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Drivers of decline and changed nest-site preference of the Baltic eider: an island-level analysis from south-western Finland

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The recent large-scale decline of Eiders (*Somateria mollissima*) in the Baltic Sea is well documented by long-term population monitoring. One hypothesis to explain the decline is increased predation pressure during breeding, but because the decline has been steep and geographically broad, multiple drivers may be involved. Here we explore whether some of these hitherto unidentified drivers relate to the breeding habitat. To this end, we performed an analysis of long-term monitoring data from ca. 300 islands from the Archipelago Sea, SW Finland, representing five geographical sub-areas, during 1993–2012. We analysed population trends and whether nest-site preference changed over time. The results showed steep population declines in the sub-areas farthest from the mainland and a more moderate decline in the sub-area closest to the mainland. The presence of breeding gulls (*Larus* spp.) on the Eider breeding island had a consistently positive effect on Eider breeding numbers throughout the study period. In contrast, the presence of breeding White-tailed Sea Eagles (*Haliaeetus albicilla*) had a negative effect on breeding numbers, but only during the early study period when the Eagle breeding population was still small. Interestingly, the sign of the effect of the distance from the nearest neighbouring island on Eider breeding numbers changed over time. Eider breeding numbers positively correlated with island size and distance to neighbouring islands in the early period, whereas exposed large islands with islands nearby were positively associated with Eider breeding abundance during the late period. Future conservation efforts should shift from site-specific conservation to population-specific management due to the shift in nest-site preference. Furthermore, the positive influence of gulls warrants the adoption of conservation measures taking interspecific interactions into consideration.

1. Introduction

Birds are considered as sensitive indicators for detecting changes in the environment they inhabit (Gregory *et al*. 2004). However, long-term monitoring data on birds should, ideally, further our understanding of the causes and consequences of change rather than simply recording them (e.g., Lindenmayer & Likens 2010). Relying solely on population trend data can result in a failure to correctly diagnose the underlying causes of population dynamics (e.g., Schaub *et al.* 2010). Mere population delineation may also be insufficient for revealing any significant shifts in population concentrations as a consequence of the changes in the environment, which may render existing monitoring schemes – typically based on fixed locations – less informative than desired (Öst *et al.* 2016). One way to overcome this difficulty is to explicitly model population trends in relation to habitat features, biotic factors including interspecific interactions, as well as anthropogenic factors. In adopting such an approach, studies using individual colonies as the unit of analysis should be particularly relevant for conservation.

Based on long-term data, the breeding population of the Eider (*Somateria mollissima*) in the Baltic Sea has suffered a steep decline in the past decades (Ekroos *et al*. 2012a), leading to a recent listing as endangered in Europe (BirdLife International 2015a). The Finnish national monitoring scheme of archipelago birds identified a decline in the breeding populations of the Eider already in the mid-1980s in the central Gulf of Finland, and the decline has also been notable in the south-western archipelago at least since 1997 (Hario & Rintala 2002). In contrast, North American population trends are more variable, but due to the decline in Europe the global Eider population has been recently listed as near threatened (BirdLife International 2015b). It therefore seems that the reasons underlying the decline of the Baltic Sea Eider population are specific to this geographic region. Despite the consensus that the species is in a state of significant decline in the Baltic, the reasons underlying the decline are still poorly understood (e.g., Ottvall 2012, Kilpi *et al*. 2015) and, at times, hotly debated (Sonne *et al*. 2012, Tillitt *et al*. 2012).

Ekroos *et al*. (2012a) discussed possible reasons for this decline and proposed a combination of changes in breeding behaviour and increased predation pressure. In a study conducted in the western Gulf of Finland, the survival of Eider females was significantly lower on open islands than on forested islands (Ekroos *et al*. 2012b). This difference was attributed to increased predation pressure on open islands (Ekroos *et al*. 2012b). The main predators of breeding eider females include non-native mammals, particularly the American Mink (*Mustela vison*; Nordström *et al*. 2002) and the White-tailed Sea Eagle (*Haliaeetus albicilla*; Kilpi & Öst 2002). The population of the White-tailed Sea Eagle has rapidly increased since the 1970s (Stjernberg *et al*. 2011).

Relevant in the context of possible predation-driven population decline, also the sex ratio of Eiders has shifted to a male bias concomitant with the population decline, one hypothesized reason for which is increased mortality of breeding females (Lehikoinen *et al*. 2008). The population size of the Eider is expected to be very sensitive to even a small increase in adult mortality, because the contribution of adult survival to the population growth rate is expected to be large in long-lived species (Sæther & Bakke 2000). Some protection from predation may be achieved by nesting in association with larids; for example, von Numers (1995) reported a positive effect of large larids (*Larus* spp.) on the occurrence of eiders in the Archipelago Sea.

Although increased predation on adults, potentially aggravated by increased secondary nest predation (see Hanssen *et al*. 2013), may be one important factor explaining the decline of Baltic Eiders, the fact that the decline has been so rapid and uniform across large geographical areas indicates that there are likely multiple factors affecting the decline (Christensen 2008, Ekroos *et al.* 2012a). One such factor may be climate, which affects particularly breeding success (Lehikoinen *et al*. 2006, Waldeck & Larsson 2013). Lehikoinen *et al*. (2006) and Rönkä *et al*. (2005) showed that cold winters negatively affected the breeding success of Eiders in the subsequent breeding season in the northern Baltic Sea. In direct contradiction to these results, however, Waldeck & Larsson (2013) showed a decrease in dry mass of Blue Mussels (*Mytilus edulis*), the staple food of Baltic Eiders, with increasing water temperatures, which sug-

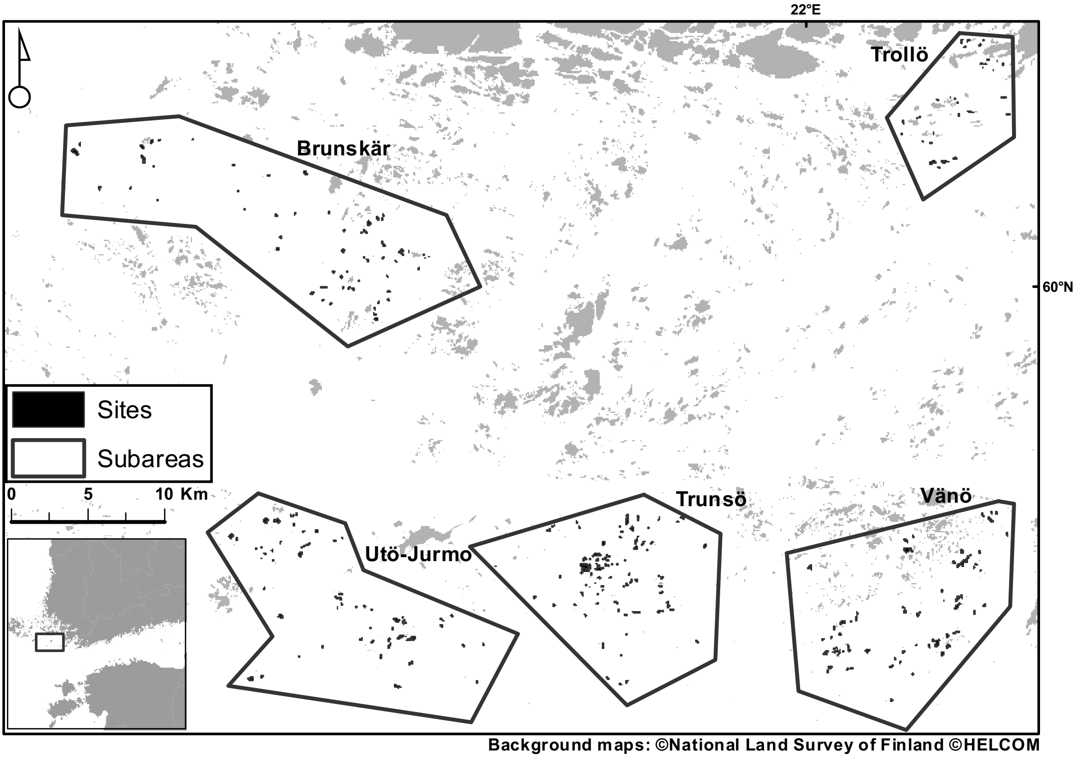

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Fig. 1. The study sites, subareas and the location of the study area in south-western Finland.

gests that cold winters may in fact offer better foraging conditions for wintering Eiders. Obviously, the relationship between winter climate and subsequent breeding success is not straightforward. Other factors affecting eider population dynamics may be related to disease or parasite outbreaks (Christensen 2008) and human presence. The latter effect may, in fact, run in both directions. On the one hand, increased human disturbance may increase nest predation and abandonment (Bolduc & Guillemette 2003). On the other hand, however, the presence of humans can also have positive effects via the "scarecrow effect", when predators avoid areas with humans thus benefiting the prey species (Leighton *et al*. 2010, Fox *et al*. 2015).

While there are a few previous studies that have modelled the habitat preferences of Eiders in the northern Baltic Sea based on census data (von Numers 1995, Heinänen *et al*. 2012), previous studies have not, to the best of our knowledge, modelled changes in habitat preference over time. We performed an analysis of long-term population trends from ca. 300 islands (called sites in this study) from the Archipelago Sea, SW Finland, representing five geographical sub-areas, during 1993–2012.

The aims of this study were twofold. First, we compared long-term population trends in the five different sub-areas. Second, we tested whether nest-site preference has changed over time, by comparing the predictors of Eider breeding numbers in the early and late study period, based on two years with as complete data as possible (1998 and 2009, respectively). These potential predictors can be broadly categorized as habitat-related factors (island exposure, distance to surrounding islands, tree cover, water depth and underwater slope), biotic factors (presence of breeding gulls, terns *Sterna* spp. and White-tailed Sea Eagles) and anthropogenic factors (distance to the nearest building). This study concerns island-level attributes influencing Eider breeding numbers, a particularly useful ecological unit of analysis for conservation purposes.

Table 1. The explanatory variables used for modelling Eider breeding numbers during the early (1998) and late (2009) study period. The variable name, metric and definition are given. Variables marked with "*" were removed from the analyses due to high correlation with another variable.

Variable	Metric	Definition
Exposure	m^2	The area of land within a 500 meter buffer around each study site
Area	ha	The area of the study site
Distance any island	m	Distance to nearest island
Distance > 0.5 ha island*	m	Distance to nearest island larger than 0.5 ha
Tree crown cover	%	The mean tree crown cover of the study site
Mean depth*	m	The mean depth within a 200 m buffer
Mean slope	degree	The mean underwater slope within a 200 m buffer
SD Height	m	The standard deviation of the Digital Elevation Model (DEM)
Larus marinus	*n*	The number of breeding pairs of Greater Black-backed Gulls
Larus argentatus	*n*	The number of breeding pairs of Herring Gulls
Small gulls	*n*	The number of breeding pairs of Common or Black-headed Gulls
Sterna sp.	*n*	The number of breeding pairs of terns
White-tailed Sea Eagle	*n*	The number of active White-tailed Sea Eagle territories within a 5 km buffer
Buildings	m	Distance to the nearest building; both permanent and summer houses

2. Material and methods

2.1. Study species and study area

Eiders in the northern Baltic Sea breed on both small open islands with sparse vegetation cover and on larger wooded islands (Kilpi & Lindström 1997). There is also nest-site-specific variation in concealment, ranging from nests on bare rock without any cover to barely visible nests hidden under bushes or trees (Öst & Steele 2010). The Eider is a highly philopatric species, meaning that the females return to breed to their preferred breeding island year after year (Öst *et al.* 2011).

The study area is located in the Archipelago Sea in South-Western Finland (Fig. 1). The grouping of sites to sub-areas is based on geographical proximity and the sub-areas are non-overlapping (Fig. 1). Of the sub-areas, Trollö is located closest to the mainland (mean distance 23 km) and is the least exposed (mean land area surrounding the sites 7.2 ha) whereas Utö–Jurmo is the furthest from the mainland (mean distance 74 km) and the most exposed (mean land area surrounding the sites 2.2 ha). Exposure was calculated as the amount of land area surrounding the individual sites within a 500 m buffer zone. Trollö has the highest mean tree crown coverage and Brunskär has the lowest, being 22.4% and 15.8%, respectively. When looking at the number of active White-tailed Sea Eagle territories inside or within 5 km of the sub-areas in 2009, Brunskär had the highest numbers with 5 territories and Trunsö and Utö–Jurmo the lowest numbers with 3 territories each.

The Eider monitoring data, as well as the data on the number of breeding gulls and terns, were collected under the Archipelago Bird Census, a monitoring scheme based on standardized methods for counting breeding birds in the archipelago (Koskimies & Väisänen 1991). The dataset used in this study covered over 300 sites (skerries, islets and islands) over a time period of 20 years (1993–2012). Not all sites have been counted each year, so there is variability in the data. For the population trend analyses, all available data was used and for the breeding preference analysis, a year at the beginning and at the end of the study period were chosen based on the maximum number of sites counted in both years. The years 1998 and 2009 were chosen with the same sites ($n = 179$) counted in both years, from the Vänö, Utö–Jurmo and Brunskär sub-areas (Fig. 1). Data from the Trollö sub-area was not available for the breeding preference analysis since Eider breeding censuses at this site were initiated in 2001. The explanatory variables used for the modelling of Eider breeding numbers are shown in Table 1. Of these variables, mean underwater slope was included in the modelling because mussel densities have been shown to increase with declining slope, i.e., shallow waters around the breeding sites (Westerbom *et al*. 2008). We included also mean depth because studies have shown higher numbers of Eiders feeding in waters 0–6 m deep, rather than at depths of 6–12 m (Larsen & Guillemette 2000).

2.2. Statistical analysis

To analyze population trends and annual indices for the Eider populations, we used the program Trends and Indices for Monitoring Data (TRIM; Pannekoek & van Strien 2005). TRIM is specifically designed for analysis of time-series count data with missing observations, by estimating the missing observations using models fitted with existing observations. Also serial correlations are taken into account in TRIM by using a Generalized Estimating Equations (GEE) approach. The program uses log-linear models to predict an imputed annual index from observed count data. The imputed counts are the observed counts, when observations are present or the estimated counts when observations are missing. The annual index value is then calculated by dividing the count total for the respective year with the count total of the first year. Overall trends in yearly indices were computed, taking into account the uncertainty of the indices (Pannekoek & van Strien 2005). These trends were expressed as multiplicative slopes, i.e., as yearly multiplication factors (1 = stable) and were classified into categories according to statistical significance and magnitude. For instance, a "moderate" decline refers to a statistically significant decline, but not significantly more than 5% per year, whereas a "steep" decline refers to a significant decline exceeding 5% per year (Pannekoek & van Strien 2005). To include only the significant change points, i.e., years, insignificant change points were deleted, with a significance level of 0.05.

To analyze potential changes in nest-site preference during the early versus the late study period, we started by conducting a multiple regression analysis on distance matrices (MRM; Lichstein 2007), using the MRM-function in the "ecodist" package (Goslee & Urban 2007). This statistical tool takes into account the spatial structure of the response variable, representing a multivariate extension of a partial Mantel's test using several explanatory variables. This analysis allowed us to incorporate geographical distances between sites as an explanatory variable and also to determine how much of the variance in the response is explained by geographical and environmental distances, respectively (Lichstein 2007). The environmental distances here refer to the between-site differences in the values of the explanatory variables.

We started by running the analysis using only the response and the geographical distances. The results showed low values for R^2, the coefficient of determination, for both analyses (1998: $R^2 = 0.000094$; 2009: $R^2 = 0.000028$), meaning that the geographical distances between the sites explained very little of the differences in Eider numbers between the sites, suggesting low level of spatial autocorrelation. Thus, we were able to proceed with the analyses using raw data instead of using the distance matrices.

We analyzed the number of breeding Eiders in the years 1998 and 2009 using a Generalized Linear Model (GLM). We started with a full model, i.e., the model with all the explanatory variables included, using Poisson errors and log link function. In case of pairs of highly correlated variables (Spearman correlation: $|\rho| > 0.7$), one of them was excluded prior to testing, in order to avoid collinearity (see Table 1). Model selection was conducted with the dredge-function in the "MuMIn" package (Barton 2015) using Akaike's Information Criterion corrected for small sample size (AICc) as selection criterion. Due to overdispersion in the fitted models (1998: $z = 3.1266$; $p < 0.001$; 2009: $z = 3.6012$; $p < 0.001$), we fitted Negative Binomial GLMs with log link function instead using the glm.nb-function in the "MASS" package (Venables & Ripley 2002). We tested for overdispersion using the dispersiontest-function in the "AER" package (Kleiber & Zeileis 2008). The percentage explained deviance was calculated according to Zuur *et al*. (2009):

$$100 \times (\text{null deviance} - \text{residual deviance}) / \text{null deviance} \qquad (1)$$

All the analyses on nest site preference were performed with R (R Development Core Team 2013).

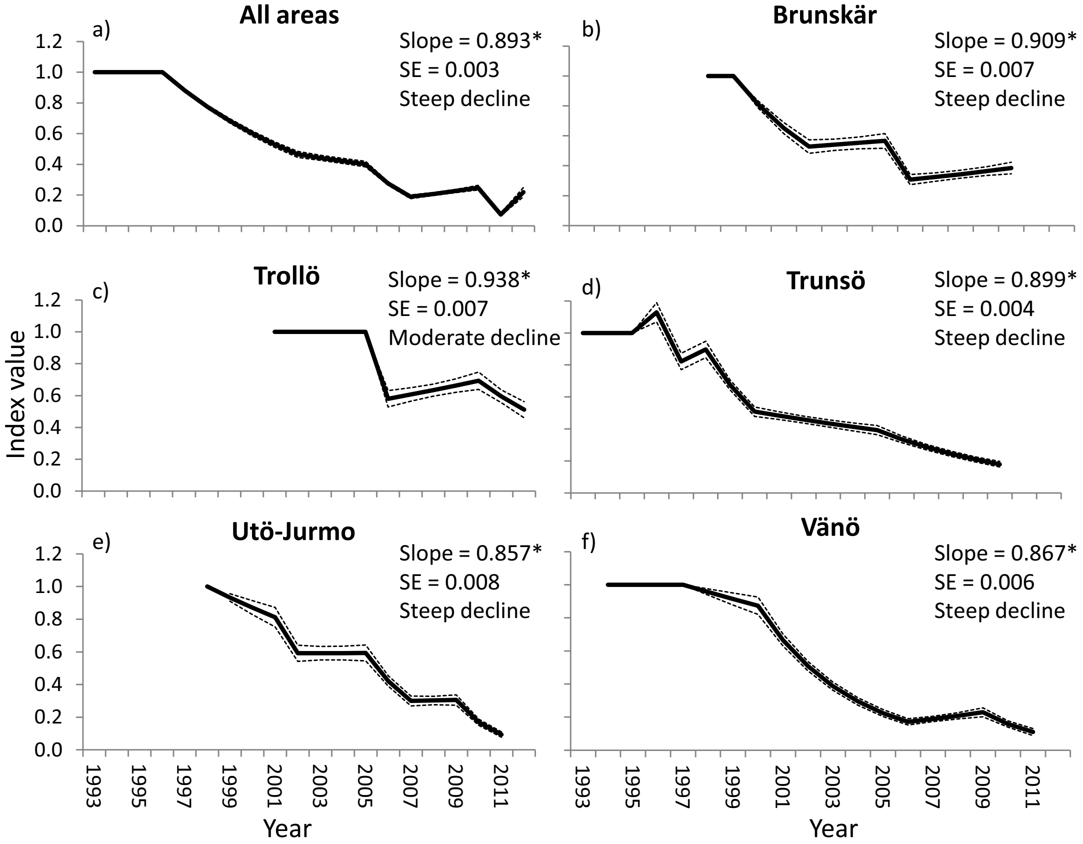

Fig. 2. The trend indices (± SE) calculated by TRIM for each subarea and for all data combined. Multiplicative slopes for the respective areas, reflecting average percentage change per year, have been added with * indicating significant slopes (*p* < 0.05), with respective standard errors. Shown is also a verbal classification of the severity of the decline as interpreted by the TRIM software; a decline significantly exceeding 5% per year is considered steep, whereas a decline not significantly exceeding 5% is considered moderate.

3. Results

3.1. Population trends according to sub-area

There was a decline in Eider breeding numbers in all the sub-areas (Fig. 2). However, the population decline was steep in the four sub-areas farthest from the mainland, whereas the sub-area closest to the mainland, Trollö (Fig. 2c), only showed a moderate decline.

3.2. Breeding numbers and nest-site preference in the early vs. late study period

Eider breeding numbers in 1998 were significantly explained by island area, the mean underwater slope surrounding the islands, the distance to the nearest island, the number of breeding Common Gulls (*Larus canus*) or Black-headed Gulls (*Chroicocephalus ridibundus*), the number of breeding Great Black-backed Gulls (*Larus marinus*), the number of active White-tailed Sea Eagle territories within 5 km and the mean tree crown coverage on the islands (Table 2). Eider females preferred large islands with less tree crown coverage in 1998, situated far away from the nearest neighbouring island, and characterized by a shallow underwater slope surrounding the islands (Table 2). The number of larids (*L. canus, C. ridibundus* and *L. marinus*) breeding also had a positive effect on the number of breeding Eiders, whereas active White-tailed Sea Eagle territories within 5 km had a negative effect (Table 2).

Table 2. The explanatory variables significantly associated with the number of breeding Eiders in 1998. Slope estimates, standard errors of the estimates (SE) and *p*-values (Pr(> |*z*|)) are provided.

Variable	Estimate	SE	Pr(> |*z*|)
(Intercept)	3.852	0.566	< 0.001
Island area	0.366	0.057	< 0.001
Distance to nearest island	0.002	0.0006	< 0.005
Mean underwater slope	–0.286	0.074	< 0.001
Tree crown cover	–0.051	0.025	< 0.05
Number of breeding *L. canus* or *C. ridibundus*	0.062	0.018	< 0.001
Number of breeding *L. marinus*	0.420	0.092	< 0.001
Number of active Sea Eagle territories	–0.830	0.260	< 0.005

Degrees of Freedom: 178 total; 171 residual
Explained deviance: 37%

Table 3. The explanatory variables significantly associated with the number of breeding Eiders in 2009. Slope estimates, standard errors of the estimates (SE) and *p*-values (Pr(> |*z*|)) are provided.

Variable	Estimate	SE	Pr(> |*z*|)
(Intercept)	3.053	0.606	< 0.001
Island area	0.383	0.063	< 0.001
Distance to nearest island	–0.0009	0.0006	0.149
Mean underwater slope	–0.126	0.069	0.071
Tree crown cover	–0.065	0.025	0.01
Exposure	–0.000005	0.000003	0.067
Standard deviation of elevation model	–0.343	0.143	< 0.05
Number of breeding *L. argentatus*	0.096	0.031	< 0.005
Number of breeding *L. marinus*	1.142	0.207	< 0.001

Degrees of Freedom: 178 total; 170 residual
Explained deviance: 39%

Eider breeding numbers in 2009 were significantly explained by island area, mean underwater slope surrounding the islands, the mean tree crown coverage, the standard deviation of the digital elevation model, the amount of land area surrounding the sites (exposure), the distance to the nearest island and the number of breeding Herring Gulls (*L. argentatus*) and Great Black-backed Gulls (Table 3). Female Eiders preferred large exposed islands with less tree crown coverage, less changes in elevation and a shallow surrounding underwater slope in 2009, and which were close to the nearest neighbouring island (Table 3). The number of large gulls (*L. argentatus* and *L. marinus*) breeding also had a positive effect on the number of breeding Eiders (Table 3).

4. Discussion

We were able to show that the rate of population decline differed between geographical sub-areas (Fig. 2). The overall population trends suggest a steep decline in all sub-areas except at Trollö (Fig. 2c), where the decline was moderate. It is important in this regard that the Trollö sub-area is located closer to the mainland than the other subareas (Fig. 1). Our data also show that the nest-site preference of Eiders has changed over time, as indicated by a change in some of the predictors of Eider breeding numbers between the early and late study period. In particular, the sign of the effect of distance from the nearest neighbouring island on Eider breeding numbers changed over time. Eider breeding numbers positively correlated with island size and distance to neighbouring islands in the early period, whereas closely-clustered, exposed large islands, with less variation in elevation were positively associated with Eider breeding abundance during the late period. Furthermore, the presence of breeding gulls had a consistently positive effect, whereas increasing underwater slope and mean tree crown cover had a consistently negative effect, on Eider breeding numbers throughout the study period. Interestingly, the presence of breeding White-tailed Sea Eagles had a detectable negative effect on Eider breeding numbers only during the early study period, for possible reasons discussed below.

As argued by Hario *et al*. (2009), poor fledging success may be a potential factor contributing to the declining population trend. A study by Hollmén *et al*. (2002) suggested that a reovirus killing ducklings may provide a possible explanation for the poor fledging success in the western Gulf of Finland in the late 1990s. While this coincides with the start of the population decline in our study areas, a previous study investigating the prevalence of another virus found a lower antibody prevalence in Eiders from Utö (located in the study area) than in Eiders from the Gulf of Finland (Hollmén *et al*. 2000). While one cannot draw direct conclusions on the importance of disease on the decline of the Eider population in the Archipelago Sea, there is no direct evidence of poor reproductive success caused by disease in our study area. Because the decline in our study area has been steeper than in areas where the decline has been attributed to poor fledging success, the cause for the decline could be attributed to increased adult mortality, as suggested by Ekroos *et al*. (2012b). As a long-lived species, the eider population is expected to be sensitive to adult mortality (Sæther & Bakke 2000) also stressed by Öst *et al*. (2016). It is also noteworthy that the number of White-tailed Sea Eagle territories is much higher in the Archipelago Sea than in the Gulf of Finland and this has been the case since the return of the eagle in the 1970s (Stjernberg *et al*. 2013).

We find it unlikely that temporal shifts in the food resource availability of Eiders would have affected the differential population trends observed in the five sub-areas. The density of Blue Mussels has been shown to increase with increasing exposure (Westerbom *et al*. 2008). This finding is in apparent contradiction to our observation that Trollö, the sub-area showing the least population decline, is also the least exposed with a mean of 7.2 ha area of land surrounding the study islands. Conversely, the steepest population decline was observed at Utö–Jurmo (Fig. 2e) which is also the most exposed sub-area, where the mean area of land surrounding the sites is only 2.2 ha. A significant negative effect of increasing underwater slope, which also acted as a proxy for Blue Mussel densities (Westerbom *et al.* 2008), was observed both in 1998 and 2009, so no detectable shifts in the preference of this variable seem to have occurred.

A salient feature of our results is that while the predictors of Eider breeding numbers are largely similar with those identified by previous research during the early study period (1998), these similarities become less evident during the latter study period. Thus, in 1998, the positive effect of island size on Eider breeding numbers (Table 2) is in line with the results obtained by von Numers (1995). Terrestrial predator avoidance may explain the positive relationship between Eider breeding numbers and distance to the nearest island (Nordström & Korpimäki 2004; Table 2). Perhaps reflecting a greater susceptibility to mammalian predation, the mean tree crown coverage had a negative effect on Eider breeding numbers. Intriguingly, this result seems at odds with the less steep population decline observed in Trollö, the sub-area with the highest mean tree crown cover (Fig. 2c).

Finally, the positive effect of larids (*L. marinus, L. canus* and *C. ridibundus*; Table 2) was also found by von Numers (1995). Aggressive colonial breeders, such as larids, may provide shelter from predators when defending their own nests as well as early warning of approaching predators, which may reduce predation rates of waterfowl adults and nests (reviewed in Holopainen *et al*. 2015). In our study area, however, particularly large gull species are declining, and based on the data used for the nest site preference analyses the average number of breeding Herring Gulls on the islands decreased from 1.8 in 1998 to 0.6 in 2009. The corresponding values for Great Black-backed Gulls are 0.6 in 1998 and 0.2 in 2009, respectively. This general decline in gull populations often occurs on the same islands which also host breeding Eiders; these islands have also experienced increased predation by White-tailed Sea Eagles (Hario & Rintala 2014).

The results of the 2009 analysis (Table 3) show similarities, but also some striking differences, with those of the 1998 analysis. This analysis again demonstrated the positive effect of island area and the presence of large larids on Eider breeding numbers, as well as the negative effects of underwater slope and tree crown cover. The negative effect of the standard deviation of island elevation suggests a recent preference for flatter breeding islands. The positive effect of larids is expected, given that co-nesting with larids is adaptive in terms of reducing predation risk and considering that predation on incubating females, particularly by White-tailed Sea Eagles, has increased over the study period (Jaatinen *et al*. 2011). The effect of breeding Herring Gulls was significant in 2009 but not in 1998, which may reflect the overall decline in their breeding numbers. When the breeding numbers of Herring Gulls are lower, the direct negative effect of predation on the Eider ducklings may be compensated for by the protection this species offers against other predators. Interestingly, the distance to the nearest island showed a negative relationship with Eider breeding numbers in 2009 (Table 3). This dissimilarity compared to the early study period could point to a change in nest-site preference by breeding Eiders. In the outer archipelago islands are more scattered compared to the inner archipelago. This result may therefore be explained by dispersal of established breeders from the outer to the inner parts of the archipelago, by the fact that Eiders have declined less in the inner archipelago, or by recruiting first-time breeders preferentially settling in the inner archipelago. In light of previous empirical work, large-scale dispersal of already established breeders may be the least important of these three non-exclusive alternatives. This view is supported by the fact that dispersal distances between subsequent breeding seasons are very short in Baltic Eiders (Öst *et al.* 2011) and that shifts between nesting islands are rare (Ekroos *et al*. 2012b). In contrast, the third alternative, preferential settlement of recruiting females in the inner archipelago, is worthy of further consideration. Thus, fidelity to natal breeding colonies (i.e., natal philopatry) may not be the rule in Eiders breeding in northern Baltic, based on the finding that genetic differentiation between islands is absent (Öst *et al*. 2005), and similar results were also indicated by a recent comparative demographic analysis of two well-studied Eider populations in the northern Baltic Sea, Tvärminne and Söderskär (Öst *et al.* 2016). Clearly, the mechanisms underlying a change in the geographical breeding distribution of Eiders merit further investigation.

Exposure of the breeding colony was significant only in the 2009 analysis (Table 3). Eider breeding numbers increased with less land area surrounding the breeding colony, i.e., with increasing exposure, a result also found by von Numers (1995) and Heinänen *et al*. (2012). As described in the Methods, we included this variable in the analysis because Westerbom *et al.* (2008) showed increasing Blue Mussel densities with increasing exposure. Heinänen *et al.* (2012) interpreted exposure to be important due to less predation pressure by terrestrial predators on more exposed islands. Enhanced predation pressure by terrestrial predators from 1998 to 2009 (see Jaatinen *et al*. 2011) could therefore be the reason why this variable was important only in 2009. Large surrounding land areas may also support permanent populations of predators, so an increase in establishment of predators on large islands in the archipelago could also drive this shift.

An interesting open question is why we detected a negative effect of White-tailed Sea Eagle breeding abundance on Eider breeding numbers only during the early study period, when eagle breeding numbers were, in fact, lower than during the late study period. This result is intriguing at first sight, in the light of previous studies showing that the species may have a considerable impact on waterfowl populations, both in the Baltic Sea (Kilpi & Öst 2002) and worldwide (Hipfner *et al.* 2012). There are at least two non-exclusive explanations. First, from a purely statistical point of view, it is conceivable that the nature of this explanatory variable changed over the study period. Whereas the number of active Eagle territories tended to behave more like a categorical variable during the early study period (territories were largely either absent or present), variation in this variable was more of a continuous nature in the late study period (values ranging from 0 to ca. 5 territories per site). This change may affect the ability to detect any significant effects of Eagle breeding density on Eider breeding numbers. Another possibility is that the number of White-tailed

Sea Eagle territories does not account for the number of non-breeding eagles in the area. It may even be the case that the presence of territorial eagles may diminish the effect of the non-territorial eagles, so that it may actually be beneficial for the Eiders to breed near a territorial eagle pair, particularly when the density of non-territorial eagles is high (Kenyon *et al*. 2007). For future studies, we therefore recommend that the effect of eagles should be assessed through direct observation of the presence of eagles and their hunting behaviour regardless of their breeding status.

To conclude, our results suggest a shift in nest-site preference of the Eider in the Baltic Sea. From a conservation perspective, this means that what is protected today, may not be suitable for this species tomorrow. The management efforts should therefore not only be directed at protecting certain habitats, but they should increasingly focus on managing existing colonies. Another major take-home lesson is the importance of interspecific interactions, particularly those between gulls and nesting Eiders, since these interactions appear vitally important for maintaining sustainable populations of not only Eiders, but also other waterfowl, in the future.

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Haahkan väheneminen ja muutokset pesimäpaikan valinnassa

Haahkan viimeaikainen laaja väheneminen Itämeren alueella on hyvin dokumentoitu pitkäaikaisseurannoissa. Yksi hypoteesi vähenemiselle on lisääntynyt pesimäaikainen saalistuspaine, mutta koska väheneminen on ollut niin jyrkkää ja maantieteellisesti laajaa, vähenemisen takana on luultavasti useampia syitä. Tässä tutkimme ovatko jotkin näistä tuntemattomista syistä mahdollisesti haahkojen pesimäympäristöön liittyviä. Tätä varten analysoimme vuosina 1993–2012 Saaristomereltä kerättyä saaristolinnuston pitkäaikaisseuranta-aineistoa, kattaen n. 300 saarta viideltä maantieteelliseltä osa-alueelta. Analysoimme populaatiotrendejä, sekä oliko pesimäympäristön valinnassa tapahtunut muutoksia.

Tulokset osoittivat jyrkkiä vähenemisiä osa-alueilla jotka sijaitsivat kauempana mantereesta, kun taas lähimpänä mannerta sijaitsevassa osa-alueessa väheneminen oli ollut vähemmän jyrkkää. Lokkien pesimisellä haahkojen pesimäsaarilla oli koko tutkimusjakson ajan positiivinen vaikutus pesivien haahkojen määrään. Toisaalta, merikotkalla oli negatiivinen vaikutus pesivien haahkojen määrään, mutta vain tutkimusjakson alkupuolella, kun kotkien määrät olivat vielä pieniä. Mielenkiintoinen tulos oli myös se, että lähimmän saaren etäisyyden vaikutus muuttui positiivisesta negatiiviseksi tutkimusjakson aikana. Pesivien haahkojen määrä korreloi positiivisesti saaren koon ja lähimmän saaren etäisyyden kanssa tutkimusjakson alkupuolella, kun taas tutkimusjakson loppupuolella pesivät haahkat suosivat suuria, ympäriltään avoimia, saaria, joissa oli muita saaria lähellä. Pesimäsaarien valinnan muutoksen vuoksi, pitäisi tulevat suojelutoimenpiteet kohdentaa pesimäpaikkojen sijaan populaatioiden hoitoon. Lisäksi, lokkien positiivinen vaikutus viittaa myös lajien välisten vaikutussuhteiden tärkeyteen suojelutoimenpiteitä suunniteltaessa.

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