

Interspecific variation in hatching success among three sea duck species at one breeding site in the Baltic Sea

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Abstract

Understanding variation in survival and reproduction is key for conservation and management of bird populations. By compiling and analysing data on hatching success (*i.e.* proportion of nests with at least one hatched egg) from Common Eider *Somateria m. mollissima*, Velvet Scoter *Melanitta fusca* and Red-breasted Merganser *Mergus serrator*, all breeding on a single island in the Baltic Sea, we demonstrate that species-specific variation can be distinct even when nests are found in the same habitat on a relatively small study site. A total of 3,316 nests was found, and hatching success was determined for 2,890 nests during a four-year study period (2021–2024). Both Common Eider and Velvet Scoter exhibited considerable interannual variation in hatching success. Hatching success for Common Eider was highest in the two last years, but in the first two years for Velvet Scoter. Red-breasted Merganser showed more stable and generally higher hatching success than the other two species. Lack of covariation between species over the years indicates that species-specific traits such as phenology and behaviour (*e.g.* defence-mechanisms to avoid nest predation) may override other local factors influencing breeding success. Our results suggest that knowledge of annual variation in hatching success cannot be applied to other closely related species, even when those species are found breeding in the same area and habitat and may even share nesting sites.

Keywords: breeding ecology, diving ducks, incubation behaviour, nest site preferences, predation.

Understanding patterns of survival and reproduction is key for conservation and management of bird populations. Sea ducks breeding in the Baltic Sea have been the focus of conservation initiatives over the last few decades due to declining abundance (Dagys & Hearn 2018; Lehikoinen *et al.* 2022; HELCOM 2023). High mortality of breeding females (Ekroos *et al.* 2012b), low hatching success (Öst *et al.* 2018), and low survival of ducklings (Desholm *et al.* 2002) are well documented drivers of the decline of the most well-studied species, the Common Eider *Somateria m. mollissima*; hereafter referred to as Eider. However, there have been few studies of breeding success and survival for other sea duck species breeding in the Baltic Sea (Skov 2011; Kilpi *et al.* 2015). Consequently, it is difficult to determine whether population drivers identified for the Eider are applicable to other ground-nesting sea duck populations within the same flyway.

Eider nesting success can show considerable interannual variation in the Baltic Sea, where years with low success rates typically are more common than the opposite (Hario & Rintala 2006). The Common Eider is a capital breeder (Sénéchal *et al.* 2011), and interannual variation in breeding success has widely been ascribed to female pre-breeding condition (Bustnes *et al.* 2002; Mohring *et al.* 2022). Pre-breeding condition affects the female's ability to invest in laying large clutches, reduce the recess periods required during incubation, and rear the ducklings (Erikstad *et al.* 1993; Erikstad & Bustnes 1994; Bustnes *et al.* 2002; Hanssen *et al.* 2003; Öst & Steele 2010). Increasing predation pressure has

been reported as a determinant of lower survival rates for Eider females in the Baltic Sea since the mid-1990s (Ekroos *et al.* 2012a; Tjørnløv 2019). For long-lived waterbird species, such as sea ducks, adult mortality is often described as the major driver of population dynamics (Ekroos *et al.* 2012b; Christensen & Hounisen 2014) but this may depend on population and site-specific characters (Gunnarsson *et al.* 2013; Rintala *et al.* 2022). Predation pressure on nests and young may also have strong effect on population dynamics and this has likely increased for Eiders in the Baltic Sea over the last 20–30 years (Lehikoinen *et al.* 2022), potentially interacting with predator-induced disturbance of females during incubation and brooding (Stien & Ims 2016). Two main predators – the White-tailed Eagle *Haliaeetus albicilla* and the invasive American Mink *Neogale vison* – have been identified as key factors limiting reproduction and survival in Finnish Eider colonies, with other mammalian predators also potentially playing an important role locally (Kilpi *et al.* 2015; Jaatinen *et al.* 2022). Contraction of the breeding distribution of Eiders along the Finnish coast has occurred, where islands with open habitat in the outer archipelago have been abandoned by breeding females due to predation by the White-tailed Eagle (Öst *et al.* 2016).

In addition to the Eider, the Velvet Scoter *Melanitta fusca* (hereafter Scoter) and the Red-breasted Merganser *Mergus serrator* (hereafter Merganser) populations have also declined in the Baltic Sea region in recent decades (HELCOM 2023). However, there was a significant positive trend in the numbers of both Scoters and Mergansers

breeding in the Swedish Baltic archipelago between 2015 and 2024 (Green *et al.* 2025). Furthermore, considerable regional differences in population dynamics of the Scoter within the Baltic Sea have been found (Hartman *et al.* 2013). For Scoter and Merganser, the underlying mechanism behind reported population declines within the Baltic Sea are largely unknown. Eiders, Scoters and Mergansers overlap in wintering areas within the so-called Baltic/Wadden Sea flyway (Fransson *et al.* 2001; Dagys & Hearn 2018; Lehikoinen *et al.* 2022). While Scoters and Eiders have similar dietary preferences (mainly benthic invertebrates; Fox 2013) the Merganser is piscivorous (Sjöberg 1985). All three species are ground-nesting birds, and the literature suggests similarities in nest site preferences (Craik & Titman 2009; Hartman *et al.* 2013; Lehikoinen *et al.* 2022).

In this study, we aim to investigate whether hatching success varies among species and between years, and discuss possible factors influencing the patterns found. Earlier studies have used different definitions of breeding or nesting success. Here we define hatching success for Eider, Scoter and Merganser nests as those with at least one egg hatched. Our data were collected during four breeding seasons (2021–2024) on an island in the Swedish Baltic Sea archipelago hosting relatively large numbers of breeding pairs for all three species. Over the four-year period, a total of 3,320 nests belonging to the three species were located, and hatching success was assessed for 2,890 nests. Based on earlier findings, which highlighted predation pressure on incubating females and clutches

as a driver of population dynamics, we predicted low hatching success of all three species. However, given that local conditions have been reported to have high influence on hatching success (Tjørnløv 2019) and since our study is restricted to one relatively small island, we hypothesised that hatching success would covary among the three species between years. Eiders and Scoters have overlapping feeding preferences (Fox 2013; Dagys & Hearn 2018; Laursen & Møller 2022; Lehikoinen *et al.* 2022) and therefore we also expected a higher degree of covariation between these two species, in comparison with the Merganser.

Methods

Study area

Data on number of nests and hatching success of Eiders, Scoters and Mergansers were collected at Hävringsö Island in the outer part of the Oxelösund Archipelago (58.603°N, 17.315°E; Fig. 1), in the middle of the Baltic Sea. Hävringsö is a rocky island of *c.* 11.1 ha in size, and sparsely covered by shrub, bushes and a few trees. There are 13 private cabins on the island, but human presence is generally limited to short-term visits during weekends and public holidays, mainly in late spring and summer. White-tailed Eagles breed on the island in some years, but no land-living mammalian predator has ever been reported on the island. Targeted and successful eradication campaigns of American Mink closer to the coast have successfully prevented their establishment in our study site. During our observations, we identified additional potential avian predators breeding annually

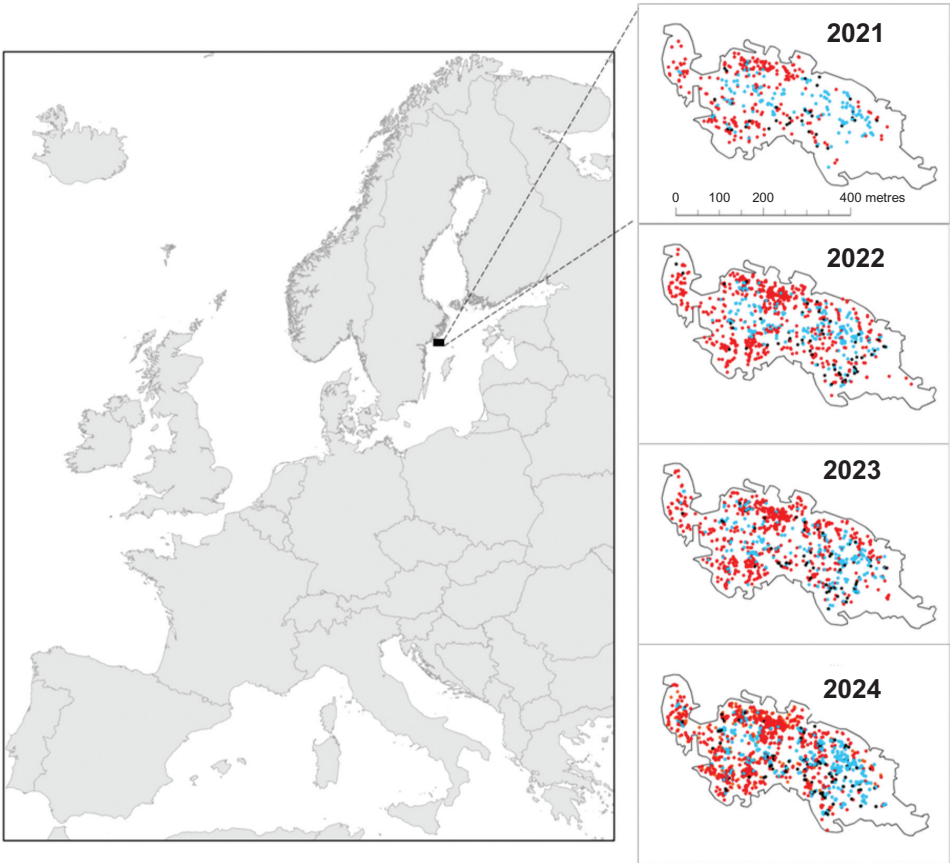


Figure 1. Map depicting the study site within the Baltic Sea. Detailed maps of Håvringe Island indicate the positions of nests found in years 2021–2024 inclusive. Red dots = Common Eider, blue dots = Velvet Scoter and black dots = Red-breasted Merganser nests.

on the island, including Herring Gull *Larus argentatus* (15–25 pairs), Common Gull *Larus canus* (numerous pairs), Greater Black-backed Gull *Larus marinus* (2–5 pairs), and Carrion Crow *Corvus cornix* (5–10 pairs).

Data collection

The first Eider females start nesting in late April, and our monitoring of the nests started between 24–28 April in all years.

With a few exceptions (*e.g.* when volunteer field staff were available), two persons searched the entire island weekly for Eider nests from late April to the first week of June (in total 12–16 working days/year). Because Mergansers and Scoters have a longer nesting period, the monitoring period was extended for these species, although the total survey effort remained comparable in terms of working days per

species. The first Merganser nests were typically found towards the end of the Eider fieldwork (varying between 18 May and 9 June), and the first Scoter nests were typically found later than those of the other species (3–11 June). Searching for Scoter and Merganser nests was continued until 5 August and, during the search for nests, we also revisited known Eider nests to determine nest fate. The entire island was searched over a period of 2–4 days depending on number of Eider nests revisited, but also on weather conditions and the total number of nests. Generally, the surveys for Scoter and Merganser were conducted at 10-day intervals. A final attempt to find remaining nests was made in late August. During the last visit of each season (20–30 August), 5–10 (min–max among the study years) incubating Scoter females were usually found. These late nests were recorded as nests with unknown fate. As field work (including boat transportation) had to be adapted to weather conditions, the dates for field work varied slightly between years.

When a nest was found it received a nest identity (ID), and its location (GPS-coordinates (Garmin GPSMAP 67i)) and the status of the nest (*i.e.* incubating female or nest with eggs) were noted. The nest ID was written on marking tape and this was then placed in view, fixed to a twig as close as possible to the nest, so that the nest could be identified during revisits without disturbing the incubating female. Nests that had already been predated at the time of the first encounter were also included in the data and analysis. During each search for new nests, previously marked nests were revisited on

each occasion to determine their fate. The fate of each nest was determined and assigned to one of three groups: (1) hatched (at least one egg membrane or duckling found in the nest); (2) predated (eggs found predated or nest found without any egg remnants); and (3) abandoned (nest contained cold eggs without signs of predation).

In the present study, predated and abandoned nests were merged into one category, *i.e.* we only distinguished between hatched and failed nests. Unknown fate was noted when a nest was not revisited when breeding was over, typically because of limited time or staff resources. This category however also included nests that could not be relocated, even when searched for, or when the outcome for the nest could not be determined for other reasons. The nests of unknown fate were included in the nest count data but were omitted from further analysis.

Statistical approach

To test for differences in hatching probability between years and species, we applied a logistic generalized linear model (GLM), including species, year (as a factor) and the interaction term (year*species). Multiple comparisons were subsequently conducted to test for significant effects between years and species using the Tukey method to adjust *P* values for family-wise error rates. Model diagnostics were performed to assess residual patterns and verify that model assumptions were reasonably met. All analyses were performed using R (R Core Team 2024) using multiple comparisons in the *multcompView* package (Graves *et al.* 2024).

Table 1. Descriptive data on nest fate (H = hatched, F = failed, *i.e.* abandoned or predated, and NA = unknown). Hatched nests were defined as those where one or more eggs hatched. Percentage (%) values given for each category are per year (2021–2024), for each species (Common Eider, Velvet Scoter and Red-breasted Merganser).

Year	2021			2022			2023			2024			TOTAL
Category/Species	H	F	NA	H	F	NA	H	F	NA	H	F	NA	
Eider	47	146	93	308	187	117	505	120	85	548	134	52	2,342
%	16	51	33	50	31	19	71	17	12	80	18	7	
Scoter	71	45	17	132	38	23	112	99	5	101	94	10	747
%	53	34	13	68	20	12	52	46	2	49	46	5	
Merganser	24	4	6	40	7	9	53	7	5	55	13	4	227
%	71	12	17	71	13	16	82	11	7	76	18	6	

Results

In total 3,316 nests were recorded (2,342 Eider nests, 747 Scoter nests and 227 Merganser nests) and nest fate could be determined in 2,890 cases (87% of all nests; Table 1). The number of nests located each year was on average 586 for Eiders, 187 for Scoters and 57 for Mergansers over the study period (Table 1). For all three species, the number of nests was lowest in the first year (2021), but this more than doubled for Eiders between the first and second year of the study, while Mergansers and Scoters showed relatively smaller increases (Fig. 2).

The probability of hatching differed significantly between the three species, with the highest probability (over years) observed

in Mergansers followed by Scoters and Eiders (Fig. 3, Table 2, Table 3). The significant interaction terms for species and years (Fig. 3, Table 2) demonstrate that the hatching probability did not covary between species and years. However, there was a significant variation in hatching probability between years for both Eiders and Scoters. The probability of hatching was significantly different between all years for Eiders ($P \leq 0.04$ in all cases; Fig. 3, Table 4) whereas it differed significantly only between the years 2021–2022, 2022–2023 and 2022–2024 for Scoter ($P \leq 0.02$ in all three cases; Fig. 3, Table 4). For Mergansers there was no significant difference in hatching probability between years ($P \geq 0.32$, n.s. in all cases; Fig. 3, Table 4).

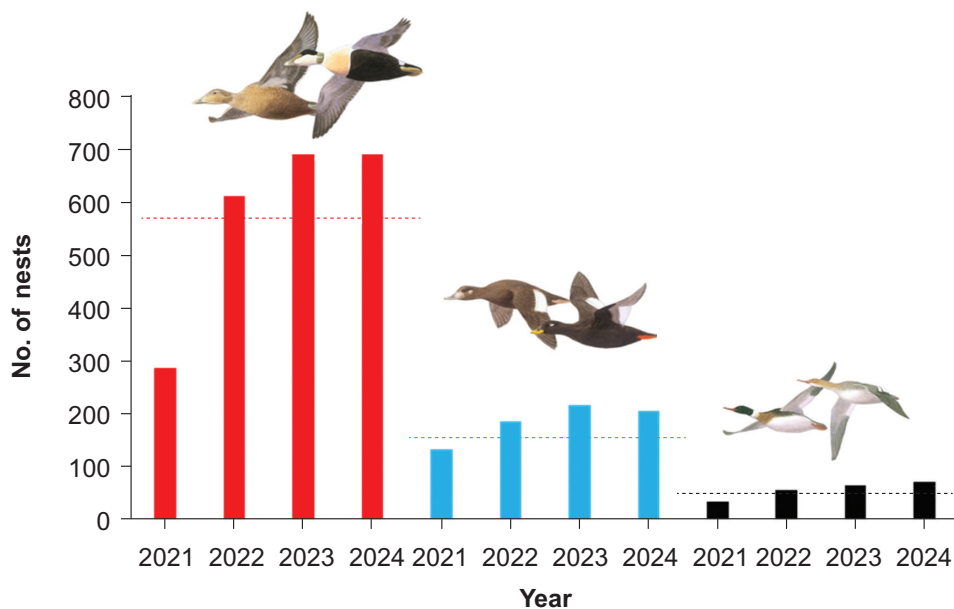


Figure 2. Number of nests found each year for Common Eider (red columns), Velvet Scoter (blue columns) and Red-breasted Merganser (black columns) on Håvringsø Island during 2021–2024. Dashed lines indicate the mean number of nests found for each species over the study period.

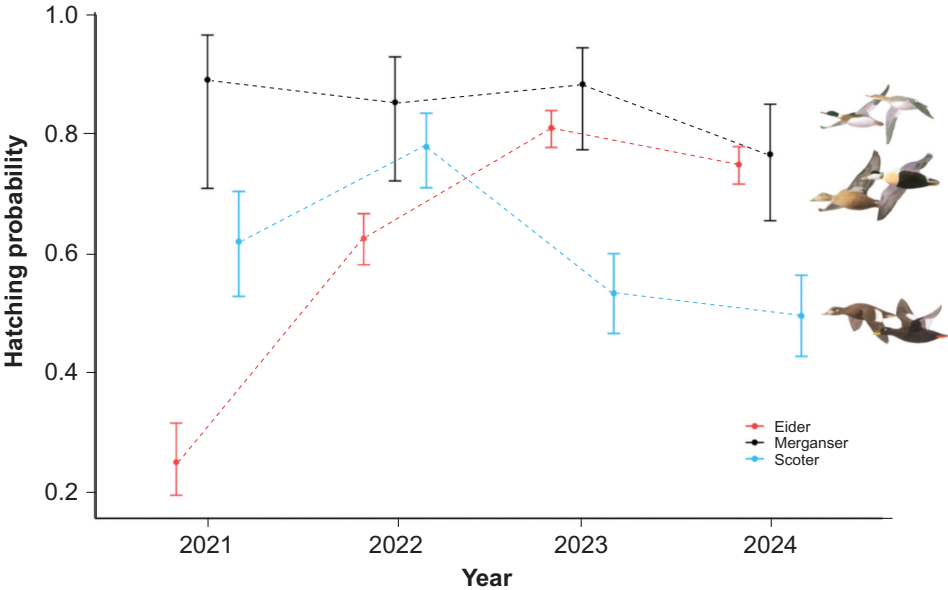


Figure 3. Predicted means (with 95% CI values) for the hatching rate (≥ 1 egg hatched in the nest) each year of Common Eider (red, Eider), Velvet Scoter (blue, Scoter) and Red-breasted Merganser (black, Merganser), for the period 2021–2024 inclusive. The dashed lines illustrate differences between years, but it should be noted that years were treated as discrete units in the analysis.

Table 2. Overall effects from the likelihood ratio (LR) tests in the binomial regression model assessing the effects of year (2021–2024), species (Common Eider (Eider), Velvet Scoter (Scoter), and Red-breasted Merganser (Merganser)), and their interaction on hatching success (≥ 1 egg hatched in the nest). All effects were statistically significant. Pairwise comparisons between years and species are provided in Table 3 and Table 4.

Variable	LR χ^2	d.f.	P value
Year	226.5	3	< 0.001
Species	69.4	2	< 0.001
Year*Species	159.6	6	< 0.001

Discussion

Our study shows considerable variation in the hatching success of Eiders and Scoters whereas Mergansers showed more stable and generally higher hatching success between years. Contrary to our expectations, we observed diverging patterns between species over time, indicating that species-specific traits influence hatching success, even for nests on the same island and in the same habitat.

We predicted that the annual nesting success of Eiders and Scoters would show a high degree of covariation, on the grounds that these two species share basic traits such as diet preference. Furthermore, Eiders and Scoters overlap in nest site selection, and it

Table 3. Pairwise comparisons of hatching success (≥ 1 egg hatched in the nest) recorded for the different species (Common Eider, Velvet Scoter and Red-breasted Merganser) within each year, based on the estimated marginal means (EMMs) derived from the logistic model (see Tables 1 & 2). Pairwise comparisons were adjusted using Tukey's method.

Species (pairwise)	Year	Estimate	s.e.	z-ratio	Adj. <i>P</i> value
Eider–Merganser	2021	−3.19	0.63	−5.03	< 0.001
Eider–Scoter	2021	−1.59	0.25	−6.26	< 0.001
Merganser–Scoter	2021	1.60	0.64	2.49	0.03
Eider–Merganser	2022	−1.24	0.42	−2.96	0.01
Eider–Scoter	2022	−0.75	0.21	−3.61	< 0.001
Merganser–Scoter	2022	0.50	0.45	1.11	0.51
Eider–Merganser	2023	−0.57	0.42	−1.37	0.36
Eider–Scoter	2023	1.31	0.17	7.67	< 0.001
Merganser–Scoter	2023	1.88	0.43	4.42	< 0.001
Eider–Merganser	2024	−0.09	0.29	−0.32	0.94
Eider–Scoter	2024	1.11	0.16	6.79	< 0.001
Merganser–Scoter	2024	1.20	0.31	3.87	< 0.001

is not uncommon for Scoters to reuse Eider nests within the same year (N. Liljeback, pers. obs.). Thus, species-specific differences in nest-site selection alone are unlikely to explain the lack of covariation between Eider and Scoter hatching success during the study period. Hatching success was highest during the last two years for Eiders, reaching 75–80%, while hatching success for Scoters was highest the second year. Eiders and Scoters differ in their breeding phenology, which may expose the incubating females to different challenges in terms of weather conditions, predator abundance and vegetation cover. In contrast, there is substantial overlap in the breeding phenology

of Scoters and Mergansers, and nests of the two species are often found in the same bush or thicket at our study site, although Mergansers generally preferred denser and more thorny thickets for nesting (authors' own observations). Yet the Merganser showed little variation in annual hatching success, and our study suggests more similarity in hatching success across years with Eiders rather than Scoters. If annual predation risk varies within the breeding season (*i.e.* in relation to differences in species phenology alone), we would expect detectable covariation over time for Mergansers and Scoters rather than for Mergansers and Eiders. Moreover, breeding in dense

Table 4. Pairwise comparisons of hatching success (≥ 1 egg hatched in the nest) recorded in the different years of the study, for each species (Common Eider, Velvet Scoter, and Red-breasted Merganser), based on the estimated marginal means (EMMs) derived from the logistic model (see Tables 1 & 2). Pairwise comparisons were adjusted using Tukey’s method.

Year (pairwise)	Species	Estimate	s.e.	z-ratio	Adj. P value
2021–2022	Eider	−1.61	0.19	−8.45	< 0.001
2021–2023	Eider	−2.55	0.19	−13.08	< 0.001
2021–2024	Eider	−2.19	0.19	−11.74	< 0.001
2022–2023	Eider	−0.94	0.14	−6.80	< 0.001
2022–2024	Eider	−0.58	0.13	−4.61	< 0.001
2023–2024	Eider	0.36	0.13	2.69	0.04
2021–2022	Merganser	0.34	0.74	0.46	0.97
2021–2023	Merganser	0.07	0.73	0.10	0.99
2021–2024	Merganser	0.91	0.67	1.35	0.53
2022–2023	Merganser	−0.26	0.57	−0.46	0.97
2022–2024	Merganser	0.57	0.49	1.15	0.66
2023–2024	Merganser	0.83	0.49	1.70	0.32
2021–2022	Scoter	−0.77	0.27	−2.88	0.02
2021–2023	Scoter	0.36	0.24	1.50	0.44
2021–2024	Scoter	0.51	0.24	2.14	0.14
2022–2023	Scoter	1.12	0.23	4.88	< 0.001
2022–2024	Scoter	1.27	0.23	5.51	< 0.001
2023–2024	Scoter	0.15	0.20	0.78	0.86

vegetation, resulting in low predation rate by avian predators and high nesting success, seems to be a general pattern in other Merganser populations (Craik & Titman 2009; Craik *et al.* 2018; Thimot *et al.* 2020).

For Eiders, the hatching rates recorded for the last three years of our study are within, or close to, the range reported for birds breeding in Finland (0.60–0.97;

Hermansson *et al.* 2023), and are notably higher than for Eider colonies in North America although our first year is more comparable (0.32–0.43; Bolduc & Guillemette 2003). The nesting success of Mergansers has also been studied in North America, with hatching rates slightly lower than in our study (0.45–0.74; Craik & Titman 2009). For Scoters, no directly comparable data were found; however, studies of the closely

related species White-winged Scoter *Melanitta deglandi* reveal substantial differences between studies (e.g. 0.35 reported by Traylor *et al.* 2004, contrasting with 0.72 reported by Brown & Brown 1981), with our results falling within this range.

Other studies of Eiders in the Baltic Sea region suggest that predation pressure influences female survival rates as well as hatching success (Ekroos *et al.* 2012b; Jaatinen *et al.* 2022). In our study area, however, mammalian predators (apart from marine species, e.g. the Grey Seal *Halichoerus grypus*) have not been observed. Thus, the increased hatching success for Eiders after 2021 may suggest relaxation from avian predation pressure during the nesting period. One possible mechanism behind this pattern may be that avian predators such as White-tailed Eagles choose other areas for feeding as a response to increased human activity (field work) during our first study year. As our field working efforts stayed relatively constant, returning predators may therefore gradually have found our study-island becoming less attractive over the 4-year study period. Local ornithologists, hunters and cabin owners on the island report, anecdotally, high abundance of White-tailed Eagles and low nesting success of incubating Eiders and Scoters before the initiation of our study. According to the “scarecrow” theory, human presence can provide protection by scaring off predators (Leighton *et al.* 2010). As a case in point, Eider females have been found to aggregate in zones with frequent human presence (Fox *et al.* 2015). For Caspian Tern *Hydroprogne caspia* (Lötberg *et al.* 2022), Kittiwake *Rissa tridactyla* (Anker

Nilssen *et al.* 2023) and Common Murre *Uria aalge* (Hentati-Sundberg *et al.* 2023), human presence has been described to act as a deterrent for White-tailed Eagle predation, resulting in improved breeding success of these ground-nesting birds. Beyond the direct effect of predation, hunting White-tailed Eagles also flush incubating Eider females from their nests, thereby exposing eggs to crows *Corvus* sp. and gulls *Larus* sp. (Stien *et al.* 2010; Stien & Ims 2016). Our presence during fieldwork may have influenced predation risk for Eiders from White-tailed Eagles, but we cannot separate factors affecting eagle abundance from other factors affecting Eider productivity, such as variation in local climate (Dey *et al.* 2018) or the pre-breeding condition of the females (Erikstad *et al.* 1993).

If Scoters and Eiders respond differently to predation by White-tailed Eagles and other avian predators, or to human presence (including field workers), this may contribute to the lack of covariation in annual hatching success between species in our study. But knowledge on differences in the incubation strategies and female behaviour of the three species investigated are limited. One example of a key behaviour that may influence species-specific hatching success is the incubating female's ability to withstand gulls trying to drive her off the nest, which has been documented for Eider (Götmark & Åhlund 1989; Swennen *et al.* 1993). Moreover, in an experimental removal of crows, Stien *et al.* (2010) found that Eider hatching success increased, primarily due to unattended nests not being predated. The use of wildlife cameras placed at Eider nests as a pilot study in our area suggests that

similar behavioural defences used against gulls are also effective against crow predation (own observation). Unfortunately, we have not yet been able to perform similar camera studies on the two other species. Nonetheless, predation on adults, nests and chicks has been emphasised as a driver of population decline for Scoter populations, not only in the Baltic Sea (Hario *et al.* 1986; Nordström *et al.* 2002) but also for the small remnant population breeding in the Caucasus (Kiknavelidze *et al.* 2024; Özkoç *et al.* 2025), and Scoters has been reported as regular prey of the White-tailed Eagle (Ekblad *et al.* 2016). However, during our study period the presence of White-tailed Eagles may also have changed due to the species' first nesting attempt on the island in 2022. The species is known to be territorial year-round (Krone *et al.* 2013) and this may affect the number of eagles visiting the vicinity of our study site. The eagles failed breeding at an early stage in 2022, abandoned the nest late in 2023 but managed to rear one young in 2024. Further, predation risk for incubating duck females and their nests may also vary on a fine spatial scale (*e.g.* due to vegetation), and even though the species overlap in nest site selection, our observations reveal that Scoters generally select denser vegetation than Eiders, which may affect predation risk and hatching success. Vegetation and concealment may play central role in avoiding nest predation in ducks (Craik & Titman 2009; Hermansson *et al.* 2023).

We recognise that the low number of nests of all species found during the first year can be partly attributed to our ability to locate nests, which likely increased over the

course of our initial fieldwork season. However, we contend that this possible “experience-effect” should have been most pronounced for Merganser, as they prefer denser vegetation (Craik & Titman 2009) and we had less knowledge about Merganser and Scoter nest site preferences compared to Eider. Consequently, other underlying mechanisms may have contributed to the perceived increase of Eider nests. As our study is limited to a four-year period, trend analyses and discussions of the potential underlying causes of changes in nest numbers over time are not feasible with the data at hand. Nonetheless, our data offer promising avenues for future research on local population development, which may add knowledge to guide conservation and management of the three study species, especially considering that predation risk may influence breeding propensity of Eider females (Öst *et al.* 2018; Nicol Harper *et al.* 2021) which may add knowledge to guide conservation and management of the three study species. This is particularly relevant given the contrast between our data which indicate an increasing number of nests and hatching rate for Eiders, when there is a general decline in breeding numbers elsewhere along the Baltic Sea.

Conservation and management of waterbird populations require detailed information on reproductive success as baseline data. Recently, initiatives to increase precision in forecasting waterbird population development have been launched in Europe, particularly in the context of adaptive harvest management. These processes have highlighted the importance of reproductive data for management of sea ducks and other

waterbird species (Madsen *et al.* 2015). Further, obtaining such data has been identified as a major challenge for adequate population modelling (Nicol Harper *et al.* 2021). Our study provides an initial insight into patterns of hatching success among three diving duck species in the Baltic Sea. Naturally, longer time series are necessary to draw conclusions about long-term trends, but this represents an important first step and a valuable contribution to ongoing conservation and management efforts. The present study also strongly suggests that variation in nesting success of one species cannot be applied to other closely related species, even when those species are found breeding in the same area and habitat.

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Photographs: Sea duck species breeding in the Baltic study area – Common Eider (upper), Red-breasted Merganser (middle) and Velvet Scoter (lower), by Niklas Liljebäck.