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RESEARCH ARTICLE

Living with the enemy: the return of an apex predator is associated with habitat shifts in a common but rapidly declining prey population

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Abstract

Context The recovery of some apex predators has led to concerns for endangered prey that may have developed risky habitat selection tactics during predator-free eras. Environmental heterogeneity affects predator–prey coexistence, but spatial redistribution of prey has rarely been studied. A predator–prey system with white-tailed eagles and common eiders provides a unique opportunity to study the effect of returning predators on an abundant but declining prey population.

Objectives Our objective was to investigate how the physical environment affects predator–prey relationships and subsequently the spatial redistribution of the prey population over time, and to perform a large-scale assessment of the population status and distribution of eiders in the North-Eastern Baltic Sea.

Methods Using extensive survey data from the Finnish coast from 1997 to 2020 on predator and prey breeding numbers, we constructed a spatiotemporal model explaining the distribution of eiders on > 3600 islands across highly variable coastal regions. We

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assessed how the proximity of nesting eagles affected eider abundance, mediated by properties related to physical nest shelter (archipelago type and island forest cover).

Results Breeding eider numbers decreased on exposed islands particularly near eagle nests, while they increased near eagle nests in the sheltered archipelago. We observed population-scale predator-induced shifts in the breeding distribution, likely reflecting both excess mortality on exposed islands and a shift of the population core to low-risk habitats.

Conclusions We show that a returning predator can affect the distribution and density of its prey in a habitat-specific manner, which is important to consider in parallel with effects of human-induced ecosystem changes during conservation planning.

Keywords Breeding distribution · Conservation conflict · Habitat selection · Predator–prey dynamics · Raptor

Introduction

Successful conservation efforts and a ban on pesticides have led to the recent recovery of some apex predators formerly on the brink of extinction (Hailer et al. 2006; Chapron et al. 2014). The recovering populations often return to formerly inhabited areas (Silliman et al. 2018), where they may encounter naïve prey that have altered their behaviour to exploit the predator-free environment (Berger et al. 2001; Bonnot et al. 2016). Learned antipredator responses can be lost in a population already in the first isolated generation (Blumstein et al. 2004; Kauffman et al. 2007). Apex predators play an important role as top-down regulators and the relaxed predation pressure associated with their disappearance may increase prey populations, followed by a decrease to previous or lower levels if the predator population rebounds (Terborgh et al. 1999; Hegel et al. 2010; Ripple et al. 2014). From a conservation point of view, the return of apex predators may jeopardise prey population persistence, which ultimately leads to conflicts between the conservation of the predator and its prey, especially for prey species that may become endangered (Hipfner et al. 2012; Marshall et al. 2016; O'Brien et al. 2018).

Predator–prey interactions include both consumptive (direct predation) and various non-consumptive (indirect) effects. Non-consumptive effects include a range of behavioural adaptations that, as a response to the predator, alter prey behaviour in ways that reduce fitness, i.e., affect growth, reproduction or survival (Sheriff et al. 2020). For example, intensified predation pressure may cause prey to shift their habitat use to sites that facilitate early predator detection or decrease the likelihood of being detected by the predator or simply avoid encounters (Lima 2009; Ng'weno et al. 2017). The physical environment and the type of shelter it provides is therefore a key factor affecting the success of predator avoidance. Avian nesting is strongly influenced by predation risk for both the incubating parent and the offspring (Lima 2009). Anti-predator strategies include changes in habitat and nest-site selection (Powell and Frasch 2000; Chalfoun and Martin 2010), aggregated nesting and proximity to more aggressive species for protection (Kopachena 1991; Holopainen et al. 2015; Rocha et al. 2016) as well as avoidance of nesting close to established raptor nests (Lima 2009; Møller et al. 2017). The fitness outcomes of different strategies may vary depending on the predator assemblage, and a strategy that provides protection against one type of predator may render the prey more susceptible to another type of predator (Ringelman 2014). Furthermore, the optimal antipredator strategy of breeding adults may conflict with the optimal strategy for avoiding offspring predation (Öst et al. 2022). Nesting in concealed sites may increase under elevated predation risk due to enhanced preference for such sites (e.g., Lima 2009; Bellamy et al. 2017; Mohring et al. 2022) or because individuals settling in suboptimal habitat experience higher mortality (e.g., Ekroos et al. 2012a), but it has rarely been studied how prey numbers change depending on the degree of protection offered by physical landscape properties and the available shelter. For example, remote, barren and treeless islands are hard to access but offer little or no shelter compared to larger and more complex islands with both physical shelter offered by cliff formations and neighbouring islands, as well as biotic shelter in the form of vegetation and trees.

Island nesting is a common adaptation of seabirds to reduce predation from terrestrial predators (Spatz et al. 2014). As a response to the spread of invasive minks and raccoon dogs in the Baltic in the late twentieth century, seabirds increasingly started to nest on remote, isolated islands (Nordström and Korpimäki

2004; Brzezinski et al. 2020). Populations of seabirds and waders nesting in the Baltic Sea in northern Europe have undergone substantial changes during the last century, some increasing and others declining (Pöysä et al. 2013; Below et al. 2019). Notably the common eider (*Somateria mollissima*, hereafter eider), one of the most numerous waterfowl in the Baltic, has experienced a population decline of 60% by 2009 compared to the peak numbers in the mid-1990s (Ekroos et al. 2012b). This decline has resulted in serious concern about the fate of this species, which is currently classified as endangered (EN) in the Finnish red list (Lehikoinen et al. 2019) as well as in the 2021 European red list for birds (BirdLife International 2021). One apparent reason for the recent decline has been increasing predation by the white-tailed eagle (*Haliaeetus albicilla,* hereafter WTE), the top avian predator of the Baltic Sea (Ekroos et al. 2012a; Öst et al. 2022). Recovering WTE and bald eagle (*Haliaeetus leucocephalus*) populations have contributed to both local and wider scale declines in seabirds in Europe and North America, respectively (Hipfner et al. 2012; Henson et al. 2019; Bregnballe et al. 2022). Due to persecution, WTEs were almost driven to extinction in the Baltic in the early twentieth century and therefore protected in Finland in 1926 (Pohja-Mykrä et al. 2012). However, pesticides and continued persecution drove the population back to the brink of extinction in the mid-1970s. Extensive conservation efforts helped the population to recover (Högmander et al. 2020), and in 2019 its status was set to LC in the red list of Finland (Lehikoinen et al. 2019).

Eiders are the main prey of nesting WTEs in the archipelago of the Baltic Sea, constituting 21% of the diet (Ekblad et al. 2016). The predation targets mainly incubating females and ducklings. In long-lived species like the eider (Coulson 1984), adult survival is a crucial factor for maintaining population size (Saether and Bakke 2000; Öst et al. 2016), while reduced offspring survival may have further negative repercussions of population persistence (Gaillard et al. 1998; Öst et al. 2016, 2022).

The predator–prey system with WTEs and eiders provides a unique opportunity to study the effect of a returning predator on an abundant but declining prey population. This study had two objectives: (A) to perform a large-scale assessment of the population status and distribution of eiders in the north-eastern Baltic Sea, and (B) to investigate how the physical environment interacts with the predator–prey relationship and subsequently affects the spatial redistribution of the population over time. Both consumptive and non-consumptive effects can be expected to play a role in the system. This is because female eiders show high fidelity to their breeding island (Öst et al. 2011; Ekroos et al. 2012a) but may choose not to breed based on predation experienced in the previous season (Öst et al. 2018). In contrast, new recruits may show less site fidelity (Öst et al. 2005; Kurvinen et al. 2016), which may allow them to more actively choose safer nesting islands, or ones already containing established breeders, to settle on.

We used extensive nation-scale long-term monitoring data on both the eider and the WTE population, focusing on the declining phase of the eider population (1997–2020). For the population status assessment, we first constructed a baseline spatiotemporal model (0-model) that included environmental, spatial and temporal variables explaining the changes in eider population abundance on islands along the Finnish coast. On top of the baseline 0-model, we formulated a set of extended models to test for possible WTE-induced shifts in the numbers of eiders breeding on different islands. We tested three alternative hypotheses: (a) eagles had no effect on eider distribution, (b) eider distribution shifted away from eagle nests, and (c) the effect of the proximity of WTEs changed over time. Assuming that a nesting WTE pair has observable effects on the local eider breeding population, we predicted that the decline in eider breeding numbers should be steeper in the vicinity of a WTE nest. We further hypothesized that nesting on islands where the nests would be less exposed to WTEs would be beneficial for eiders. We thus predicted (1) a temporal shift of the core of the eider population from the barren outer archipelago where they are exposed to WTEs towards the less exposed inner archipelago, (2) that in the vicinity of WTEs, islands with more protective forest cover would show less decline in eider numbers compared to those offering less protective forest cover or (3) a shift to both the more sheltered inner archipelago and islands with more tree cover. The spatiotemporal models with added WTE impacts (see above) were applied with the aim of helping to understand how long-lived species with high site-fidelity may respond to—and cope with—the growing predation pressure by a returning apex predator.

Materials and methods

Study area and species

The study area covers the Finnish coast from Virolahti in the east to Kokkola in the north (Fig. 1). The north-eastern Baltic Sea shows a spatial salinity gradient, ranging from 5–6‰ in the central parts of the Baltic proper to 3‰ in the Gulf of Bothnia and the Gulf of Finland (Furman et al. 2014).

The eider is a large sea duck, which in the Baltic feeds mainly on blue mussels (*Mytilus trossulus*), requiring a salinity of at least 4.5‰ (Westerbom et al. 2002). Due to the low salinity, blue mussels do not occur in the inner gulfs of the Baltic Sea. The eider distribution mainly follows the distribution of blue mussels along the coast, even though smaller numbers of eiders nest in the inner low-salinity gulfs of the Baltic Sea. Eiders nest on the ground, either exposed while relying on cryptic coloration, or under protective vegetation (Öst and Steele 2010). The nest is typically located 10–60 m from the shore (Laurila 1989) and females show high breeding philopatry to their chosen nesting island (Öst et al. 2011). In addition to WTEs, adult eiders are mainly predated by invasive mammals; minks (*Neogale vision*) and raccoon dogs (*Nyctereutes procyonoides*) (Öst et al. 2018; Jaatinen et al. 2022). Hooded crows (*Corvus corone cornix*) and large gulls *Larus* spp. are the primary nest predators (Hermansson et al. 2023), and broods at sea are depredated by gulls and—increasingly—by WTEs (Öst et al. 2018). In Tvärminne in the northern Baltic Sea, the proportion of female eiders killed at their nest is on average 5.6% over the past three decades (1990–2020), showing a sharply increasing time trend (annual range 0–16.8%) (Öst et al. 2022).

The white-tailed eagle is a large raptor closely associated with water (Ferguson-Lees and Christie 2001). Fish is the main prey in inland landscapes while birds, mostly waterfowl, constitute most of the prey in the middle and outer archipelago (Nadjafzadeh et al. 2016; Ekblad et al. 2016, 2020). WTEs mature at an age of about 5 years and after settling they have high site-fidelity and defend a breeding territory, on which they have one or multiple nests (Cramp 1980).

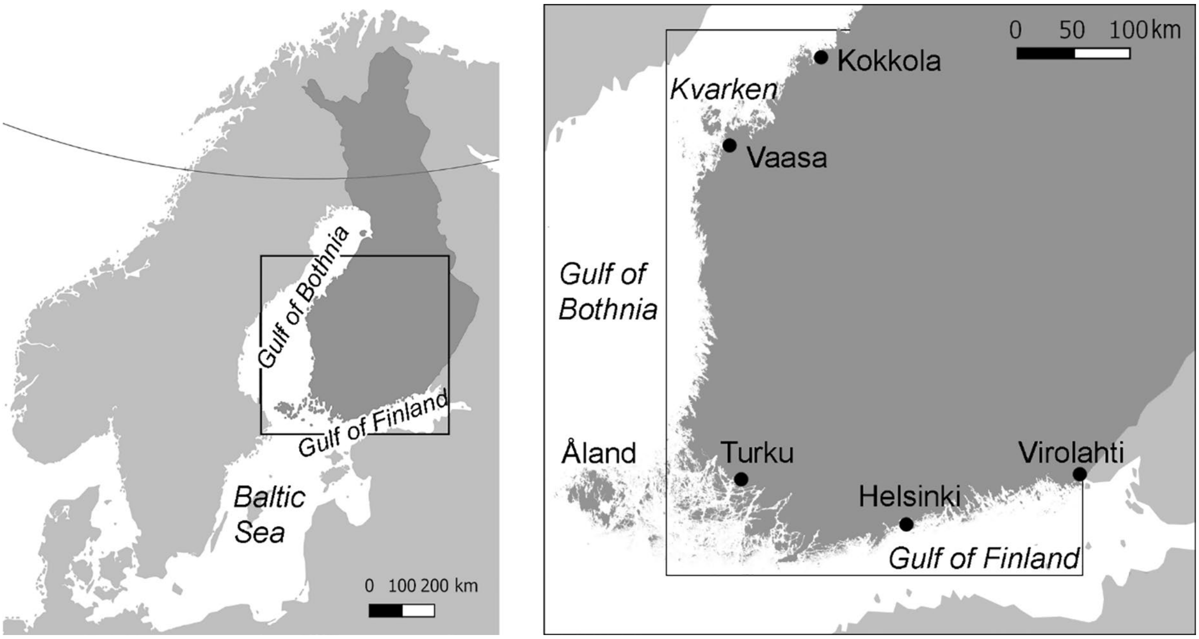


Fig. 1 Map of the Baltic Sea (left) and the study area (right). Names of waters are written in italics. The box indicates the study area

White-tailed eagle surveillance, territory status and occupancy modelling

The WTE population in Finland has been monitored since 1973 by the White-tailed eagle working group, which was affiliated with WWF Finland until 2019 and thereafter with Osprey Foundation. WTEs nowadays nest along the entire coast (Online Resource 1), and the population has increased steadily (Lokki et al. 2024). Annually, almost all known territories are surveyed by volunteers. Most nest monitoring take place over a one-month period starting in mid-May when the nestlings are half-grown and of appropriate age for ringing, because disturbance during the early nesting phase can induce nest failure. Breeding status was previously determined by climbing to the nest or observing from the ground using binoculars or telescopes. Nowadays, also helicopter flights and camera-equipped drones are used. Annually about 80 volunteers participate in the field work and data collection along the coast.

A breeding attempt is recorded when at least one of the nests in the territory has been decorated (Balotari-Chiebao et al. 2016; Högmander et al. 2020, Online Resource 2). The WTE pairs stay in their territories also in summers when they skip breeding, or the breeding attempt fails. Sometimes the known nests in the territory are undecorated though the pair is seen on the territory. This may be because they have an unknown nest or chose not to breed. As the territories are large, the eagles may be on the territory even when not seen. These pairs are considered "missing". As the population grows, new territories are emerging, and there might be a lag before they are found.

To account for imperfect detection and eliminate small-scale oscillations in the series, we fitted a basic dynamic occupancy model (MacKentzie et al. 2002) to the survey status data using the package unmarked in R (Fiske & Chandler 2011; Kellner et al. 2023). All variables (initial occupancy, detection-, colonization- and extinction probability) were set to ~ 1. In the model input data, the territories were coded 1 in years when observed occupied, 0 when surveyed but no breeding signs or eagles were detected, and as missing (NA) when not surveyed. For new territories, the preceding year was coded as NA and the years before that to 0. The output of the model produced a matrix with yearly probabilities of occupancy (0–1) for each territory. Years with confirmed occupancy in the surveys get the value 1, and a probability of occurrence (a number between 0 and 1) is calculated for all years coded as 0 or NA. According to the model, e.g., unoccupied gaps of one to 2 years have a high probability of being occupied, while the probabilities dropped considerably with larger gaps.

For the annual island-specific eider survey data, we categorized the WTE occurrence into three categories based on the distance to the nearest active WTE nest: (1) immediate vicinity, when the nearest nest was within 2 km of the island; (2) within hunting distance, when the nearest nest was between 2 and 10 km away; and (3) not in range, when no active territories were found within 10 km. The above categorization was based on the maximum hunting radius of territorial WTEs, estimated at ca 10 km (Ekblad et al. 2020). The territories of successfully nesting pairs do typically not overlap, so only the distance to the closest pair is relevant. In years when the WTEs nested successfully, we used the coordinates of the occupied nest, and in years with unsuccessful breeding, the mean coordinates of the nests.

For each eider breeding island and year, we estimated the probabilities that the data point belonged to each category (1–3) and simply classified the data point into the category with highest probability. The probability of belonging to category 1 equals the probability that at least one occupied territory is within 2 km (hereafter denoted as P_{2km}). This is calculated as one minus the probability that all candidate territories are unoccupied, i.e., $P_{2km} = 1 - \Pi(1 - \mathbf{p}_i)$, where $\mathbf{p}_i$ is a vector with the occupancy probabilities of all candidate sites within 2 km (typically there is only one, if any). If no candidate territories are within 2 km, then $P_{2km} = 0$. Next, the probability of belonging to category 2, i.e., that the nearest active WTE territory is at 2–10 km, is calculated as: $(1 - P_{2km}) \times P_{10km}$. Here P_{10km} is the probability that at least one candidate territory is occupied at a the 2–10 km distance and is calculated according to the same logic as P_{2km}. Finally, the probability of belonging to category 3, is $(1 - P_{2km}) \times (1 - P_{10km})$.

Importantly, we used the occupancy status of the preceding year (t–1) in the modelling, because predation experienced in the previous season affects the decision of whether or not to breed in the subsequent year (Öst et al. 2018) and may occasionally also lead to a change of breeding island (Öst et al. 2011).

Furthermore, also depredated eider nests are included in the eider surveys, creating a possible time-lag in the effects of eagles on eider breeding numbers. Finally, it has been shown that the fear of nesting avian raptors persists for years after the predator has disappeared (Burgas et al. 2021).

Archipelago bird censuses and eider count data

The number of breeding eiders in Finland is monitored in the archipelago bird censuses coordinated by the state-owned organisation Metsähallitus. Though officially initiated in 1984, censuses have been made in several areas since the 1940s (Hildén 1987; Hario and Rintala 2002). Eider breeding numbers are estimated by at least two annual counts of successful (actively incubating or already hatched) and unsuccessful (depredated or abandoned) nests performed according to guidelines and reported as pairs (Koskimies and Väisänen 1991). At the southern coast, the first count is performed around mid-May, and at the northern coast in early June. The second count is performed two to three weeks later. Annually around 50–80 persons participate in the surveys and, within the study area, an average of 500 islands (100–1200) are surveyed (Online Resource 3). The goal is to obtain a long-term data series from sample areas along the coast, and although some areas have been counted more frequently than others, these data nevertheless offer the most comprehensive survey so far for estimating eider occurrence along the Finnish coast. In addition, we obtained eider counts from additional areas and years directly from own data series as well as from municipalities, associations, and private persons. In some cases, pair numbers were reported as a sum for groups of multiple islands. In cases where separated counts from these islands were available from other years, we distributed the summed numbers on the separate islands according to the proportions from previous and/or subsequent years. If the islands were approximately the same size, summed pairs were distributed evenly among the islands. This redistribution concerned on average 6.2% of the observations per year, and 7.4% of the number of breeding females. We excluded islands > 20 ha, as eiders predominantly occur on smaller islands and only a few islands larger than this were included in the monitoring data. We also excluded islands north of the 63° 57’ latitude, where eiders are virtually absent, and the Åland Islands, due to lack of census data. Furthermore, we excluded one island that, according to visual inspection of the data, clearly was an outlier that fell outside the general pattern. This large (seven ha) island with a mean height of only three meters, to one side facing a large land and to the other open sea, has outer archipelago characteristics but the proportion of land within 5 km is 40% and it is the only island with a high proportion of land close to a WTE nest in the first half of the study period, when there nested substantial numbers of eiders, and including it produces exaggerated estimates for the inner archipelago.

Eider breeding island properties

The physical attributes of the breeding islands in fragmented archipelagos are crucial for modelling species occurrence (Rönkä et al. 2008). We used a selection of physical parameters found to be important predictors for the occurrence of eiders in island-level studies (size, latitude and longitude, archipelago zone, and forest cover; von Numers 1995; Rönkä et al. 2008; Kurvinen et al. 2016; Table 1) to model the island-specific breeding numbers of eiders and subsequently the potential interactions of these factors with the effects of WTEs. Latitude and longitude are relevant because eider numbers are decreasing towards the gulf interiors due to a lack of blue mussels, and we were further interested in exploring potential differences in population trends between the two gulfs. Possible collinearity of explanatory variables was assessed with the Variance Inflation Factor (VIF) and none of these variables exceeded the threshold of 3 (Zuur et al. 2010).

Island size explains the distribution of many island-nesting birds, where some species prefer smaller and other larger islands. Larger islands provide more space and habitats for nesting birds, but also for their predators (Rönkä et al. 2008). Many birds that nest in the Baltic archipelago avoid nesting in forests, and since larger islands tend to have more forest cover, suitable nesting habitats do not necessarily increase in proportion with the island size. In the models, that have logarithmic link functions, we used the natural logarithm of island size (lnSize) as an explanatory variable to account for the abundance–area relationship in the model. We set this variable to zero when calculating any model predictions

Table 1 Fixed effects explanatory variables used to model the number of eiders breeding on a focal island (n = 3648)

Variable	Description	Range	Median
Year	Year when data were collected	1997–2020	2008
Island size (Size; lnSize)	Island size in hectares; lnSize is its natural logarithm	0.01–19.5 ha	0.6 ha
Latitude (Lat)	Latitude (ETRS89) at the centroid of the island	6,629,182–7,100,246	6,670,934
Longitude (Lon)	Longitude (ETRS89) at the centroid of the island	172,762–541,194	290,209
Proportion of land (Land)	The percentage of land area within a radius of 5 km from the centroid of the island	0.06–82.85%	10.55%
Forest cover (Forcov)	Median forest cover of the island (%)	0.00–83.00%	12.00%
White-tailed eagle occurrence (WTE)	Categorical variable with three levels describing occupancy of white-tailed eagle territories in the vicinity of the island in the previous year - Closest occupied WTE nest/territory within a radius of 2 km from the centre of the island - Within 2–10 km radius from the island - No occupied territories within 10 km		

Shown are the variables and their abbreviations, descriptions, range and medians

(e.g., in figures illustrating the results), implying that the model prediction can be interpreted as the density of eider pairs per ha, on a “model island” with a size of 1 ha. An interaction between latitude, longitude and year was used to roughly model the spatiotemporal trends in the Gulf of Finland in the south (ENE–WSW gradient) and the Gulf of Bothnia in the west (NNE–SSW gradient, Fig. 1). To avoid artificial boundaries, i.e., manually choosing where to draw borders, we measured the proportion of land within a 5 km radius (Land; continuous variable; Fig. 2) instead of the traditional division into inner, middle, and outer archipelago (Häyrén 1900; von Numers 1995). A high proportion of land indicates inner archipelago, with islands of all sizes, often forest covered and close to each other, and a low proportion of land indicates outer archipelago, towards which the islands gradually become smaller and more separated from each other (von Numers 1995). The forest cover dataset, primarily developed for forested areas, had a resolution of 16 × 16 m, where the value of each pixel shows the percentage of the pixel being forest covered. We used the median value for the island from the latest available data (2019; Mäkisara et al. 2022). Due to the pixelated nature of the data, some pixels included water areas up to 8 m around islands. Visual inspection revealed that seagrass around islands caused erroneous values for some pixels. To correct for this error affecting estimated medians on small islands, we set the forest cover for all islands smaller than 0.07 ha (represented by 1–3 pixels) to 0%.

Spatial data and artwork

All island characteristics were calculated with Qgis 3.12. The coordinates (Lat and Lon), island area (Size) and the proportion of land (Land) were calculated from the National Land Survey of Finland Topographic Database in vector format (scale 1:10000). The forest cover data were obtained from the Natural Resources Institute Finland (Luke) (Mäkisara et al. 2022). The figures were created with Qgis, R and PhotoShop.

Research questions and models

We first constructed a spatiotemporal model describing eider breeding numbers (density) on islands along the Finnish coast (0-model), to which we added further predictors to address our hypotheses. We assessed whether the occurrence of WTEs in the previous year affected the breeding numbers of eiders and whether these potential effects depended on archipelago type and forest cover. The research hypotheses and corresponding models are presented in Table 2.

Statistical analyses

All statistical analyses were performed using R version 4.4.1 (R Core Team 2024). This study targets the declining phase of the eider population; hence, to identify the turning point, we first conducted an

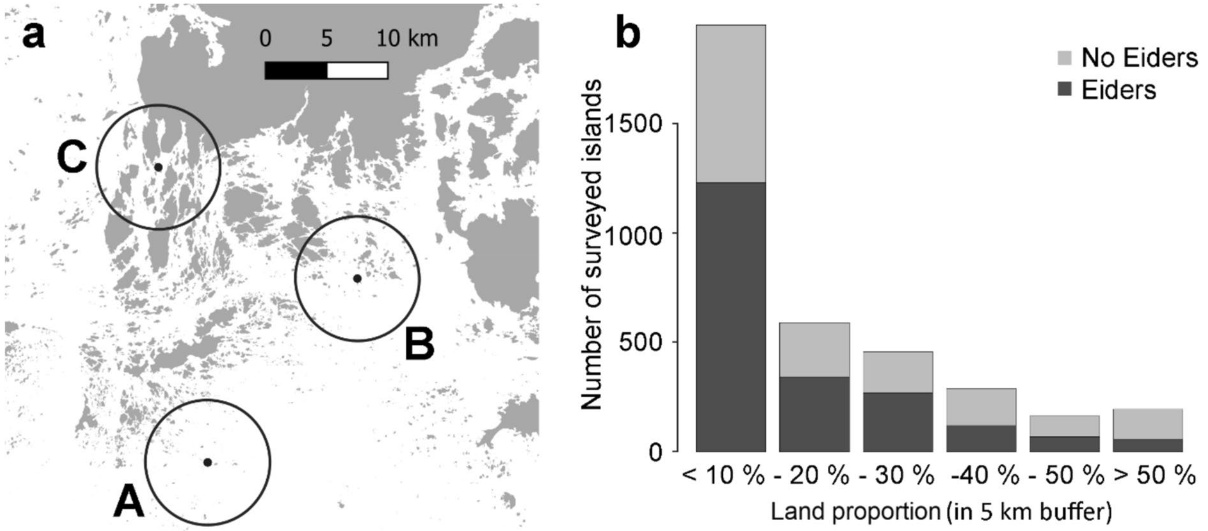


Fig. 2 **a** Illustrative map showing three islands with a 5 km radius representing different archipelago zones. Island A is situated in the outermost archipelago and has a land proportion of 1.5% (10% quantile). Island B is situated in the outer-middle archipelago and has a land proportion of 10.6% (median) while Island C represents the inner-middle archipelago and has a land proportion of 42% (90% quantile). **b** Histogram showing the number of surveyed islands in terms of the proportion of land within a 5 km radius from the centre of the island. The dark part of the bar shows the number of islands where eiders have been found breeding at least once, while the light part indicates islands with no breeding records of eiders

overall eider population trend estimate based on all available count data from 1980 to 2020 (N counts from islands where eiders bred at least once = 17,443, N unique islands = 2295) using the package rtrim (Bogaart et al. 2020), based on the TRIM-software (Pannekoek and van Strien 2005), a common tool for monitoring bird population sizes designed to deal with spatially and temporally irregular data. No covariates were used in this analysis. The baseline was set to 1980, as there was not enough data from preceding years. We identified the population peak to 1997 (see Results) and as we in subsequent analyses focused on the declining phase of the population, we used the count data from 1997 to 2020 for all subsequent modelling. Eventually, our data on breeding eiders consisted of 18,516 island-counts from 3648 different islands (Online Resource 3). Here, we use an index instead of absolute population abundance or population density, as the intention is here only to illustrate relative population changes. Using population indices is very common for such purposes, while presenting reliable average population densities or populations sizes would require strong assumptions and extrapolation to unsurveyed islands with the current methods.

To fit the 12 models described in Table 2, with the island-specific number of breeding eider pairs as the response variable, we applied generalised linear mixed models (GLMMs) with a logarithmic link-function and negative binomial error distribution, accommodating the overdispersion of the data. The models were fitted using package glmmTMB (Brooks et al. 2017). Island size was log-transformed and included as a predictor lnSize as such. The predictors Lat, Lon, Year (study year as a continuous variable), Land (proportion of land) and Forcov (forest cover) were standardised to zero mean and unit variance using the function 'scale'. The products of the interacting continuous variables were not rescaled; direct interactions of the scaled variables were used. The performances of the models were compared using AIC (Burnham and Anderson 2002). To avoid pseudoreplication and to account for the unequal monitoring frequency of islands and years (unbalanced data), we included the factor variables Island_ID and Year_f as random effects on the intercept in all models. In the model, these components describe the spatial and temporal variation unexplained by the predictors. We also modelled the spatial autocorrelation of the observations as an additional random

Table 2 Research hypotheses with associated candidate models (for parameter descriptions, see Table 1)

Hypotheses	Model (fixed effects)				Nr
Spatiotemporal baseline model describing the changing eider occurrence in the Finnish archipelago	lnSize + Lat × Lon × Year	+ Land	+ Forcov		0a
The proximity of WTEs have a negative effect on the number of eiders	lnSize + Lat × Lon × Year	+ Land	+ Forcov	+ WTE	0b
The eiders decline more in the proximity of WTEs	lnSize + Lat × Lon × Year	+ Land	+ Forcov	+ WTE × Year	0c
The eider distribution has shifted towards the inner archipelago (with more land)	lnSize + Lat × Lon × Year	+ Land × Year	+ Forcov		1a
The eider distribution has shifted towards the inner archipelago and WTE proximity has a negative effect on the eider distribution	lnSize + Lat × Lon × Year	+ Land × Year	+ Forcov	+ WTE	1b
The proximity to a WTE nest has different effects depending on archipelago type	lnSize + Lat × Lon × Year	+ Land × Year × WTE	+ Forcov		1c
The eider population has declined more on unsheltered islands	lnSize + Lat × Lon × Year	+ Land	+ Forcov × Year		2a
The eider population has declined more on unsheltered islands and WTE proximity has a negative effect on the eider distribution	lnSize + Lat × Lon × Year	+ Land	+ Forcov × Year	+ WTE	2b
The eider population has declined more on unsheltered islands in the proximity of WTEs	lnSize + Lat × Lon × Year	+ Land	+ Forcov × Year × WTE		2c
The eider distribution has shifted towards the inner archipelago and towards more sheltered islands	lnSize + Lat × Lon × Year	+ Land × Year	+ Forcov × Year		3a
The eider distribution has shifted towards the inner archipelago and towards more sheltered islands and WTE proximity has a negative effect on the eider distribution	lnSize + Lat × Lon × Year	+ Land × Year	+ Forcov × Year	+ WTE	3b
Full model: The proximity to a WTE nest has different effects depending on archipelago type and forest cover (shelter) of the island	lnSize + Lat × Lon × Year	+ Land × Year × WTE	+ Forcov × Year × WTE		3c

The response variable in all models is the number of eiders breeding on the island. An interaction term in the table indicates that in addition to this interaction, all lower-level interactions and the corresponding main effects were also included in the model. The factor variables Year_f and Island_ID were included as random effects on the intercept, along with the position of the island (in 2 × 2 km squares, see "Spatial autocorrelation")

Hypothesis: Physical attributes are affecting the redistribution of the eider population

0) No spatiotemporal interactions beyond the geographical ones

1) Temporal effect of proportion of land, i.e. archipelago type (interaction Land × Year)

2) Temporal effect of forest cover, i.e. shelter (interaction Forcov × Year)

3) Temporal effects of both archipelago type and forest cover (shelter)

Hypothesis: The proximity to nesting white-tailed eagles affects the redistribution of the eider population

a) no WTE effect

b) WTE effect (proximity)

c) Temporally changing WTE effect (interaction WTE × Year) effect, with a distance-based correlation structure (see below). Additionally, we ran the models including a temporal autocorrelation structure available in the package glmmTMB, but as the model that did not include temporal autocorrelation was better supported (ΔAIC = 0.64), temporal autocorrelation was left out from the final model.

Spatial autocorrelation

Spatial autocorrelation is likely to occur in geographically extensive data sets such as this one (Dormann 2007). The level of spatial autocorrelation was quantified by Moran's Index, which is a measure of how closely clustered specific items are in the 2D-space, on different distances, applying the package 'spdep' (Bivand and Wong 2018). The data showed significant spatial autocorrelation, especially with distances < 10 km. To allow for spatially autocorrelated data in our models, we applied the spatial exponential covariance structure available in package glmmTMB. A distance matrix based on the coordinates of the observations was calculated and used as a random effect in the model. In our extensive dataset, the calculations were not possible to execute on island level, because the number of possible combinations became too large. We therefore created a grid of 2 × 2 km squares for the Finnish coast and assigned each island to the corresponding square. We then used the location of the centre of the squares to derive the distance matrix. The model including spatial autocorrelation performed better than a simpler model without it (ΔAIC = 791), and therefore, spatial autocorrelation was included in the final model.

Model validation

The random effects Year_f and Island_ID were explored for normality, which is one of the model assumptions. The random effects of Year_f did not differ significantly from normality (Shapiro–Wilks normality test, n = 24, p = 0.72) which the Island_ID did (n = 3648; Shapiro-p < 0.001), but visual inspection of the Q–Q plot of the random effects of Island_ID revealed a slight skewness of the data, not indication major violations of the model assumption. Further, we explored the Dunn–Smyth residuals of the fitted model, which according to visual inspection were close to normally distributed.

Results

Population size

The eider population grew rapidly from the beginning of the surveys in 1980. The population peak occurred in 1996–1997, when the number of eiders was around 260% of the initial population size in 1980 (TRIM analysis; Fig. 3). Thereafter, the population trajectory has followed a steep decrease of approximately the same magnitude until 2007, after which the population size has fluctuated around approximately the same levels as in the early 1980s (Fig. 3).

Model selection

The full model (3c, Table 2) was the best supported, compared to the second-best model (1c, with ΔAIC = 8.96), and was thus used for inference. The two highest ranked models included the interaction Land × Year × WTE, but also models including the interaction Land × Year ranked higher than any model lacking this interaction. All models containing the interaction between WTE and Year were higher ranked than the corresponding models lacking them (Online Resource 4).

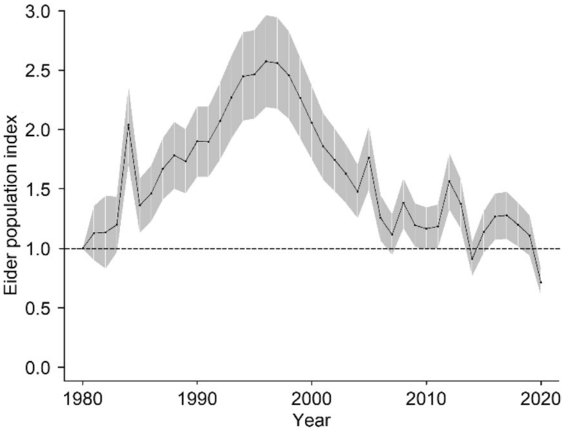
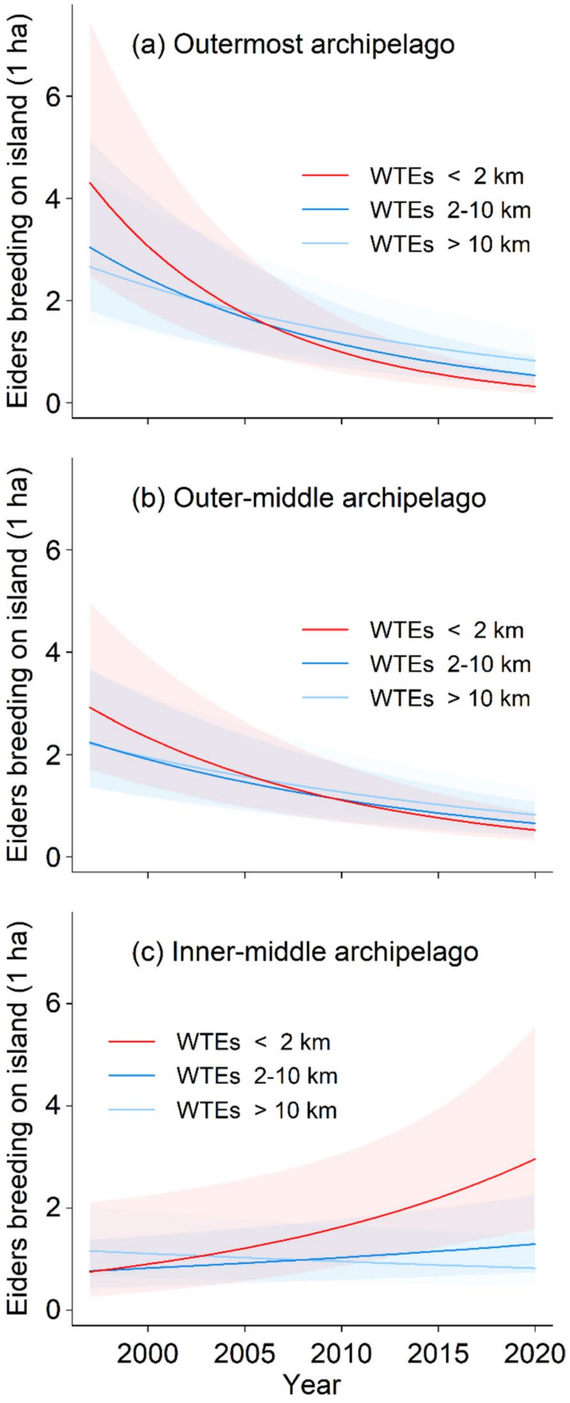


Fig. 3 The eider population size development in the northeastern Baltic Sea. The abundance indices are scaled so that 1980 has the value 1. The grey bars represent 95% confidence intervals

Fig. 4 Temporal changes in eider density of surveyed islands ▶ (breeding numbers of eiders per 1 ha island) in different archipelago zones (Land) and with regard to the proximity to white-tailed eagle (WTE) nests. The panels show the estimates from the model presented in Table 3 for **a** the outermost archipelago with 1.5% land (10% percentile), **b** 10.5% land (outer-middle, median) and **c** inner-middle archipelago with 42% land (90% percentile) within a 5 km buffer around each island (Fig. 2). In each panel, curves illustrating the predictions are shown for islands < 2 km (red), 2–10 km (dark blue) and > 10 km (light blue) from the closest WTE nest. The shaded areas represent the 95% confidence intervals. Latitude, longitude, and forest cover were fixed to their means



Eider abundance in relation to archipelago structure, WTE occurrence and time

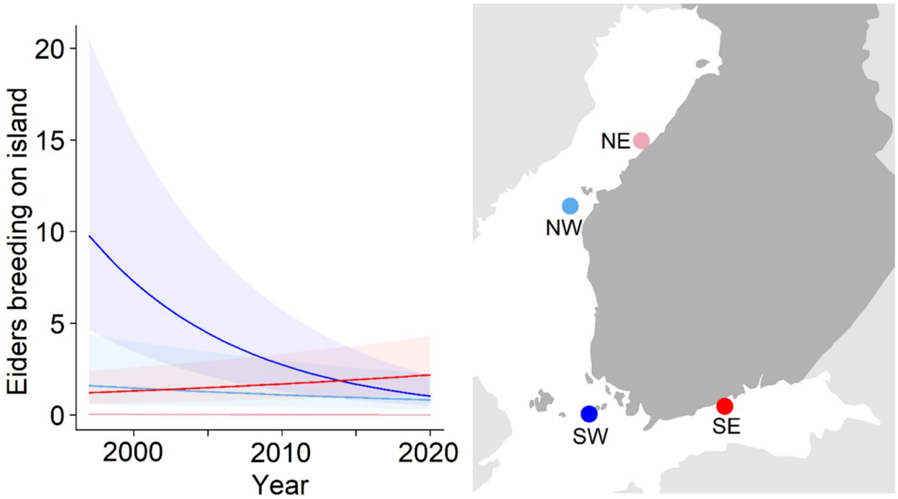
The three-way interaction Year × Land × WTE indicates that eider numbers responded differently to WTE proximity depending on the proportion of land around the island (corresponding to archipelago type). When the eider population peaked in 1997, there were more eiders in the outer (low proportion of land) than in the inner archipelago (high proportion of land), and the highest numbers were found on islands within 2 km from the closest WTE nest (Fig. 4a, b). In the inner archipelago, the eider numbers were somewhat higher > 10 km from WTE nests than in the proximity of the nests (Fig. 4c, Table 3). During the time-period 1997–2020 the eider numbers declined in the outer archipelago, steepest on islands < 2 km from WTE nests (Fig. 4a). In the end of the period, the highest eider numbers in the outer archipelago were found on islands > 10 km from WTEs. In contrast, in the inner archipelago the eider numbers decreased on islands > 10 km from WTE nests but increased on islands in the vicinity of WTE nests (Fig. 4c). The three-way interaction Forcov × Year × WTE was also significant, but only for islands 2–10 km from WTE nests and not nearly as important as the corresponding interaction with Land (Table 3). Densely forested islands generally experienced a less steep decline in breeding numbers. On islands with low forest cover, eiders showed a more pronounced decline near WTE nests than away from them, while the opposite pattern seemed to be true for forested islands. However, this effect was small and statistically significant only for islands in the 2–10 km range, presumably because of the far greater sample of islands in this category compared to the < 2 km group.

Table 3 Parameter estimates with standard errors (SE), Wald Z statistics (χ^2) and statistical significances (p) of the best-supported model (3c in Table 2) explaining variation in the number of breeding eider pairs on islands at the Finnish coast

Predictor	Estimate (± SE)	$\chi2$	*P*
Intercept	0.25 ± 0.25	0.99	0.3206
lnSize (ha)	0.70 ± 0.02	795.05	< 0.0001 ***
Year	− 0.24 ± 0.03	61.81	< 0.0001 ***
Lon	− 0.74 ± 0.22	11.72	0.0006 ***
Lat	− 1.62 ± 0.30	29.53	< 0.0001 ***
Land	− 0.18 ± 0.09	3.56	0.0592
WTE		8.87	0.0118 **
2–10 km	− 0.08 ± 0.03	7.62	0.0058 **
< 2 km	0.02 ± 0.08	0.09	0.7658
Forcov	− 0.36 ± 0.04	81.51	< 0.0001 ***
Lon × Year	0.28 ± 0.01	391.59	< 0.0001 ***
Lat × Year	− 0.09 ± 0.03	7.46	< 0.0063 **
Lon × Lat	− 1.03 ± 0.38	7.50	< 0.0062 **
Year × Land	0.10 ± 0.02	31.34	< 0.0001 ***
Land × WTE		8.07	0.0177 *
2–10 km	0.06 ± 0.03	3.14	0.0766
< 2 km	0.25 ± 0.10	6.46	0.0110 *
Year × WTE		1.06	0.5881
2–10 km	−0.00 ± 0.02	0.02	0.8895
< 2 km	−0.06 ± 0.02	0.99	0.3189
Year × Forcov	-0.00 ± 0.02	0.02	0.9019
Forcov × WTE		2.23	0.3279
2–10 km	−0.05 ± 0.03	1.81	0.1785
< 2 km	−0.08 ± 0.08	0.96	0.3271
Lon × Lat × Year	− 0.24 ± 0.03	48.06	< 0.0001 ***
Year × Land × WTE		63.47	< 0.0001 ***
2–10 km	0.17 ± 0.02	48.73	< 0.0001 ***
< 2 km	0.37 ± 0.07	26.43	< 0.0001 ***
Year × Forcov × WTE		10.65	0.0049 **
2–10 km	0.08 ± 0.02	10.48	0.0012 **
< 2 km	0.02 ± 0.06	0.08	0.7712

lnSize is the logarithm of the island size. The predictors Year, longitude (Lon), latitude (Lat), proportion of land (Land) and forest cover (Forcov) were all scaled. The predictor WTE is a three-level factor 'no nests within 10 km from the island', 'nests within 2–10 km' and 'nests < 2 km'. Estimates are given in relation to the 'no nests within 10 km' -group (intercept). ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

Fig. 5 Large-scale spatiotemporal trends of the eider population in the north-eastern Baltic Sea. The graph shows predicted breeding numbers of eiders per ha on surveyed islands at high and low latitudes and longitudes along the Finnish coast. The corresponding places are shown on the map



Geographical gradients and temporal shifts in eider distribution

The number of eider pairs increased with the size of the island. The three-way interaction between Year, Lat and Lon showed that eider numbers were highest in the southwest and decreased towards the north (Gulf of Bothnia) and east (Gulf of Finland) in the beginning of the study period. However, breeding numbers of eiders decreased steeply at low latitudes (SW) and more modestly at high latitudes (NW) during 1997–2020. The longitudinal trend was the reverse, with a temporal increase in eider numbers towards east at low latitudes (SE). In terms of coastal geography, the eider numbers decreased with a remarkable 90% in the Archipelago Sea (SW) and declined moderately in the Gulf of Bothnia (NW/NE) but increased in the eastern part of the Gulf of Finland (SE) (Fig. 5, Table 3).

The proportion of land (Land) and forest cover (Forcov) were set to their means, and WTE occurrence to nests within 2–10 km from the island. The shaded areas show the 95% confidence intervals.

Discussion

Our study demonstrates a clear spatial redistribution of the prey population (eiders) caused by habitat-specific trends in breeding numbers due to increasing predation pressure by an apex predator (WTE). Key habitat determinants of trends in breeding abundance were island exposure and forest cover, both of which affect predation vulnerability, leading to a population redistribution of eiders at both smaller (forest cover-island exposure axis) and larger spatial scales (nationwide geographical gradient). The full model, including three-way interactions with time, WTE proximity and proportion of land or tree cover, was best supported, revealing complex spatial and temporal variations in the focal predator–prey interactions. Breeding eider numbers were initially highest on treeless islands of the outer archipelago but later showed the steepest declines near nesting white-tailed eagles. In contrast, islands in the inner archipelago sustained higher breeding numbers in areas closer to eagle nests. The observed spatial redistribution of the prey population may be mediated by consumptive (i.e., predation) and non-consumptive (i.e., predator avoidance) effects, as will be discussed below.

Effects of predation and the physical environment

Birds can demonstrably distinguish between, and adapt their behaviour to, different predation risks (Morosinotto et al. 2010; Mohring et al. 2022), as illustrated by several passerines that avoid nesting close to raptor and owl nests (e.g., Lima 2009; Møller et al. 2017). This behaviour is less studied in waterfowl, but intriguingly, common loons were not avoiding nesting close to bald eagle nests when both populations were increasing (Cooley et al. 2019), mirroring our findings that eider numbers were highest in the vicinity of WTE nests in the core areas—the outer archipelago—when both populations were increasing. The outer archipelago, initially used by breeding female eiders for its isolation from terrestrial predators and abundant blue mussels during the period of low predation risk, also attracted recruits to the emerging WTE population, suggesting that prey availability was driving WTE habitat preferences. While remote islands in the outer archipelago offer nesting grounds safe from terrestrial predators (Spatz et al. 2014), this environment offers only limited protection from aerial, visually oriented predators (Lima 2009). However, the rapid recovery of WTEs—predators belonging to a different guild than the mammalian predators dominating during the apex predator-free period—may partly explain the delayed response to the returning threat, as female eiders persisted in nesting in the exposed outer archipelago until their numbers collapsed. Nevertheless, selection of nest sites offering visual protection is not without trade-offs, as nests with greater cover can potentially impede the incubating female's ability to quickly escape mammalian predators (Öst and Steele 2010).

Both consumptive and non-consumptive effects can explain the decrease of eiders in the outer archipelago. Female survival is lower on open, treeless islands (Ekroos et al. 2012a) while non-consumptive predation costs may be realized through intermittent breeding—a common strategy in eiders (Coulson 1984)—as predation risk in itself is associated with a higher probability of skipping breeding (Öst et al. 2018). Nest predation may have indirect carry-over effects by reducing future reproductive activity (Hanssen and Erikstad 2013), or by inducing breeding dispersal (Lima 1998). Established breeders, however, show high fidelity to their breeding island (Öst et al. 2011; Ekroos et al. 2012a), whereas fidelity may be less pronounced in recruits. Hence, natal dispersal is likely to be more extensive than breeding dispersal (Öst et al. 2005; Kurvinen et al. 2016), and potentially the primary driver behind the shift of the population core towards the less exposed inner archipelago. As the eider is a social species, the recruits may concurrently settle successfully inwards in the archipelago where established breeders are still occurring, which may further reinforce the shift in the core distribution of the population.

Humans can have a repelling effect on predators (Leighton et al. 2010) and in addition to physical shelter, the inner archipelago may offer indirect protection for the eiders, as human presence is more concentrated near the mainland. Subadult WTEs are shown to avoid human settlement (Tikkanen et al. 2018; Balotari-Chiebao et al. 2021), while the eiders have learned to seek shelter by and breed close to humans if necessary (Fox et al. 2015). The inner archipelago may offer relaxed predation pressure from WTEs as they are opportunistic hunters that feed on the most profitable prey (Ekblad et al. 2016). In the inner archipelago, offering shelter for the eiders, suitable shallow fishing grounds yield more profitable prey for the WTEs (Nadjafzadeh et al. 2013), which feed almost exclusively on waterfowl in the outermost archipelago but predominantly on fish in the inner archipelago (Ekblad et al. 2016). Finally, successfully breeding WTEs defend their territories against non-breeding WTEs, which may have a positive impact on eider breeding success and survival in areas with high aggregations of subadult WTEs. As a parallel example, nesting in association with territorial bald eagles (*H. leucocephalus*) has been suggested as a strategy to reduce predation risk for nesting great blue herons (*Ardea herodias*), as resident eagles may help to keep the more numerous non-breeding eagles away from the heronries (Kenyon et al. 2007).

Future prospects of the predator and prey populations

The rapid decline of the eider population since the mid-1990s (Ekroos et al. 2012b) was preceded by a corresponding growth of the population since 1980. The eider population might thus be reverting back to levels it had before the population growth in the absence of its main natural predator. It could also be reaching historically low levels, but we currently lack historical data to confirm this. However, the rate at which the eider population has been declining is of concern, while the WTE population continues to grow. Moreover, besides breeding eagles, adult and offspring eiders are extensively preyed upon by subadult and other non-breeding WTEs (floaters), whose effects are not quantifiable. The floaters, often seen foraging in groups of several individuals, can target specific islands regardless of the spatial limitations set by a nest site. At least locally, the effect of this predation can be larger and more unpredictable than that of the sedentary breeders.

Our study provides rare evidence that a predator can cause a substantial shift in the geographic centre of the prey species' distribution within a few decades. Consequently, eiders are likely to face a trade-off between food availability—blue mussels decrease towards the mainland—and predator avoidance—the inner archipelago may provide safer breeding grounds. The shift in the prey's distribution is consistent with life-history theory, because long-lived species should prioritize their own survival over reproduction (e.g., Gaillard and Yoccoz 2003). Importantly, these distributional changes may have dire repercussions on eider population persistence in the long run. World-wide, single-species protection plans have contributed to the successful recovery of some apex predators while failing to consider ecosystem level consequences and effects on other species, highlighting the need for multispecies action plans (Marshall et al. 2016; Cruz et al. 2019). With the current status of the WTE population (LC), that shows no signs of food-deprivation (Dementavičius et al. 2020), it would be important to limit any artificially boosted survival of subadult WTEs by minimising subsidies in the winter, such as discarded hunting remains and fish. The future prospects of both the eider and WTE populations are, however, also strongly influenced by ongoing, unpredictable human-induced ecosystem changes such as habitat loss, climate change, eutrophication, hazardous substances and the inadvertent spread of invasive predators. Considering that the initial reasons for the earlier eider population decline are still unclear, continued monitoring of the populations is ever more crucial, as well as research targeting especially the prey selection of WTEs, the role of sub-adult WTEs and the effects of multiple stressors (e.g. Bårdsen et al. 2018; Jaatinen et al. 2022).

Conclusions

The return of a predator belonging to a different guild than the prey currently is familiar with can have a significant impact on its prey (Ehlman et al. 2019). We showed that the nesting WTEs most likely had an impact on the eider numbers, this impact depending on the physical attributes of the breeding islands and reflecting a complex interplay of direct and indirect effects of predation. The decline was most dramatic on exposed, unsheltered islands in the outer archipelago where incubating eiders were an easy prey for aerial predation. The core of the eider population has experienced a shift towards the inner archipelago, where the predation pressure by WTEs is lower, while navigating the trade-off between food availability and predator avoidance. The returning predator has thus contributed to reshaping of the distribution of eiders on the population scale in the north-eastern Baltic, leaving former core areas almost unpopulated. To ensure the protection of both predator and prey species, conservation planning measures should include multispecies models at the ecosystem level (Marshall et al. 2016). Furthermore, it is important to consider that the required conservation efforts may vary in different habitats and with time due to complex predator–prey interactions in a changing environment.

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Author contributions The initial study conception and design were made by CE and TL, and the final study questions were formulated by CE, TL, AL, MÖ and KJ. AB and TS managed the waterfowl databases and censuses, and HL managed the white-tailed eagle database. CE analysed the data with contributions from AL and HT. CE and TL led the writing of the manuscript with major contributions by MÖ. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data is available at https://doi.org/10.5281/zenodo.15723442 (Ekblad et al. 2025).

Declarations

Competing interests The authors declare no competing interests.

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