

# Whooper Swans *Cygnus cygnus* nesting on offshore islands – a new occurrence or a well-forgotten old phenomenon?

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## Abstract

In recent years, the first cases have been observed of Whooper Swans *Cygnus cygnus* nesting on the offshore islands and coasts of the eastern Baltic Sea, in Finland and the Leningrad region of Russia. Based both on our own data and a review of the literature, we suggest that the tendency for Whooper Swans to breed on offshore islands was probably the result of the actively growing population having widely colonised the majority of suitable lakes across the continental regions of Finland. This view is supported by Whooper Swans not yet being recorded nesting on Sweden's numerous coastal islands, where the breeding density of the species is considerably lower. As further supporting evidence, the literature review also found that Whooper Swan nesting in the marine landscape has not been observed anywhere else within its current range. We additionally provide a synthesis of reports made by M.A. Menzbir about Whooper Swans nesting on the northeastern coast of the Caspian Sea in the second half of the 19th century. Based on both historical and current data from other authors, however, we conclude that these claims were in error and that the birds were most likely nesting on coastal freshwater lakes, which were very numerous in the lowlands around the Caspian Sea during the cooler climate conditions of > 100 years ago.

**Keywords:** Baltic Sea, breeding biology, *Cygnus cygnus*, habitat preferences, Whooper Swan.

As a result of considerable anthropogenic pressure during the first half of the 20th century, numbers of the Whooper Swan *Cygnus cygnus* in Europe declined markedly,

with breeding birds disappearing from the southern half of its former range (Isakov & Ptushenko 1952; Cramp & Simmons 1977; Brazil, 2003). European breeding areas were

restricted to Iceland (*i.e.* the main breeding grounds of the Icelandic population; the Whooper Swan is considered a rare breeding species in the very north of Scotland) and to limited areas in northern Sweden and Finland, as well as the taiga and parts of the forest-tundra zone of European Russia (Isakov & Ptushenko 1952; Bauer & Glutz von Blotzheim 1968; Brusewitz 1971; Cramp & Simmons 1977). During the 1950s–1970s, following adoption of laws to protect the species and environmental change (*e.g.* climate warming and an increase in arable farming) which improved conditions for the species at nesting and wintering sites, Whooper Swan numbers in Europe began to recover and its breeding range expanded. The species was found nesting increasingly further south (Keller *et al.* 2020), notably in Sweden and Finland from the 1950s onwards (Lammi 1983; Svensson *et al.* 1999), and it has now also bred in Latvia, Lithuania and in Poland since 1973 (Baumanis 1975; Nedzinskas 1980; Švažas *et al.* 1997; Lipsbergs 2000; Tomiałojc & Stawyrzyk 2003; Boiko *et al.* 2014), and in Estonia since 1979 (Luigujõe *et al.* 2002; Boiko & Luigujõe 2024).

Whooper Swan numbers also decreased in northwestern Russia during the 20th century, and by the 1970s the species no longer bred in the Leningrad region (Malchevsky & Pukinsky 1983). Population growth and expansion of the swans' breeding distribution began to become evident in all regions of northwestern Russia from 1980–1990 (Kuznetsov & Babushkin 2012; Hokhlova & Artemjev 2002; Fetisov 2021, but these processes were much slower than in the Baltic countries (Keller *et al.* 2020).

In northwestern Russia, the Whooper Swan has settled exclusively on freshwater inland waterbodies, mainly lakes and ponds. It thus differs from the Mute Swan *Cygnus olor*, which inhabited a wide range of offshore islands and coastal sites during the early stages of its expansion in the Baltic region (Berglund *et al.* 1963; Tenovuo 1975; Renno & Paakspuu 1987; Mägi *et al.* 1992; Andersen-Harild 1994). Although adult Whooper Swans have been found in coastal waters (on Korovinskaya Bay and Pechora Bay) in the Russian arctic at the end of the 20th century, nests were located only in the delta region of the Pechora River and in nearby shrub and forest tundra, with reports of Whooper Swans nesting on Lovetskiy Island in Pechora Bay not confirmed (Shchadilov *et al.* 2002; Yu. Mineev and K. Brides, pers. comm.). Elsewhere, the phenomenon of Whooper Swans nesting on offshore islands in the Baltic Sea has only been noticed in recent years (Valkama *et al.* 2011; Kouzov *et al.* 2021; Kouzov & Kravchuk 2023).

Here we therefore aim to describe the emergence of this apparently new feature of habitat selection by Whooper Swans nesting in the Baltic region, through a literature review and by presenting our own data on the swans nesting in the eastern part of the Gulf of Finland.

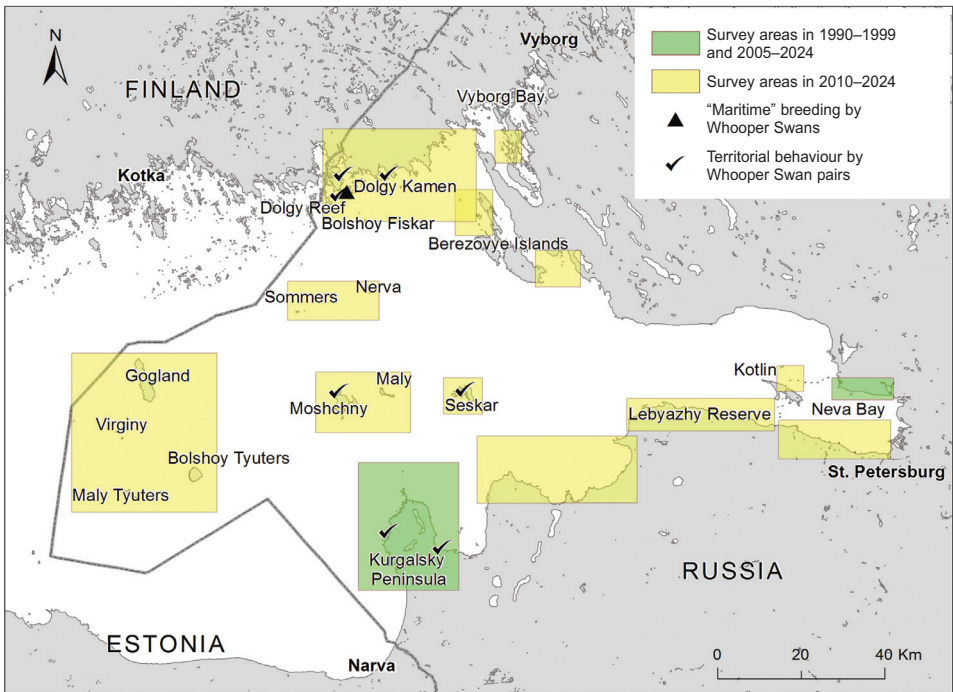
## Methods

Information on Whooper Swans nesting in the Leningrad Region was collected as part of our studies of breeding biology and migrations of waterbirds in 1990–1999 and 2005–2024. During these years, we covered most of the coasts and islands of the Gulf of Finland. Fieldwork was conducted along

the southern coast of the Gulf of Finland (between St. Petersburg and the Kurgalsky Peninsula) and the northern coast of Neva Bay in February–May, with islands near the Kurgalsky Peninsula, as well as central and northern islands in the eastern part of the Gulf of Finland, visited in May–June (Fig. 1). Nests on small unforested islands (< 15 ha in area) were searched during a continuous survey, in which the observer walked the area in a zigzag pattern with 2–3 m intervals between waypoints. On larger forested islands, a 20–30 m coastal strip was surveyed using the same method. The route surveys conducted of Whooper Swan nesting habitats (marshes, *plavni*) along the mainland

coast were made either from the land (by car) or by boat. Territorial pairs were searched for and recorded. If nests were found they were visited to take measurements including: the diameter, height and material of the nest, distance to water and height above water level, clutch size (*i.e.* number of eggs) and the incubation stage of the clutch. Incubation stage was determined by a water test – *i.e.* from the angle of inclination and the extent to which eggs floated on being placed in water (Mednis 2002). The coordinates of each nest were also recorded using a GPS navigator.

In addition to our own data, we also analysed data from a review of the extensive



**Figure 1.** Map of the Gulf of Finland with detailed description of the study area, survey areas and points where nesting and territorial behaviour by Whooper Swans was recorded on offshore islands in the Russian part of the Gulf of Finland.

literature available (128 publications) on the range of the species. This enabled us to trace the changing status of the Whooper Swan in our study area through time, as well as to assess the extent to which the species nested in marine biotopes over its entire range. Papers were sourced by entering keywords (“Whooper Swan”, “nesting”, “islands”) into academic search engines such as Scopus, Web of Science and ResearchGate. Since some regional publications of interest may not be reflected in these sources, we also searched Yandex and Google by entering keywords both in English and in the national languages of the countries being searched.

Furthermore, we analysed data on Whooper Swan nesting in Finland obtained from an open access data repository (Finnish Biodiversity Information Facility 2024), considering only records with breeding index values of 7, 71–75, 8, 81–82 (*i.e.* confirmed breeding). Breeding events without exact coordinates but recorded in quadrats which suggested that they may be on inland lakes on the mainland were omitted from the analysis. A total of 192 records of confirmed breeding in island areas or directly on the seashore between 1973–2023 were sampled. All data were freely available and distributed under a CC BY 4.0 license.

## Results

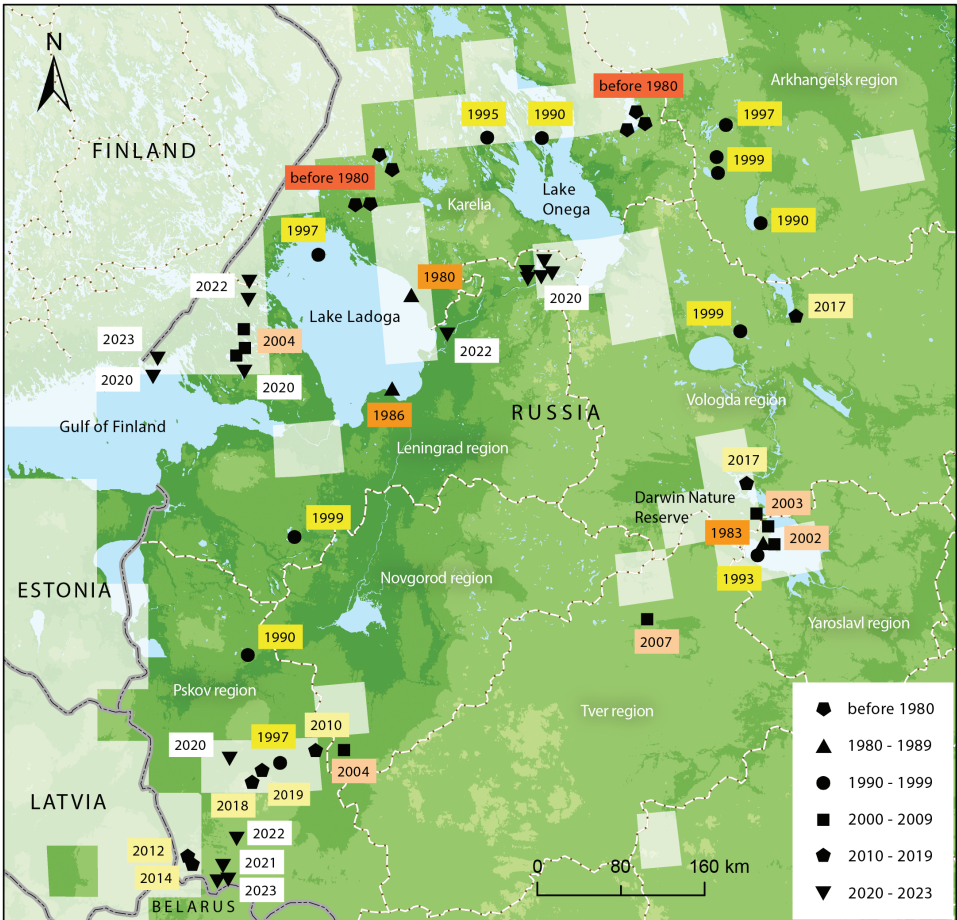
### Whooper Swans breeding the Leningrad Region and adjacent areas of northwest Russia

#### *Literature review*

During the 1980s and 1990s, Whooper Swans started nesting in the Darwin Nature

Reserve in the southern Vologda region of Russia, and in the first 10 years of the 21st century, up to 27 pairs bred at the site (Kuznetsov & Babushkin 2012; Fig. 2). An increase in the Whooper Swan numbers and the expansion of their breeding area to the south were also noted in Karelia during this period (Hokhlova & Artemjev 2002). At the same time, Whooper Swans began to repopulate the Leningrad Region, nesting on southern Lake Ladoga (Vysotsky 1998) and Lake Vyalie in the south of the region during the 1980–1990s (Golovan & Kondratyev 1999) and, at the beginning of the 21st century, on Lakes Bolshoye Rakovoye, Okhotnichye and Melkovodnoye in the northern part of the Karelian Isthmus (Iovchenko 2011; Khrabry 2020). In recent years, the species has continued breeding on the Karelian Isthmus, including on Lake Volochaevskoye (Khrabry 2020), in the north of the Leningrad region on a small lake near the settlement of Torfyanovka (Loseva & Rychkova 2023) and on three small lakes near the settlement of Kuznechnoye (iNaturalist 2024). Reports of breeding in recent years have also come from the northeast of the Leningrad Region – from lakes in the Tihvinsky district, from the Nizhne-Svirsky Reserve (Oliger 2022), from Ivinsky Spill and also on a number of other lakes in the area (Khrabry 2020). In total, we estimate that there are about 20–24 pairs of Whooper Swans nesting in the Leningrad region (Khrabry 2020; Kouzov *et al.* 2021; Loseva & Rychkova 2023; iNaturalist 2024).

Since 2012, Whooper Swans have been observed nesting further south, on lakes in the southern part of the Pskov region



**Figure 2.** Years in which Whooper Swan nests and broods were first recorded in northwest Russia according to published data and iNaturalist. The earliest years are marked in red, the latest in white, and all intermediate years are distributed according to a gradient from red to white. Pale green areas represent confirmed breeding areas of the Whooper Swan according to the European Breeding Bird Atlas (Keller *et al.* 2020). Note that some points may indicate more than one nest.

(Fetisov 2005, 2014, 2015, 2021; Grigoriev 2018, 2019, 2020; Pukinskaya 2024; Shemyakina & Yablokov, 2013). In total, 14–15 pairs may nest in the region (Fig. 2). Additionally, 1–2 pairs have nested on lakes and bogs in the southwest of Novgorod region since 2004 (Arkhipov *et al.* 2015;

Zueva 2011, 2024), and in 2007–2008 one pair was reported nesting in the Tver region (Komarova *et al.* 2015).

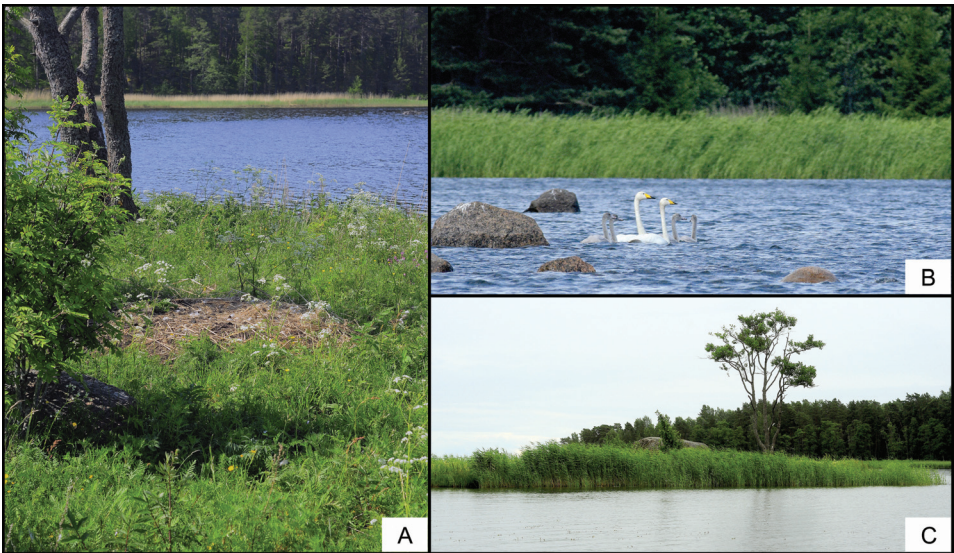
#### *Field observations*

In May–June 2008–2015 we recorded six territorial pairs of Whooper Swans in the

eastern part of the Gulf of Finland. These were found on the western shore of the Kurgalsky Peninsula in 2008, on the eastern shore of the Kurgalsky Peninsula and on Moshchny Island in 2013, on the eastern shore of the Kurgalsky Peninsula and on Dolgy Kamen Archipelago in 2014, and on the Seskar Archipelago in 2015. In all cases, the birds showed territorial behaviour and chased Mute Swans from the area of coastal water that they were defending. However, no nests or broods were found.

On 4 July 2020, in the Dolgy Kamen archipelago on a small moraine island in the stream between Krutoyar Island and Dolgy Kamen Island, a swan nest was found which had long been abandoned by the birds, and the eggshells were already pulverised. A

brood of Whooper Swans with four cygnets *c.* one month old was seen nearby (Kouzov & Kravchuk 2023; Kouzov *et al.* 2021; Fig. 3A, B). Initially, we wrongly assumed that this was a Mute Swan nest, as Mute Swans are common breeders in the area. However, detailed observations and inspection of the eggshells in the following years convinced us that Whooper Swans were nesting at this site. The islet (which is *c.* 30 × 18 m in size) consists of a moraine boulder bed and large pebbles, mostly covered with short grasses, and with a narrow strip of low reeds along the shoreline (Fig. 3C). A pair of Whooper Swans continued nesting on this island during 2020–2024 inclusive, hatching 4–5 cygnets each year, and no eggs were ever found (destroyed



**Figure 3.** Photographs of Whooper Swans breeding in our study area, in the eastern part of the Gulf of Finland, showing: (A) nest after hatching on an unnamed islet between Krutoyar and Dolgy Kamen Islands (7 June 2021); (B) pair with 4 cygnets near Bolshoy Pogranichny Island (*c.* 1 km from the assumed nest, 7 July 2020); and (C) general view of the islet in the stream between Krutoyar and Dolgy Kamen Islands, where Whooper Swans nested in 2020–2024 (4 July 2020).

or dead in the nest) once the brood had departed (Kouzov & Kravchuk 2023; Loseva & Rychkova 2023). The nest was in the same location each year, with the decayed remains of the previous year's nest mound providing the base for the new one.

With 8–12 pairs of Mute Swans also breeding annually in the Dolgy Kamen Archipelago, differences in breeding behaviour by the two species were noted. Firstly, all Mute Swans nested on small rocky skerries mainly in the outer part of the archipelago and their broods were subsequently observed here as well, in the open water near the rocks. The Whooper Swans nested in the inner part of the archipelago (Fig. 1) and broods were held near semi-submerged vegetation. Secondly, the Mute Swan broods moved away along open water when a boat appeared, and the adults never left their nestlings. In contrast, in such cases of danger, the Whooper Swans tended to hide small cygnets in dense reeds, after which the adult swans swam 150–200 m away, where they exhibited agitated behaviour and would even fly out of range.

In July 2022, another breeding pair of Whooper Swans (with brood) was recorded at a small water body near the A-181 Scandinavia highway, c. 17 km northeast of the islet where the Whooper Swan nests had previously been found (Loseva & Rychkova 2023). In 2023, a further territorial pair was seen on Tuman Island near the northern shore of the Gulf of Finland on 12 July, 10 km east-northeast of the nesting site on the Dolgy Kamen Archipelago.

On 26 June 2024, two more territorial pairs without broods were observed near

Ryabinovy Reef Island and on a small islet near Bolshoy Pogranichny Island. Additionally, a scattered group of 11 pairs of non-territorial Whooper Swans was observed on this archipelago. Another large group of 32 birds, including at least eight pairs, were at the Seskar Archipelago from 25–30 May 2024.

### **Baltic Sea region and northern European countries**

The wider review of the literature, for records of Whooper Swans breeding in the Baltic Sea region found that, in the mid-20th century, pairs nesting in Finland inhabited inland lakes and mossy bogs in the northern and central part of the country. Moreover, most of the growth in abundance during the second half of the 20th century occurred on inland waterbodies, but with breeding distribution expanding southwards through the country (Haapanen *et al.* 1973, 1991; Valkama *et al.* 2011). By the 1980s, of 607 nesting sites identified and confirmed in Finland, only 14 were known to be on lakes in the coastal belt (Koistinen 1983), and of these the vast majority were on the coast of the Gulf of Bothnia between Pori and Raahe. During the 1990s, however, the Whooper Swans' range expanded to coastal lakes in the northernmost part of the Gulf of Bothnia near Oulu (Auvinen 2012; Herva & Markkola 2012).

Numbers of Whooper Swans breeding in Finland reached 4,000–6,000 pairs in 2004 (Lehtiniemi 2006), and during first decade of the 21st century the breeding range covered almost the entire country (Valkama *et al.* 2011). Nesting pairs of Whooper Swans were observed along almost the

entire coastal area of the Gulf of Bothnia and the coastal areas of the Åland and southwest archipelagos during this period (Leivo *et al.* 2002; Valkama *et al.* 2011; Fig. 4). By 2014, the breeding population of Whooper Swans in the country had reached 8,400–11,500 pairs (Lehtiniemi 2014), which we estimated as corresponding to a density of 0.02–0.03 pairs/km<sup>2</sup>.

To date, nesting of Whooper Swans has also been recorded in almost the entire coastal zone of the Gulf of Finland (Valkama *et al.* 2011). However, in the coastal area, Whooper Swans overwhelmingly occupy habitats similar to their nesting sites in the continental part of the country – breeding on coastal lakes and lakes on the largest forested islands (Auvinen 2012; Herva & Markkola 2012; Valkama *et al.* 2011).

The earliest case of nesting on a sea island that we were able to find occurred in 1973, near Kälkö Island in the mouth of the Gulf of Finland (Finnish Biodiversity Information Facility 2024; Fig. 4). In the first decade of the 21st century, pairs were reported nesting along the coast and on small islands near Hailuoto in the northern Gulf of Bothnia (Auvinen 2012; Herva & Markkola 2012), and also near Pyhtää on the coast of the Gulf of Finland in 2009 (Finnish Biodiversity Information Facility 2024; Fig. 4).

There were at least two confirmed cases of nesting by Whooper Swan on the coast near Vaasa in the Gulf of Bothnia in 2011–2020: along the coast of Vätungarna Island in 2020, and in the bay of Trutören Island in 2015. On the coast and small islands in the Gulf of Finland during this

period, reliable records of Whooper Swans breeding near Helsinki have been reported: in Vanhankaupunginlahti Bay since 2014 (Citynature 2024) and in Laajalahti Bay in 2020 (Finnish Biodiversity Information Facility 2024). In 2021–2023, the number of observed “maritime nesting” swans increased many times (Finnish Biodiversity Information Facility 2024). Nesting in the marine landscape (130 cases) was observed along the entire coast of Finland, but almost half of the observations were on the coast of the Gulf of Bothnia (Fig. 5A). Of the 40 nests where the location was described accurately, almost a quarter of them were located on small offshore islets rather than in coastal reeds or inland lakes of large islands (Fig. 5B).

After Finland, the country of mainland Europe with the largest number of breeding Whooper Swans is Sweden (Nilsson *et al.* 1998; Nilsson 2002, 2014; Ottosson *et al.* 2012), where the landscape is similar to that of Finland. The number of breeding swans reached 5,400 pairs by 2010, corresponding to a density of 0.012 pairs per km<sup>2</sup>, but here the birds nest exclusively on inland water bodies (Nilsson 2014).

In Lithuania, Latvia and Estonia, the Whooper Swans initially occurred exclusively on inland waterbodies, with first nesting recorded in these countries in 1973, 1973 and 1979, respectively (Švažas *et al.* 1997; Lipsbergs 2000; Luigujõe *et al.* 2002; Švažas *et al.* 2011; Boiko *et al.* 2014; Boiko & Luigujõe 2024). By 2013, up to 600–670 pairs of swans were nesting here, increasing to > 1,000 in just Latvia and Estonia alone in 2021 (Boiko & Luigujõe 2024). Only in

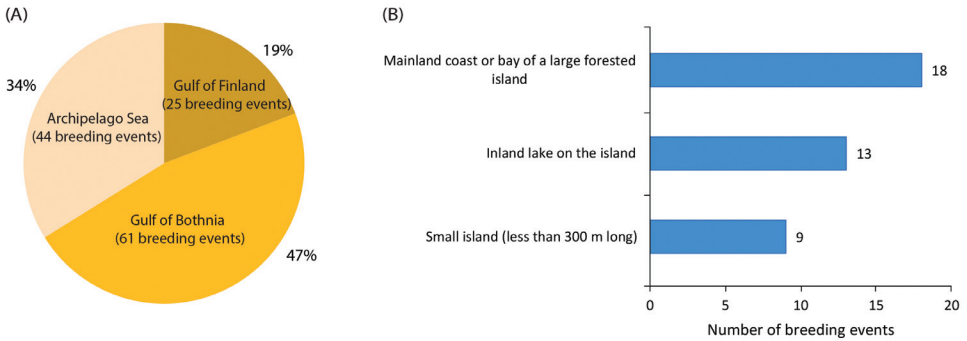




**Figure 4.** Years in which Whooper Swan nests and broods were first recorded at locations on islands and coasts of the Baltic Sea, according to Finnish Biodiversity Information Facility (<https://laji.fi>, accessed 12.02.24), and the location of the first Whooper Swan nest found on an island in Russia. The earliest years are marked in red, the latest in white, and all intermediate years are distributed according to a gradient from red to white. If the exact nest site coordinates were not specified, only records where the extent of the finding area (*i.e.* the range of coordinates) does not include a mainland area with lakes are included in the map.

the 1990s did the swans start to nest in Estonian coastal areas, and then only in freshwater bodies when near the seacoast (Luigujõe *et al.* 2002; Elts *et al.* 2018). In Latvia they are still inland breeders, with none occurring on coastal waterbodies (Boiko & Luigujõe 2024).

In other countries of the Baltic region and northern Europe (*i.e.* in southern Norway, Denmark, northern Germany and Poland), breeding Whooper Swan pairs have exclusively used inland sites from the outset (Tomiałojc 1990; Knief *et al.* 2010; Sikora *et al.* 2012; Nyegaard *et al.* 2014; Dudzik *et al.*



**Figure 5.** Whooper Swan nesting on the eastern Baltic Sea coast and islands in 2022–2023 (according to Finnish Biodiversity Information Facility 2024 and our observations). (A) Total number of confirmed breeding events in 2022–2023 for locations in the seascape (records without precise coordinates in quadrats capturing part of the mainland with lakes were not considered). (B) Landscape distribution of Whooper Swan nests (only records with coordinates accuracy of < 1,000 m were included).

2014; Shimmings & Oien 2015; Dale 2016). Within these countries, we know of only one case of a Whooper Swan nesting on a sea spit, which was near the mouth of a river in northern Norway in 1971. However, even this record is exceptional, because these birds were forced to move to this islet in a year with a very late spring, when coastal lakes were covered with ice for a long time (Myrberget 1980).

### Historical nesting by Whooper Swans on the northern coast of the Caspian Sea

For the last 60 years, the Whooper Swan has occurred in the Caspian region only during winter or on migration (Lugovoy 1963; Krivonosov 1979; Rusanov & Krivonosov 1990; Berezovikov & Gissov 2001; Berezovikov & Gissov 2012; Reutsky 2014). Yet Menzibir (1895) indicated that the Whooper Swan was a common breeding species on the coast and islands of the

northern Caspian Sea in the second half of the 19th century, citing information from N.A. Severtsov. Our detailed analysis of the literature from the late 19th to early 20th century however showed that this opinion was most likely erroneous, and that Whooper Swans nesting (in some numbers) in the region probably used freshwater lakes overgrown with reeds near the coast, rather than maritime habitat (see Supporting Materials Annex S1).

### Whooper Swans nesting in other parts of its range in Eurasia

Throughout the rest of the Whooper Swan’s range in the Palearctic, there are currently no known cases of the species nesting on offshore islands or on the coast (Isakov & Ptushenko 1952; Brazil 2003; Johnsgard 2016; Carboneras & Kirwan 2020). In areas where the species’ range borders a marine area, Whooper Swan pairs nest only on inland lakes, swamps and, less frequently, on

rivers (*ibid.*). This pattern is well documented on the Kola Peninsula (Bianki 1990; Bianki & Shutova 1987), the Kanin Peninsula (Mineev & Mineev 2011) and the Russian Far East (Krechmar & Kondratiev 1986; Brazil & Shergalin 2003). Where Whooper Swans nest in extensive river deltas such as the Pechora, Lena or Amur, they occupy lakes in the upper parts of the deltas away from the seacoast (Degtyarev 1987, 1990; Brazil & Shergalin 2003; Mineev & Mineev 2011; Roslyakov 1990; Roslyakov & Voronov 2023).

## Discussion

Our observations of Whooper Swans in the Leningrad region, with nesting now occurring at sites in the eastern part of the Gulf of Finland, suggest a probability of further increase in the numbers of pairs breeding on offshore islands in the coming years. These island areas, especially Moshchny Island and the Seskar Archipelago in the central part of the gulf, along with the northern skerries and the islands of the Kurgalsky Peninsula to the south (Fig. 1), appear to provide opportunities for an expansion of breeding by Whooper Swans in this part of the Baltic region, because they have relatively low anthropogenic pressure and large areas of suitable habitat available.

Despite the overwhelming presence of Mute Swans in the study area, we consider that competition between the two species may be reduced by differences in the ecological niches that they occupy. Breeding in a seascape, in an area where the Mute Swan has long been widely dispersed, our Whooper Swan pairs showed important

differences with the Mute Swans in their habitat preferences and protective behaviour. For instance, inter-specific differences in defensive behaviour – *e.g.* with Mute Swans having a tendency to guard their young if disturbed, whereas Whooper Swans are more likely to hide them in reeds and abandon the brood – have previously been described for swans nesting on inland water bodies (Isakov & Ptushenko 1952; Brazil 2003). This makes Whooper Swan broods highly dependent on thickets of semi-submerged vegetation, which is usually found only in the inner parts of skerries. There are also some differences in the diets of the two species, with Mute Swans feeding mainly on soft submerged vegetation and algae in the study area, whereas the Whooper Swans' diet is formed largely from harder food such as semi-submerged and swamp vascular plants, *e.g.* the roots and rhizomes of Common Reed *Phragmites australis* (Johnsgard 2016; Kouzov *et al.* 2024). The diets of newly hatched cygnets may of course be very distinct from those of adult birds, and this could form the subject of a separate study.

The literature review indicated that marine nesting among Whooper Swans is likely a new phenomenon for the Baltic region, probably related to population growth, range expansion and an increasing shortage of inland nesting sites, as illustrated for Finland (Valkama *et al.* 2011; Keller *et al.* 2020). Indirect evidence supporting this view is the absence of “maritime nesting” by Whooper Swans in Sweden, where species density is 2.5–3 times lower than in Finland and probably there is not yet a shortage of inland nesting sites.

The occurrence of “maritime nesting” of Whooper Swans in the Leningrad region, where the number and density of the species is significantly lower than in Sweden, may perhaps be explained by the dispersal of birds from Finland.

On analysing the literature, we found one peculiarity. Whilst none of the modern regional publications with nesting data mention Whooper Swans breeding regularly on offshore islands and coasts (except for the very recent occurrences in Finland and the Leningrad region of Russia), and Mark Brazil’s comprehensive review of the species’ range globally during the 20th century noted only a single abnormal case of Whooper Swans nesting on a sea spit in Norway in 1971 (Brazil 2003), caused by delayed ice melt on lakes in the adjacent mainland (Myberget 1980), some major publications describing the Whooper Swan’s breeding habitat state that it occasionally breeds on seashores in bays and estuaries with reed beds (Isakov & Ptushenko 1952; Cramp & Simmons 1977; Brazil 2003) but give references only for swans nesting on inland water bodies. This uniformity in describing occasional breeding in coastal waters suggests that the statements are derived from an older source so, since most of the species’ range lies in historical Russia, we paid special attention to old domestic records (see Results). We assumed that nesting of the species is unlikely on sea coasts with strong tidal activity, which allowed us to limit the search to inland seas, and to find some historical reports of Whooper Swans nesting in the northern Caspian Sea during the mid-19th century (see Supporting Materials Annex S1). The

middle of the 19th century was the time of major exploratory expeditions, made over a vast territory, with one or two researchers in the team often making detailed observations not only on all branches of zoology and botany, but also on geology and geography as well. The probability of some inaccurate description therefore is quite high. Consequently, one cannot but agree with Reutsky (2014) that the historical description of Whooper Swans nesting on the coasts of the Caspian Sea in the 19th century is uncertain. Moreover, if the Whooper Swan (like the Mute Swan) previously bred in large numbers on the coasts of the northern part of the Caspian Sea, and ceased to do so because of intensive hunting of flightless moulting birds in the second half of the 19th century (Menzbir 1895; Isakov & Ptushenko 1952), the question arises as to why (unlike the Mute Swan; Krivenko *et al.* 1990) it did not recolonise this part of its breeding range after protection measures were put in place in the mid-20th century.

The paleontological history of swans suggests that the Whooper Swan, like the other closely related “northern Holarctic” swans (Brazil 2003; Rees 2006), formed as a species in the Pleistocene Epoch (Brodkorb 1958, 1964; Voinstvenskiy 1960; Campbell 1980; Hargrave 1965; Howard 1964; Parmalee 1977, 1980, 1992; Northcote 1988; Martynovich 2004; Panov & Pavlova 2007), in conditions dominated by fresh glacial tundra-steppe lakes (Zeuner 1963; Frenzel 1968) rather than saline waters. The Mute Swan and closely related extinct species of swans, on the other hand, evolved presumably in the Miocene-Pliocene Epoch

(Howard 1946; Voinstvenskiy 1960; Delacour 1973; Bickart 1990; Jefferson & Lindsay 2006; Zelenkov 2013; Kouzov *et al.* 2024), in warmer climates (Velichko 1987; Kennett 1995; Steinhorsdottir *et al.* 2021), and it appears that the Mute Swan was associated with the Paratethys marine basin for much of its evolutionary history (Voinstvenskiy 1960; Dzhabarov 1966). This reinforces the view that mass nesting by Whooper Swans on offshore islands and coasts in the northern Caspian Sea area was unlikely, even though Mute Swans commonly breed in the region (Krivonosov 1987; Rusanov & Krivonosov 1990).

All reports in the literature of Whooper Swans in the northern coast of Caspian Sea during the second half of the 19th and first half of the 20th century are lacking a description of specific nesting sites and habitat use by the species. At this time, there was a gradual climate transition from a long-term cool phase to the modern warm phase (Shnitnikov 1969, 1970; Krivenko 1991, 1992), the level of the Caspian Sea was significantly higher than by the end of the 20th century (Krivenko 1991; Gavrilov 2020), and a large number of fresh and slightly saline shallow lakes covered with rich aquatic vegetation were located along its northern coast. Such water bodies were especially numerous in its northeastern part near the Ural River delta (Lavrovsky 1966; Wolftsun & Smirnov 1970; Krivenko 1991). It seems likely that Whooper Swans nested on these coastal lakes historically with a similar pattern to that currently observed, for example, in Estonia (Luigujõe *et al.* 2002; Boiko *et al.* 2014). The disappearance of Whooper Swans from this region could be

related not only to intense hunting of moulting birds (Menzbir 1895; Bostanzhoglo 1911; Isakov & Ptushenko 1952), but also to the disappearance of most of these breeding habitats as a result of climate warming and lowering of the Caspian Sea levels in the second half of the last century (Shnitnikov 1970; Krivenko 1991). The Mute Swan, which nested mainly on seacoasts and islands (Karelin 1883; Bostanzhoglo 1911; Krivonosov 1987; Krivenko *et al.* 1990; Rusanov & Krivonosov 1990), was not significantly affected by the drying of these lakes when it reoccupied the northern coast of the Caspian Sea.

Overall, we therefore consider it likely that breeding by Whooper Swans on the offshore islands in recent years is a new phenomenon for the species, not only in the Baltic region but throughout its range in the Palearctic. It may be explained in Europe by a southward shift in the swans' breeding distribution and a shortage of inland nesting habitats resulting from the increase in numbers of the species in the second half of the last century. Although whether environmental conditions on or around these islands have changed, so that they are now more suitable for swans, should also be considered.

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