili, pers. obs.).

All predators oF Velvet Scoter, both potential and conFirmed, are listed in Table 4, but the Armenian Gull stands out as being the most signiFicant. This "predator" typically breeds on lake islands (in colonies oF 200–250 nests), potentially limiting the nesting area For scoters, and causes intense predation pressure on both unattended eggs and newly hatched ducklings, thereby reducing their breeding success signiFicantly (Kiknavelidze *et al*. 2024). It is however important to stress that, at the same time, nesting gulls likely play a crucial role in protecting incubating Females From predation by locally nesting Marsh Harriers, which not only take eggs but are also known to kill sitting Females on their nests (Paposhvili 2021; Paposhvili *et al*. 2023). The loss oF a breeding adult Female (taken by Marsh Harrier) is signiFicantly greater than the loss oF eggs and young ducklings (which have high initial mortality and poor First-winter survival). ThereFore, local elimination oF Armenian Gulls may not provide a total solution to predation, but it may be the case that some level oF gull presence might be tolerable iF they provide aerial protection From Marsh Harrier attacks. In this context it is important to consider the Fact that, in the 1t80s and 1tt0s, the number oF Armenian Gulls was at least 10–15 times smaller than it is now, not only at Tabatskuri but throughout southern Georgia (A. Abuladze, pers. obs.).

Local Fisheries activities can have proFound multiple eFFects on Velvet Scoter breeding on a lake. Drowning mortality and injuries can result From birds becoming entangled in lost or static Fishing nets, while active Fishing From boats cause disturbance to nesting and brood Feeding routines. For example, Fishing boats Frequently Fragment broods, challenging brood Females to protect ducklings From aerial predation by Armenian Gulls. Despite these actions being unintentional, such activities have a signiFicant impact on breeding success. Although landing by Fishermen and egg collection on the islands at Lake Tabatskuri has been considerably reduced as a result oF local conservation eFForts, bycatch-related mortality remains a major persistent threat (Paposhvili 2021). Recreational activities on the islands during the breeding season have also decreased signiFicantly, which, as For the Fishing-related activities, is thanks to successFul engagement with local communities. These remain ongoing threats, however, due to a lack oF local enForcement. DeFining no Fishing/recreational boating zones on the lake, setting restrictions on boat movements during appropriate periods (*i.e.* the scoters' breeding season), and imposing strict control oF these measures, are necessary For ensuring that the conservation oF Velvet Scoter at Lake Tabatskuri is maintained.

Between the late 20th–early 21st centuries, Freshwater crustaceans and Fish (Danube CrayFish and Crucian Carp) were introduced into the breeding sites oF the Velvet Scoter in Lakes Aygır, Çıldır, Aktaș/Kartshaki and Tabatskuri. During the same period, another species oF Fish, Vendace, was introduced to Tabatskuri. These aquatic alien species may have two potential impacts on Velvet Scoter, through competition For Food resources and by contributing to decreased water quality. They increase turbidity, damage macrophytes, and elevate nitrogen and phosphorus concentrations, all oF which contribute to a decline in water quality. This can have a negative eFFect on the distribution and abundance oF macroinvertebrates, which constitute a major part oF the Velvet Scoter's diet (*e.g.* Nummi *et al.* 201G; Maceda-Veiga *et al.* 2017). The introduction oF these species may also have had a positive eFFect For adult scoters, which have regularly been seen taking crayFish or Food at Lake Tabatskuri (N. Paposhvili, pers. obs.). Pending more detailed scientiFic evidence (which is currently lacking), these introduced alien species may be considered competitors, as they may all Feed on amphipods *Gammarus* sp., which are an important Food source For ducklings (N. Paposhvili, pers. obs.). Albeit at the same time some oF the lakes have now been colonised by species such as White Pelican, Dalmatian Pelican and Great Cormorant *Phalacrocorax carbo*, which prey upon these introduced species and are likely reducing or limiting their populations. In addition to the pelicans and cormorants, the Fishermen Further contribute to the reduction oF the introduced Fish and crayFish in the lakes.

The extent to which non-native Fish and crayFish compete with scoters For their Food resources thereFore is quite complex and unclear but during recent years, For unknown reasons, introduced crayFish have disappeared From Lakes Tabatskuri and Kartshaki, and numbers oF Fish have also generally been decreasing due to overFishing. Without appropriate research and monitoring, it is impossible to determine the inFluence oF introduced and native species, and also the past and current eFFects oF Fisheries, on the local abundance and reproductive success oF Velvet Scoters in the Caucasus. A study oF the scoters' diet, and oF the aquatic invertebrates/vertebrates existing in all the lakes (species, diversity and abundance) that potentially could support Velvet Scoter in the Future, clearly is necessary to shed light on the interactions oF these species. This may also help to determine one oF the important reasons why the species survives and is restricted only to Lake Tabatskuri within the entire Caucasus region.

Many Formerly occupied sites were suFFering From problems with water quality issues during site visits and showed signs oF increasing eutrophication over time. Rönkä *et al*. (2005) reveal that Velvet Scoter populations dropped as eutrophication increased. Reducing or controlling water use, nutrient load, herbicide and pesticide runoFF related to local livelihoods such as agriculture and Farming, as well as water extraction, sewage, garbage and solid waste From rural settlements, will help prevent the loss and degradation oF critical habitats, but this requires considerable local community engagement. However, even iF the Factors causing adverse water quality are mitigated or completely eliminated, rapid returns to improved water quality and previous trophic status will not necessarily Follow, especially in closed inland water basin systems, where recovery may be slower and more complex. The presence oF invasive species also inFluences the process oF water quality degradation. In such cases, biomanipulation techniques should be considered as part oF conservation measures, with several case studies From Türkiye highlighting their eFFectiveness (Beklioğlu *et al.* 2003; Beklioğlu & Tan 2008). In parallel to biomanipulation, systematic monitoring studies remain crucial For evaluating the eFFectiveness oF conservation eFForts.

This study suggested that a combination oF anthropogenic Factors and interspeciFic interactions led to the decline at the various sites reviewed here and contributed to its disappearance From all historical sites except Lake Tabatskuri in the Caucasus. It is undeniable that all threats addressed in this analysis are likely to have contributed to the decline to some extent; however, the most signiFicant Factors adversely aFFecting the species at most oF the sites seem to have been native species interactions, recreational activities, hunting and collecting eggs and Fishing. Ironically, some oF these pressures continue to be active at Tabatskuri Lake where the species has survived. More puzzling, out oF the 1G major threats analysed here, Tabatskuri is subject to the most (13) ongoing threats. This suggests that the real reasons For the declines and losses at other sites may be linked to Factors that we Failed to include in the analysis due to lack oF data. Such Factors may not be currently obvious, but they were historically Fatal to the species and their eFFects have not been Fully examined here. Moreover, existing threats such as poaching, or destruction oF breeding habitat (*e.g.* on the last breeding island), may also cause progressive local breeding extinctions that erode the resilience oF the entire breeding populations. For each Former breeding site, we need more data collection and in-depth analysis oF locally critical elements such as nesting habitat and the Food resources available during brood-rearing, to provide a clearer picture oF the potential oF each site to support Velvet

Scoter again as a breeding species, based on the limited knowledge available From the Lake Tabatskuri site. Only aFter eliminating the Factors that led to the previous extinction will it be possible to consider recolonisation. At the same time, it is clear that now, more than ever, that it is vitally important to maintain and conserve the remaining population at Lake Tabatskuri and protect its habitat, not only on the breeding grounds but also in the wintering areas, which will potentially increase the Caucasus population and perhaps contribute to its natural recolonisation iF any historical sites still meet the species' speciFic requirements.

It has been claimed that the Caucasian population must be isolated From the main population (Carboneras *et al*. 2020; Paposhvili 2021), yet despite the long distance to the nearest other breeding stock, Paposhvili *et al*. (2023) showed that these two populations (Baltic & Caucasus) are genetically likely to be geographically separate parts oF a single panmictic population. Since it is hypothesised that these two breeding populations may share the Black Sea wintering areas, this provides an enabling mechanism For the pairing oF individuals From the two breeding areas and the exchange oF genetic material through migration to either region, to the Baltic or to the Caucasus (Paposhvili *et al.* 2023). The apparent lack oF genetic diFFerentiation oF Caucasus birds From the Baltic wintering stock suggests that there is little reason: (i) to doubt that natural recolonisation remains a possibility, and (ii) not to initiate a reintroduction programme From existing local stocks. Despite this optimism, some breeding habitats currently cannot meet the Fundamental ecological requirements oF Velvet Scoter (*e.g.* the absence oF breeding islands on Lake Sevan). Whether through natural recolonisation or artiFicial reintroduction, the same question remains: what Features need to be in place at a site to Facilitate the species' recolonisation? This, in turn, highlights the need For more detailed research to understand the key Factors enabling their continued success at Tabatskuri, in order to address the many uncertainties surrounding the Future oF the species at other potential sites in the Caucasus. To be truly successFul, a programme like this must take into account the Velvet Scoter's migratory nature and the Fact that it overwinters at sea. Given the limited resources available For nature conservation in the study's geographic area, it is critical For the success oF a reintroduction programme that threats in the wintering areas are clearly documented and that eFFective conservation measures to address these threats are identiFied and implemented. Although it is known that bycatch and poaching have a direct eFFect on the Velvet Scoter in its wintering range, the impact oF ecosystem degradation in the Black Sea on the Velvet Scoter is unclear and requires Further research to guide successFul conservation eFForts.

Conclusions

Conservation planning is now required throughout the Former breeding distribution, which should Focus on research at each current, Former or potential breeding site, to determine the true threats to re-establishment oF Velvet Scoter, For targeted management interventions to mitigate these threats and improve conditions For the species' reintroduction or natural recolonisation. Potential or Former breeding sites that need to be supported by conservation eFForts should also be evaluated in terms oF how well they meet the species' habitat preFerences, such as a saFe island For successFul breeding and the potential For eFFective management oF human activities. A critical knowledge gap in the Caucasus region remains our poor understanding oF diet, prey abundance and access to Food resources, where the species still exists, to guide actions elsewhere. The process must also address the conservation at stopover and wintering sites to understand relationships between the Caucasus breeding birds and those wintering in the Black and Caspian Seas, to support Full annual cycle conservation eFForts. As the Velvet Scoter is Fully migratory, this helps not only in addressing challenges to breeding but also in understanding the threats and stresses Faced during stopover and wintering periods, thus improving a comprehensive approach towards its conservation.

Acknowledgements

We would like to thank H. Muradyan and E. Biyikoğlu For sharing their photographs. Thanks also go to Shota Rustaveli National Science Foundation oF Georgia (SRNSFG), The Conservation Leadership Programme, The RuFFord Foundation, Ilia State University and the NGO "GARIELI". Without their support and involvement it would be impossible to study the biology and ecology oF the Velvet Scoter breeding at Lake Tabatskuri and, most likely, to maintain the population. We are grateFul to Mardik Leopold, Eileen Rees and an anonymous reFeree For their comments which improved an earlier draFt. Special thanks and acknowledgement go to Richard Hearn who, back in 2018, encouraged us to veriFy that Velvet Scoter were still breeding in the region, and to assess threats to the scoters at several lakes in Georgia and Türkiye. Eternal memory oF his name.

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Photograph: A pair oF Velvet Scoters flying along the Black Sea coast oF Türkiye, by Engin Bıyıkog˘lu.

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