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Research Article

Different demographic drivers of recovery in two adjacent populations of a long-lived bird of prey

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Understanding the demographic mechanisms underlying population decline or recovery is critical for conservation and management, yet similar population trends may arise from very different underlying processes. Comparing populations of vulnerable species groups like long-lived raptors in different environments can reveal how species respond to change. Here, we explore the demographic drivers of population recovery in two white-tailed eagle *Haliaeetus albicilla* populations, for which we have comprehensive data available: a mainly coastal population in the Baltic Sea region and an Arctic inland freshwater population primarily in Lapland. We analysed over 50 years of data, including breeding pair counts, productivity, ringing records, visual resightings, and genetic identification of individuals at natal nests and breeding sites. These data were combined in a Bayesian age-structured integrated population model to estimate key demographic parameters, population trends, and conduct prospective and retrospective analyses. Both populations experienced similar growth rates (Baltic Sea: 8.7% (CRI = −1.1%–16.8%), Lapland: 8.8% (CRI = −7.0–28.0%)) primarily supported by high adult survival typical for long-lived species. Despite these similar growth rates, demographic pathways differed markedly between populations: subadult survival being higher in the Baltic Sea, whereas adult survival was higher in Lapland. Both populations showed evidence of negative density dependence, and in the Baltic Sea population this appeared to operate primarily through delayed recruitment. This was associated with an increase in the non-breeding floater cohorts, suggesting increasing constraints on recruitment into the breeding population. Our results demonstrate that comparable population growth can be sustained by contrasting demographic structures, implying that monitoring and management strategies should account for population-specific processes rather than relying on trends alone. More broadly, this study highlights the value of long-term, multi-source data and integrated demographic modelling for identifying density-dependent mechanisms and understanding recovery dynamics in long-lived species.

Keywords: *Haliaeetus albicilla*, integrated population model, population dynamics, raptor, total population size

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Introduction

Understanding the mechanisms of population dynamics is essential for predicting how populations respond to environmental pressures and management actions (Sutherland and Norris 2002). Changes in population size and structure, and in the distribution of breeding pairs result from demographic processes like survival, reproduction, immigration and emigration (Newton 1998, Sutherland and Norris 2002), influenced by biotic (Krüger et al. 2002, Sillett et al. 2004, Bretagnolle et al. 2008, Lowney and Thomson 2024) and abiotic factors (Krüger et al. 2002, Marra et al. 2015, Pirotta et al. 2018, Nebel et al. 2023). Importantly, similar population trends might arise from very different combinations of these processes, particularly in long-lived species where demographic rates may compensate for one another. However, studying such complex patterns, combined with unpredictable environmental variation and stochastic events is challenging, and collecting reliable data on survival and reproduction often requires extensive monitoring (Cusser et al. 2021). Here, long-term datasets are invaluable, and comparative studies can help understand the ecological and anthropogenic factors that drive population recovery, persistence or collapse.

Integrated population models (IPMs) allow the handling of comprehensive long-term datasets. They represent a major advance in the field of population estimation by integrating multiple data from various sources (Schaub and Kéry 2022), including joint analysis of capture–mark–recapture data, population counts, and reproductive metrics. This improves estimates of population size and of 'hidden' demographic parameters, for which non-explicit data have been sampled (Besbeas et al. 2002, Schaub and Abadi 2011), and allows insights into the population structure. Estimates from IPMs enable assessments of which demographic parameters are contributing most strongly to population dynamics (Koons et al. 2016, 2017). Together, this enhances our understanding of wild animal populations and allows to support better-informed conservation strategies (Bled et al. 2017, Rushing et al. 2017, Plard et al. 2019).

Avian and mammalian predators occupy high trophic positions and are especially vulnerable to human pressures (Sergio et al. 2008, Donázar et al. 2016, McClure et al. 2018). As apex- and mesopredators, they serve as indicators of environmental health (Helander et al. 2008, Donázar et al. 2016, HELCOM 2022) and provide key ecosystem services, such as scavenging and regulating prey (Donázar et al. 2016). While many predator species continue to decline, some populations are recovering, emerging as conservation 'winners' despite past pressures (Dornelas et al. 2019, Finn et al. 2023). The comeback of Europe's large avian and mammalian predators is considered a conservation success story (Boitani and Linnell 2015). However, population growth alone does not necessarily reflect demographic stability or resilience, and recovering populations may differ substantially in their underlying structure and vulnerability to emerging threats. One of such species is the white-tailed eagle *Haliaeetus albicilla*, a top predator of coastal and lakeside ecosystems that feeds on a large variety of prey (Helander 1983, Ekblad et al. 2016, 2020, Dementavičius et al. 2020). Across Europe, the species suffered from hunting pressures, loss of habitat and environmental toxins, most notably DDT and PCBs (Helander and Stjernberg 2003, Helander et al. 2008), and went locally extinct in the western and central Europe (Love 1983). Norway was a last stronghold in northern Europe, where the species was protected in 1968 (Love 1983). In Finland, the white-tailed eagle was close to extinction in the 1920s and 1970s, but has seen a remarkable recovery (Lokki et al. 2024) potentially due to extensive conservation efforts (Nebel et al. 2025), providing an exemplary case of the general recovery of predator populations in Europe. Today, the species comes into conflict with the conservation of some prey species (e.g. eider duck *Somateria mollissima*, Öst et al. 2022) and might kill new-born livestock (O'Rourke 2014, Ekblad et al. 2020).

Two white-tailed eagle populations can be distinguished in Finland: the Baltic Sea population that inhabits mainly coastal-archipelago areas of the Baltic Sea, but also freshwater environments in southern and central Finland, and the inland population in Lapland and northeastern Finland that is primarily located north of the Arctic circle. These two populations are along a latitudinal climate gradient, characterized by shorter productive seasons and much harsher winters in Lapland, and longer growing seasons, milder climate and higher brackish-water productivity around the Baltic. The two populations are genetically distinct (Ponnikas et al. 2013), and today, there is no evidence that these two populations interbreed. However, breeding range expansion in central and eastern Finland raises the question whether this reproductive isolation might soon to be overcome. Both populations have been increasing, but there are several current and future threats on the horizon that call for their careful monitoring. Both populations are likely impacted by various environmental toxins (Isomursu et al. 2018, Sonne et al. 2020, Dietz et al. 2021), lead from ammunitions (Helander et al. 2021), and human activities (Isomursu et al. 2018), including the increasing construction of renewable energy infrastructures (Nebel et al. 2024).

In the present study, we use unique and comprehensive data to

1) construct a Bayesian integrated population model (IPM) which allows us to estimate and compare unknown population parameters between the two populations like

1) total population size,
2) population structure, including floater-to-breeder ratios (FBR),
3) immigration rates, which can inform whether the population recovery was self-sustained,
4) survival and
5) recruitment of different age classes, and
6) age at first reproduction (AFR). Finally,

2) we use perturbation analyses to identify and compare the main drivers of population recovery between the two populations (Koons et al. 2016, 2017), assess whether similar

growth rates are sustained by different demographic pathways, and test for signs of density dependence. This is a key step towards understanding the recovery of white-tailed eagle and that of other similar predators, helping assess current conservation status and identify drivers of past expansion to inform future predictions.

Material and methods

History of the white-tailed eagle in Finland

By the end of the 1960s and early 1970s, white-tailed eagle nests were being systematically documented in southwest Finland, the Åland Islands (Fig. 1, 'A') and the Northern Quark (Fig. 1, 'B') in the Baltic Sea. In the late-1990s, the white-tailed eagle expansions from southwest and Quark met in the Satakunta (Fig. 1, 'C'). In the 1990s, white-tailed eagles started to also inhabit freshwater environments of southern and central Finland. On the other hand, historically, Lapland appears to have been only sporadically occupied by breeding birds (Stjernberg et al. 2007), but a breeding population established in the mid-1970s around the water reservoirs Lokka and Porttipahta (Fig. 1, 'D'). In the late-1980s, there was a first breeding record of a white-tailed eagle pair in Koillismaa (to south of Lapland, Fig. 1, 'E') and in the 2000s even further south. It is not clear whether birds breeding in eastern Finland (Fig. 1, 'F') expanded from west, north or east from Russia. Population delimiters for this study were taken from genetic studies (Ponnikas et al. 2013).

Field data and genetic data collection

The monitoring of the Finnish white-tailed eagle populations has been conducted by the White-tailed Eagle working group that has operated under WWF Finland (1973–2019) and under the Finnish Osprey Foundation (2020 onwards). Monitoring data is available for 53 years (1970–2022) and 46 years (1977–2022) for the Baltic Sea and Lapland, respectively. Known nests were visited annually during the breeding season. Nest was determined as 'active' when there were fresh signs of activity, i.e. a nest had fresh sticks and branches brought in. The number of nestlings was determined by climbing the nesting tree, but also from the ground with binoculars, or by using drones. Where nest counts were obtained by ground observation alone, the number of observed nestlings is a conservative minimum value of brood size. Drone surveys and nest climbing are providing accurate counts.

Breeding attempts that resulted in a known fledgling or a live nestling at ringing age were considered successful, since the nests were typically not visited afterwards. Nestlings were ringed by licensed volunteers in May–early July with two metal rings. One of them had a large unique alphanumeric code allowing reading from a distance. Across the study period, on average about 69% (SD = 17) of all known nestlings were ringed, in the remaining cases the nestlings were either too old or the tree was not climbable, preventing the ringing of nestlings.

Post-fledging records were collected by reading the coded rings at winter feeding stations (Nebel et al. 2025), or opportunistically by the public between January and April in Finland (Supporting information). Adult breeding birds were identified at nest sites by photographs of the rings that are visible on the legs of a flying eagle. Recoveries of marked, dead individuals were obtained from inside and outside of Finland (Supporting information). To supplement visual resightings and inform recruitment into the breeding population, we use genotype information. Volunteers have collected 2–3 feathers from each ringed nestling since 2003 and adult feathers on or under the nest since 2001 (with most data available since 2008) during nest visits. By genotyping individuals and combining information from these two data, we could connect breeding individuals to their site and year of hatching (Penttinen et al. 2024). The genotyping also allowed us to record encounter histories of parent birds without rings and of unknown origin. A full genotyping and laboratory protocol can be found in the Supporting information.

Integrated population model

We developed an IPM to analyse the data sets jointly, but for the two populations separately. The IPM analysed three different data sets: 1) count data of the number of active nests each year (range = 2–504 and 1–113 for the Baltic Sea and Lapland populations, respectively), 2) productivity data as the number of successful broods and the total number of fledglings produced by all surveyed broods in each year (range = 3–552 and 1–124 surveyed broods), and 3) individual encounter data from a total of 5647 and 918 individuals, respectively, that include resightings from the study area, genetic encounters of unringed breeding birds of unknown origin from the study area (n = 546 and 68) and dead recoveries from inside and outside the study area of fledglings that were ringed in the study area (751 and 65). For each of these data sets we formulated a sub-model and the corresponding likelihood, and the IPM is formed by the joint likelihood, which is the product of the single data likelihoods (Schaub and Kéry 2022). In the following section, we describe the sub-models.

The core of the IPM is a female-based, stage-structured population model with a pre-breeding census. It includes 17 demographic stages (Supporting information, Fig. 2) and random annual variation in all demographic rates. Stages represent locally born individuals from age 1 until recruitment $N_{1\text{-}14}$, first-time breeders N_{15}, experienced breeders N_{16}, and immigrants N_{17} (birds breeding for the first time that were born in unknown nests inside or outside the study area). Annual transitions among stages were governed by age-specific survival s, recruitment α, site fidelity f, breeding probability b, reproductive success ψ, productivity ρ, and immigration ω. By using binomial and Poisson processes and annually variable demographic rates the model incorporates both demographic and environmental stochasticity. Specifically,

$$N_{1,t+1} \sim Pois\left(\Psi_t \frac{\rho_t}{2} s_{1,t} f_t \left(N_{15,t} + b_t N_{16,t} + N_{17,t}\right)\right)$$

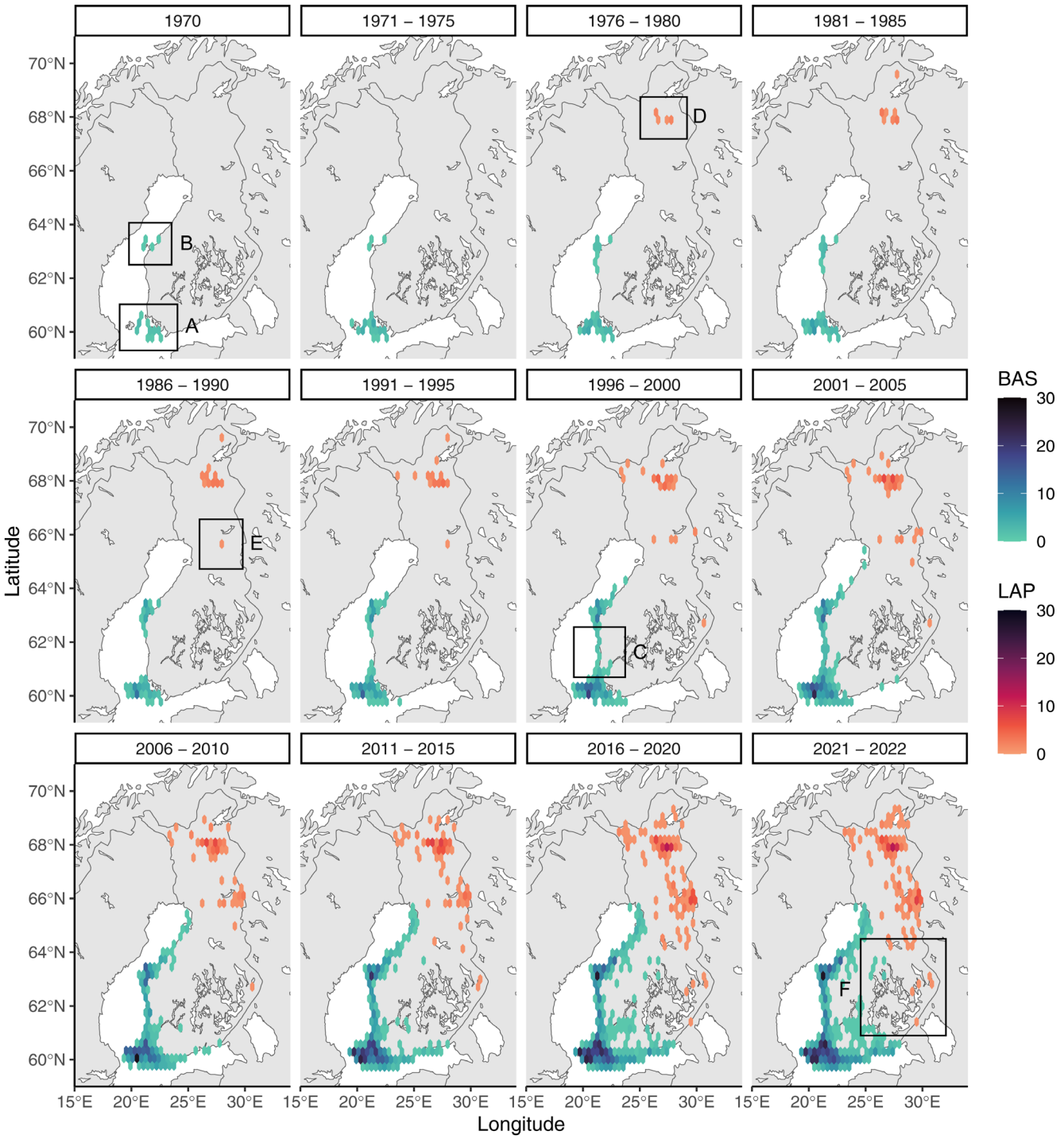

Figure 1. Maps of Finland showing the spatial and temporal expansion of two white-tailed eagle populations between 1970 and 2022. Shown are known location of active territories (if multiple nests are known, their average position was used). Dark colour tones indicate high density in the hexagon heatmap. The Baltic ('BAS', blue) population was restricted in the 1970s in the southwest Finland and the Åland Islands and the Quark and one pair in Lapland ('LAP', in orange). The pair from 1970 in Lapland is not shown as it disappeared and the LAP population only re-established in 1977. Annotations (squares and letters A–F) are referred to in the material and methods section. Years were collated to improve visual display.

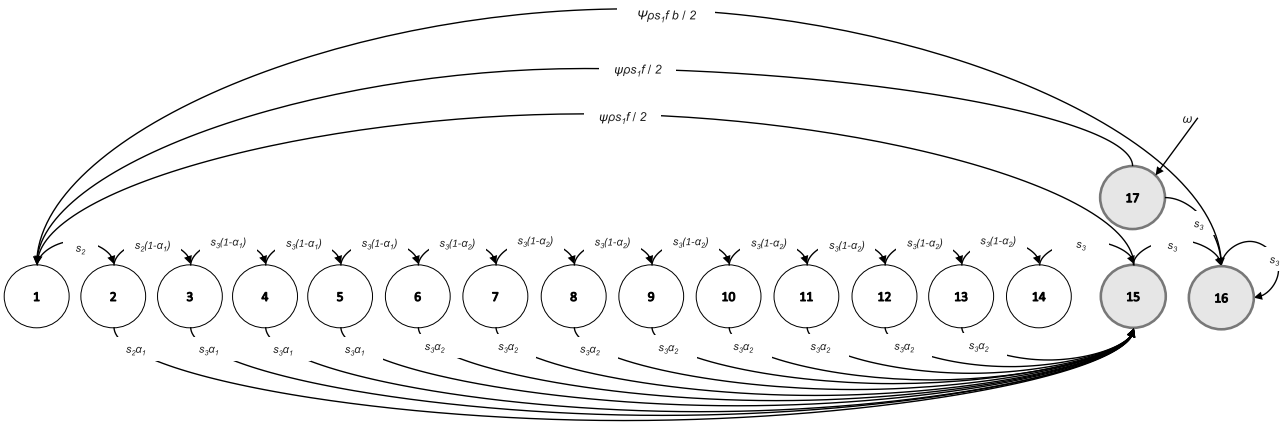

Figure 2. Life-cycle graph of the white-tailed eagle used in the integrated population model. There are 17 nodes that correspond to different ages (1–14: locally born 1-year olds–14-year olds) and states (15: locally born first time breeders, 16: experienced breeders that reproduce, 17: immigrants). Arrows depict transition from one state to the next based on demographic parameters, survival s, recruitment α, breeding probability b, reproductive success ψ, brood size ρ, and site fidelity f. The number of immigrants is ω. Empty nodes are non-breeding states, grey nodes are producing offspring every year.

$$N_{2,t+1} \sim \mathrm{Bin}\left(s_{2,t}, N_{1,t}\right)$$

$$N_{3,t+1} \sim \mathrm{Bin}\left(s_{2,t}\left(1-\alpha_{1,t}\right), N_{2,t}\right)$$

$$N_{k,t+1} \sim \mathrm{Bin}\left(s_{3,t}\left(1-\alpha_{1,t}\right), N_{k-1,t}\right) \quad \text{for } k = \{4,5,6\}$$

$$N_{k,t+1} \sim \mathrm{Bin}\left(s_{3,t}\left(1-\alpha_{2,t}\right), N_{k-1,t}\right) \quad \text{for } k = \{7,\ldots,14\}$$

$$\begin{aligned} N_{15,t+1} \sim\ & \mathrm{Bin}\left(s_{2,t}\alpha_{1,t}, N_{2,t}\right) \\ & + \mathrm{Bin}\left(s_{3,t}\alpha_{1,t}, (N_{3,t} + N_{4,t} + N_{5,t})\right) + \\ & \mathrm{Bin}\left(\begin{array}{l} s_{3,t}\alpha_{2,t}, (N_{6,t} + N_{7,t} + N_{8,t} + N_{9,t} \\ + N_{10,t} + N_{11,t} + N_{12,t} + N_{13,t}) \end{array}\right) \\ & + \mathrm{Bin}\left(s_{3,t}, N_{14,t}\right) \end{aligned}$$

$$N_{16,t+1} \sim \mathrm{Bin}\left(s_{3,t}, (N_{15,t} + N_{16,t} + N_{17,t})\right)$$

$$N_{17,t+1} \sim \mathrm{Pois}\left(\omega_t\right)$$

The observed counts of active breeding pairs (B_t) are modelled with a state-space model whose state-process model corresponds to the described population model and whose observation model links the predicted number of breeders with the observed counts using a log-normal distribution with an error term (σ_B^2) representing counting errors and model misfit:

$$B_t \sim \mathrm{logNormal}\left(\left(N_{15,t} + N_{16,t} + N_{17,t}\right), \sigma_B^2\right)$$

We assume that all 15-year olds to start reproducing if they have not reproduced so far. Site fidelity of one year olds was estimated f, and it was assumed to be one in older individuals. Hence, we allowed for natal dispersal but assumed absence of breeding dispersal, which is reasonable for a highly philopatric species (Nebel et al. 2024, Penttinen et al. 2024).

The productivity data include the number of active surveyed broods (B_t), and the total number of fledglings each year (J_t) from the number of successful broods (SB_t). The data were modelled first with a Binomial regression model:

$$SB_t \sim \mathrm{Bin}\left(\psi_t, B_t\right)$$

where ψ_t is the breeding success, the probability that a brood produced at least one fledgling.

Then, the number of fledglings were modelled with a Poisson regression:

$$J_t \sim \mathrm{Pois}(SB_t \times \rho_t)$$

where ρ_t is the mean number of fledglings raised by a successfully breeding female in year t.

A marked individual could be re-encountered alive in a year by visual observation alone, by genetic identification alone, or by both. The genetic identification furthermore informs about age-specific recruitment probability. A dead individual could also be recovered. The re-encounter probabilities of these different identifications are likely to be different. The good-

ness-of-fittestofthecurrentdata,indicatedstrongimmediatetrap-happiness (Pradel 1993), i.e. an individual encountered in the previous year was more likely to be encountered again in the current year than an individual not encountered.

We constructed a multistate capture-recapture model that jointly analyses the re-encounter and dead-recovery data, allowing for an immediate trap effect. In the Bayesian framework, multistate models are typically fitted using categorical distributions (Kéry 2010), but to overcome known problems with the MCMC samplers when live recaptures and dead recoveries are jointly analysed (Schaub and Badia-Boher 2025), and to increase computational efficiency, we re-parameterised the multistate model to use only Bernoulli distributions (Schaub et al. 2024, Schaub and Badia-Boher 2025). As the three binary processes are hierarchically linked through the latent survival state variable $\boldsymbol{z}$ (below), they collectively constitute a valid pre-parameterisation of the traditional multistate model (Schaub and Badia-Boher 2025). We define the stochastic latent state variable $\boldsymbol{z}$ that determines for each individual i in each year t whether it is alive $z_{i,t}=1$ or dead $z_{i,t}=0$. In the year in which an individual was marked, it is known to be alive. In all subsequent years, the latent state is estimated using the Bernoulli distribution governed by annual survival ($s_{a,t}$: annual survival from t to $t+1$ of an individual of age a) and the preceding latent state:

$$z_{i,t+1} \sim \text{Bernoulli}\left(s_{a,t} \times z_{i,t}\right)$$

Recruitment state was represented by another latent variable $\boldsymbol{x}$, where individuals initially marked as juveniles could recruit over time. For an individual that has not yet recruited into the breeding population in year t, $x_{i,t}=1$, while for an individual that has recruited in year t, $x_{i,t}=0$. The recruitment transition was modelled with a Bernoulli distribution as follows:

$$x_{i,t+1} \sim \text{Bernoulli}\left(\left(1-\alpha_{a,t}\right) \times x_{i,t}\right)$$

where $\alpha_{a,t}$ is the probability to recruit into the breeding population (i.e. to reproduce for the first time) at age a in year t. A combined recruitment dataset informed both populations.

The third latent state variable indicated whether an individual has dispersed to another population ($e_i=0$), or it was philopatric to the study population ($e_i=1$). This latent state variable is computed from a Bernoulli distribution with the site fidelity parameter (f), i.e.

$$e_i \sim \text{Bernoulli}\left(f\right)$$

Encounters (observations) are stored in a three-dimensional array $\boldsymbol{y}$, where the first dimension refers to the type of observation (here $n=3$, for sightings [y_1], dead recovery [y_2], genetic identification as a breeder [y_3]), the second to the individual and the third to the year. The entries in the array are either 1 if an individual was encountered in a given year with the corresponding method, and 0 otherwise. The data are then modelled with three Bernoulli distributions, with y_1 and y_2 modelling observation of ringed birds (probabilities of visual resighting, p^s and of dead recovery, r) and y_3 modelling recruited and genotyped birds (probability of genetic re-encountering, p^g):

$$y_{1,i,t} \sim \text{Bernoulli}\left(p^s_{a,t,k} \times e_i \times z_{i,t} \times \text{ring}_i\right)$$

$$y_{2,i,t} \sim \text{Bernoulli}\left(r_t \times \left(z_{i,t-1} - z_{i,t}\right) \times \text{ring}_i\right)$$

$$y_{3,i,t} \sim \text{Bernoulli}\left(p^g_{t,k} \times e_i \times z_{i,t} \times \left|x_{i,t} - 1\right| \times \text{gen}_i\right)$$

Multiplying these encounter probabilities by the current value of the latent state or the change in latent state in the Bernoulli distributions ensures that only living (z), present (e) and ringed (*ring*) individuals can be visually resighted, that only recently dead (z_{t-1}-z_t) and ringed (*ring*) individuals can be recovered dead, and only recruited individuals ($|x_{i,t}-1|$) that are alive (z), present (e) and have a genotype profile (*gen*), can be genetically re-encountered. Whether an individual was ringed ($ring_i=1$) and/or genetically identified ($gen_i=1$) are boolean variables and are known from the data. The resighting probability (p^s) can vary according to the age (a, 3 levels: 1-year, 2–3 years, >3 years old), year (t) and whether the individual has been encountered at the preceding occasion (k, 'immediate trap effect'). An immediate trap effect is not possible for individuals that are 1-year old, hence for a given year 5 resighting parameters are estimated. The genetic reencounter probability (p^g) could vary by year and also included an immediate trap effect. The probability to recover a dead individual (r), finally only varied by year, but not by the age of the individual and was the same for both populations.

The data of the Baltic Sea and Lapland populations were fitted in a single model, however, all parameters with the exception of the dead recovery probability were independent.

Model implementation

Tests for density-dependence and floater-to-breeder ratio

We tested whether the annual population growth rate λ decreases with increasing total population size ($N_{1\text{-}17}$) following a simulation approach (Schaub and Kéry 2022), which accounts for the negative correlation between λ and $N_{1\text{-}17}$ (Lebreton and Gimenez 2013). We compared the observed relationship between λ and $N_{1\text{-}17}$ with a simulated relationship between the two that would arise in the absence of density-dependence. If the observed and simulated relationships do not differ, there is no evidence for density-dependence.

To assess which demographic rates were impacted by density-dependence, we run regression models of the full posterior distributions of annual demographic rates against total

population size. As recruitment α_1 and α_2 were not informed by data until 2008, we restricted all regression models to the time 2008 until 2022 for all parameters to compare the same periods.

Calculations of the floater-to-breeder ratio (FBR) can be used to interpret the long-term viability of animal populations (Hunt 1998). We define breeders as the classes $N_{15\text{-}17}$ and floaters as $N_{3\text{-}14}$. $N_{1\text{-}2}$ were excluded from the floater calculations as these had no chance yet to recruit (Fig. 2). We calculate the FBR using the following equation:

$$FBR = \frac{\sum_{k=3}^{14} N_k}{(N_{15} + N_{16} + N_{17})}$$

Realized population growth $\log(\lambda_t)$ was calculated using the entire estimated population size of all 17 classes and using the following equation:

$$\log(\lambda_t) = \log(N_{t+1}) - \log(N_t)$$

where N_t is the total population size in year t.

Prospective and retrospective perturbation analysis and age at first reproduction

We first calculated how sensitive the realized population growth rate λ was to changes in demographic rates and in population structure (Koons et al. 2016, 2017). To do this, we computed elasticities, which represent the proportional (percent) change in λ resulting from a proportional change in each vital rate or structural component. Second, we performed retrospective perturbation analyses to identify the drivers of λ in each population (Koons et al. 2016, 2017, Schaub and Kéry 2022). We used temporal decomposition to quantify the contribution of temporal variability and covariability of demographic rates and population structure to the temporal variability of λ. The first 20 years were discarded (BAS 1970–1989, LAP 1977–1996) for this analysis, because we were interested in the demographic processes after the initial phase of the population establishment. We repeated the analysis with a 10-year cut-off (BAS 1970–1979, LAP 1977–1986) to assess the robustness of our results to the threshold choice. The 20-year cut-off was only used for the perturbation analysis.

We were further interested in estimating the age at first reproduction (AFR) between 2008 and 2022. We calculated AFR separately for each population and year to assess changes through time. AFR was derived from age-specific recruitment probabilities (α_n, n = 1–15) using the following equation:

$$AFR = \alpha_1 + \sum_{n=2}^{15} \left(n\alpha_n \prod_{i=1}^{n-1} (1 - \alpha_i) \right)$$

For a given year, AFR was calculated assuming that the age-specific recruitment probabilities estimated for that year remained constant across ages. Consequently, annual variation in AFR reflects changes in recruitment implied by α in a given year, rather than true cohort-specific temporal variation in realized AFR.

Results

Temporal population increase, population structure and demographic rates

The R-hat values of parameters were generally < 1.1 (with five exceptions of < 1.3, reflecting minor to modest non-convergence), with an average of 1.004, indicating that the Markov Chains have converged. The non-converged parameters were all estimates of population size for Lapland in the 1990s, likely due to small sample sizes. The model had a good fit (Supporting information) and Bayesian p-values were within acceptable ranges (Supporting information). One exception was dead recoveries in the Baltic Sea population, which showed a high p-value likely reflecting the low frequency and limited information content of the recovery data. Across the observation period, the estimated number of females increased at an average growth rate of 0.083 (CRI = −0.011–0.155) and 0.084 (−0.073–0.247) for the Baltic Sea and Lapland populations, respectively (Table 1, Fig. 3). This translates to 8.7% (Baltic, −1.1–16.8%) and 8.8% (Lapland, −7.0–28.0%) annual increases, respectively. In 2022, the estimated total number of females from known nests within the population was 1965 (1454–2452) for the Baltic Sea population and 259 (118–443) for the Lapland population (Fig. 3). The total number of known females for the two populations amounted to 4449 (3144–5791) individuals, assuming an equal sex ratio. In the Baltic Sea population, FBR increased over time (1995: 0.94; 2022: 1.32), while in Lapland, FBR remained stable at around 0.60–0.70 (Supporting information). The number of immigrants was generally low, but varied temporally, with higher rates during the early study years (Supporting information).

Adults from Lapland had higher survival probabilities than those from the Baltic Sea and subadults from the Baltic Sea had higher survival probabilities than those from Lapland (Table 1). Despite reproductive success being higher in Lapland and brood size being higher in the Baltic Sea (Table 1), productivity (resulting number of nestlings per breeding attempt) was similar between the two populations (Lapland: 0.862, 0.644–1.058; Baltic Sea: 0.815, 0.345–1.098, p (BAS < LAP) = 0.564).

Furthermore, site fidelity f was higher in the Baltic Sea population than in the Lapland population. The mean number of female immigrants ω was much higher in the Baltic Sea compared to Lapland, but the immigration rate, expressed as the number of immigrants per locally hatched birds, was overall similar (Baltic Sea: 0.09, 0.02–0.29; Lapland: 0.11, 0.01–0.35). The estimates of the nuisance parameters can be found in the Supporting information.

In both populations, subadult survival s_2 was higher than juvenile survival s_1 and recruitment increased with age, with older birds having higher recruitment probabilities than

Table 1. Posterior means and 95% credible intervals (CRI) for different demographic parameters, annual survival s_1 (probability to survive from fledging until 1 June the following year), s_2 (probability to survive one year when in ages 1–3), s_3 (probability to survive one year when four years old or older); recruitment into the breeder state α_1 (probability to recruit at ages 2–5 years), α_2 (probability to recruit at ages 6–13 years), reproductive success ψ , brood size ρ (number of nestlings per successfully breeding female), breeding probability b of experienced breeders; site fidelity f (probability to remain in Finland), and number of immigrants ω. Values are shown for the Baltic Sea ('BAS') and inland ('LAP') population. Column p (BAS < LAP) refers to the posterior probability that a given demographic parameter is differentin BAS than in LAP and quantifies the strength of evidence. A value close to 1 indicates that the parameter is lower in BAS than LAP, a value close to 0 indicates that the parameter is higher in BAS than LAP.

	Population				
	Baltic Sea		Lapland		
Parameter	Mean	95% CRI	Mean	95% CRI	p (BAS < LAP)
Juvenile survival s_1	0.891	0.871–0.911	0.881	0.806–0.944	0.397
Subadult survival s_2	0.950	0.940–0.961	0.913	0.870–0.951	0.031
Adult survival s_3	0.894	0.884–0.904	0.940	0.922–0.956	1.000
Recruitment α_1	0.032	0.018–0.050	0.065	0.012–0.162	0.797
Recruitment α_2	0.214	0.145–0.307	0.205	0.034–0.511	0.393
Reproductive success ψ	0.512	0.466–0.555	0.606	0.570–0.639	1.000
Brood size ρ	1.592	1.558–1.626	1.422	1.346–1.502	< 0.001
Breeding probability b	0.979	0.913–1.000	0.901	0.592–0.998	0.185
Site fidelity f	0.928	0.884–0.968	0.661	0.568–0.756	0.000
Immigrants ω	8.585	5.774–11.984	1.463	0.602–2.443	0.000
Population growth log (λ)	0.083	−0.015–0.213	0.084	−0.080–0.318	0.506

young ones (Table 1). However, CRI intervals of recruitment for Lapland were very wide, indicating strong uncertainty. Across all years, mean AFR for the Baltic Sea population and the Lapland population was 9.4 (7.6–11.6) and 9.2 (5.7–13.2), respectively.

Evidence of density-dependence

We found evidence that both populations are subject to density-dependence (Supporting information), with the probability of the posterior distribution for the actual data being smaller than the reference distribution without density-dependence (Baltic Sea = 0.999; Lapland = 0.891). The regression models showed that recruitment α_2 and subadult survival s_2 in the Baltic Sea were negatively affected by population size (Supporting information), although the decline was more pronounced for α_2 than s_2 (Fig. 4). Recruitment declined from 0.267 (0.099–0.581) in 2008 to 0.166 (0.073–0.264) in 2022 (Fig. 4), increasing AFR from 9.0 (7.3–11.0) to 10.2 years (8.8–11.8). Reproductive success ψ showed a positive relationship with population size in the Baltic Sea (Fig. 4), from a probability to breed successfully of 0.578 (0.521–0.633) in 2008 to 0.659 (0.617–0.698) in 2022. There was no evidence of density dependence or temporal effects for any of the other demographic rates in either population (Supporting information).

Prospective and retrospective perturbation analyses

Realized population growth rate λ was most sensitive to changes in adult survival s_3 in both populations, followed by changes in subadult survival s_2. Other demographic rates (s_1, f, ψ, ρ) had lower elasticities, indicating that changes in these parameters have a smaller effect on λ. Population growth was little sensitive to a change in population structure. An increase in the proportion of breeding individuals results in an increase of λ while an increase in the non-breeding individuals has a slight negative effect on λ. Results were similar for both populations (Fig. 5).

The temporal variability in different parameters contributed to the fluctuations in λ, but with some differences between the two populations. In the Baltic Sea, the contribution of temporal variation was low across most parameters, but with high contribution from adult survival s_3, and reproductive success ψ. In Lapland, contributions were more spread out, with high uncertainties and all their CRIs include 0, limiting interpretability. Results were consistent between the 20-year (Fig. 5) and 10-year cut-off (Supporting information).

Discussion

Since the 1970s, the two white-tailed eagle populations in northern Europe increased annually by an average of 8.7–8.8%, increasing from 8 (3–15) to 4449 (3144–5791) known female individuals in 2022. While the point estimates of annual population growth rates are robustly positive, their uncertainties are wide and including negative values, especially for the Lapland population, indicating some estimation uncertainty. Although the annual increase has been similar, the two populations have relied on different demographic pathways to achieve recovery with subadult survival, brood size and site fidelity being higher in the Baltic Sea than in the Lapland population, and adult survival and reproductive success being higher in the Lapland than in the Baltic Sea population. Our results demonstrate that similar population growth rates can arise from distinct demographic mechanisms, showing that recovery dynamics cannot be inferred from population trends alone. The contrasting demographic pathways furthermore indicate that population assessments based solely on population trends might obscure spatial heterogeneity, which can only be resolved using spatially

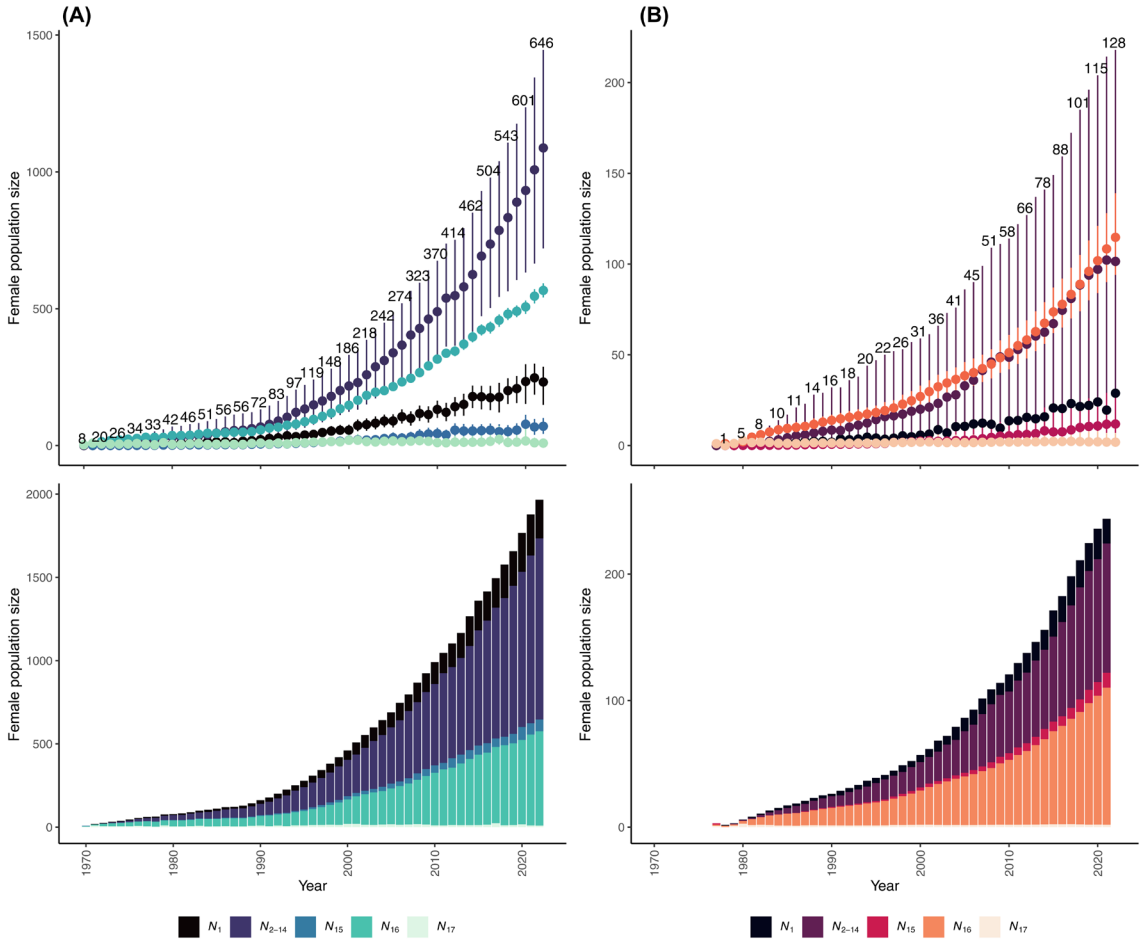

Figure 3. Population development based on the output from the integrated population model for the two white-tailed eagle populations investigated in this study. The Baltic Sea population (blue, column A, 1970–2022) and the inland Lapland population (red, column B, 1977–2022) have increased dramatically in the past decades. Different shades of colour relate to different age classes. From darkest to lightest: one year olds N_1, non-breeding 'floaters' N_{2-14}, first-time breeders N_{15}, experienced breeders N_{16}, and immigrants N_{17}. Error bars depict 95% CRI. Numbers indicate female breeding population size, only every second year is shown due to graphic constraints.

explicit population assessments (Zipkin and Saunders 2018, Gantchoff et al. 2022). We further show that negative density dependence is present in both populations, but only in the Baltic Sea, a delay in the onset of reproduction could be identified as the driving mechanism.

A comparison of demographic parameters, their elasticity and temporal contribution

Differences in demographic pathways in the two populations likely reflect variation in environmental conditions or human pressures between the regions, with winter conditions playing a central role. In the Lapland population, winter likely represents a major survival challenge, as watersheds remain frozen until later spring and food availability might be limited. Under these harsh conditions, only the fittest subadults may survive, resulting in a high-quality adult cohort characterized by high survival and reproductive success. Despite the severity of winter conditions, adult survival in Lapland was high, suggesting that sufficient food resources (likely carcasses) must be available to support resident birds through winter. Adults might also be stronger competitors for limited resources during winter. In addition, the lower human population density and reduced competition for nest sites in Lapland may further contribute to high adult survival.

In contrast, subadults in the more southernly Baltic Sea population may benefit from milder winter conditions, potentially reducing subadult mortality. However, adults in this region may face greater risks associated with higher human presence (Isomursu et al. 2018, Nebel et al. 2024) or increased competition among conspecifics, which could negatively affect adult survival. It should be noted that at least some individuals from Lapland migrate to the Baltic Sea area during winter, and the extent to which wintering areas of subadults from the two populations overlap remains unknown. Consequently, inter-population interactions and competition during the non-breeding season cannot be excluded.

Together, these patterns suggest a change in dominant demographic constraints along a latitudinal and habitat

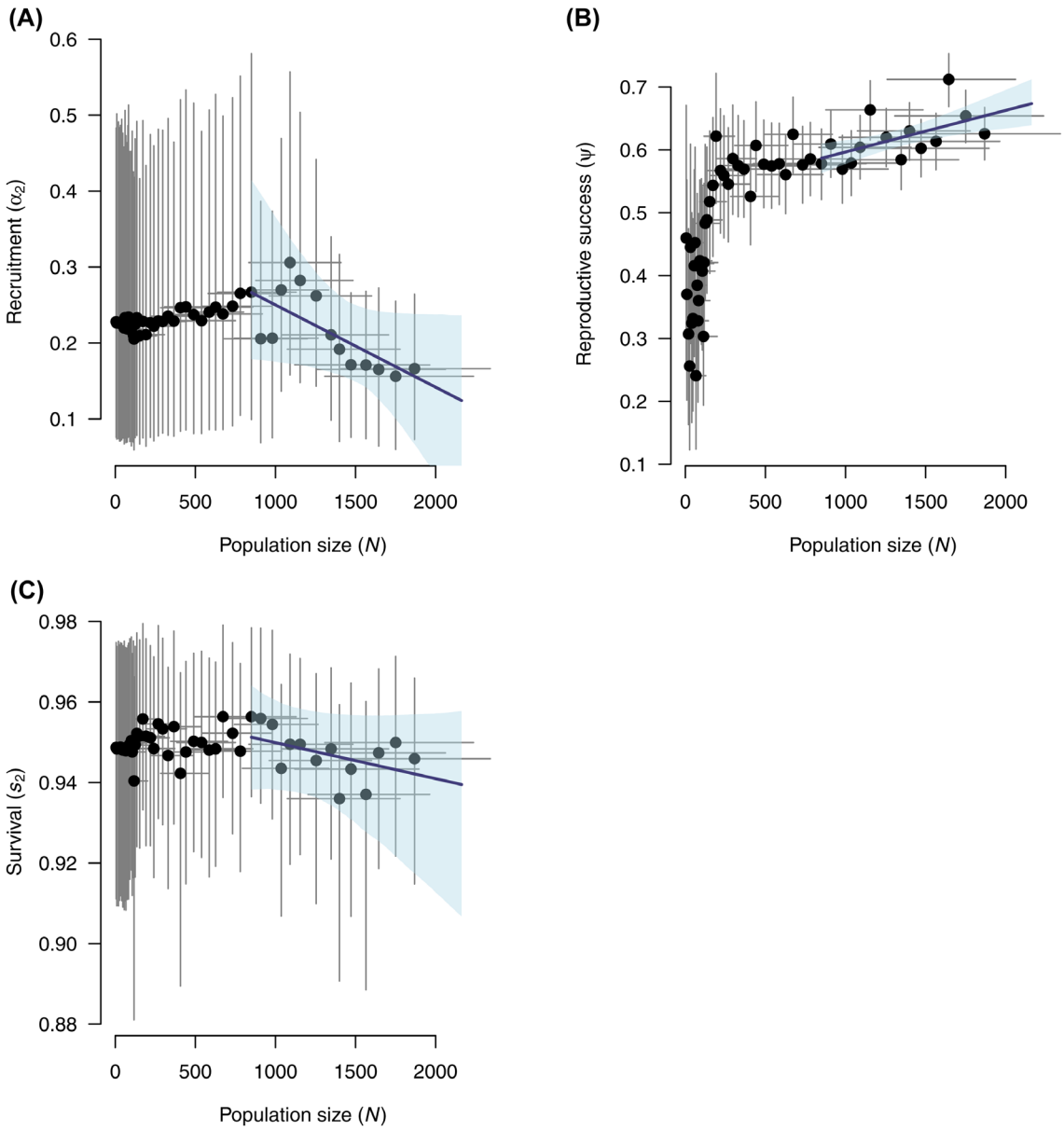

Figure 4. Annual estimates of recruitment α_2 (A), reproductive success Ψ (B) and subadult survival s_2 (C) plotted against estimated population size in the Finnish Baltic Sea (BAS) population of white-tailed eagles. Between 2008 and 2022, recruitment α_2 and subadult survival s_2 are negatively associated with population size, reproductive success ψ positively. Dots show posterior means, and lines show 95% credible intervals. Blue regression lines show the predictions based on the estimated regression coefficients, light blue shades 95% credible intervals. All regressions were restricted to the time period of 2008 to 2022 due to a lack of genetic information prior to 2008.

gradient. Our findings demonstrate that population recovery can be driven by distinct demographic pathways even when population growth rates are similar. This demonstrates the limitations of relying on population trends alone to assess population health or to identify region-specific conservation challenges.

Elasticities revealed that adult survival had the strongest influence on population growth in both populations, a pattern consistent with observations in other long-lived species (Sæther and Bakke 2000, Newton 2010, van de Kerk et al. 2013). The contribution analysis indicated that temporal variability in population growth was strongly influenced by fluctuations in adult survival and reproductive success. The protection of nest sites and cessation of illegal persecution, together with the ban of DDT likely improved both survival and breeding performance. Immigration was low and did not contribute significantly to population increase, indicating little gene flow within the Baltic Sea metapopulation (population genetic studies like Hailer et al. 2007, Ponnikas et al. 2013) and that the population recovery was largely self-sustained. However, immigration tended to be relatively stronger in the first study years (Supporting information),

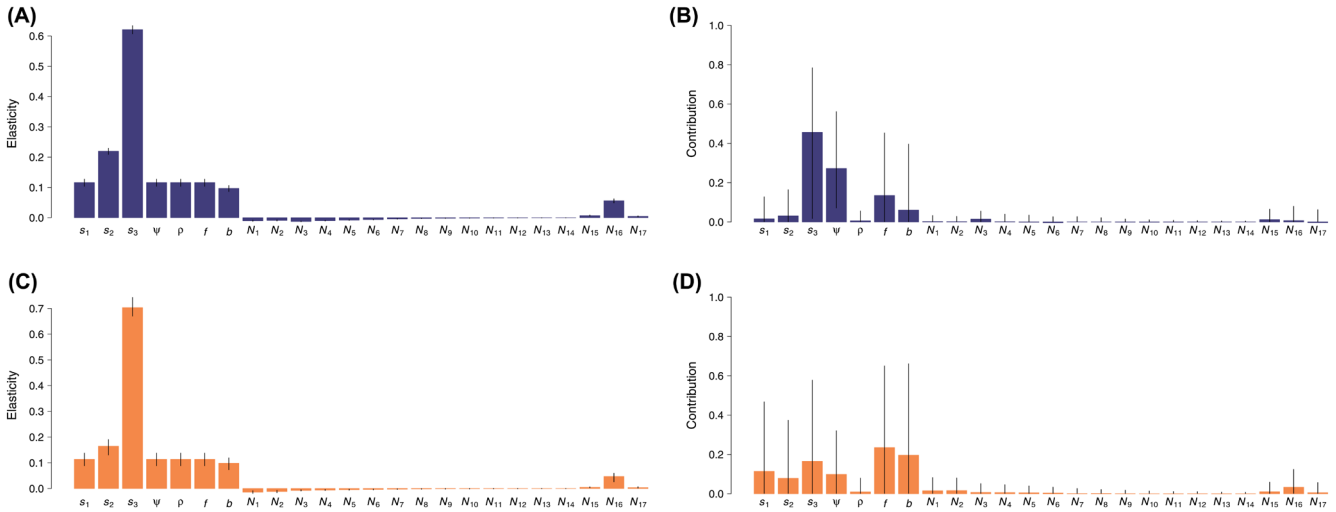

Figure 5. Elasticity of the realized population growth rate (λ) to changes in the demographic parameters and in population stage structure, and the relative contribution of the variability of the demographic rates and of population stage structure to the temporal variability in realized population growth rate for the Baltic coast population (blue, A and B) and the inland Lapland population (orange, C and D). The bars show the posterior means, the vertical lines indicate the limits of the 95% CRI. The values are calculated from the result of the integrated population model considering the period from 1990–2022 (BAS) and 1997 – 2022 (LAP). s_1, s_2, s_3: age-specific survival; ψ: reproductive success, ρ: brood size; f: site fidelity; N_1–N_{14}: locally born, not recruited individuals of different ages; N_{15}: locally born, recruited first-time breeders, N_{16}: experienced breeders, N_{17}: immigrants.

suggesting that it could have played a more pronounced role in the initial establishment of the population. The contributions to temporal variability in population growth rate were wide and overlapping across vital rates, originating from the large estimation uncertainties of the demographic rates and their temporal variances and covariances. The incorporation of environmental covariates will be essential next step to estimate demographic rates more accurately and to better resolve the drivers of population growth rate variation in these recovering populations (Knape et al. 2023, Martin et al. 2026).

Density-dependence in the Baltic Sea population

Regulatory mechanisms through negative density-dependence primarily affect the non-breeding cohorts, in particular floaters. Floaters must likely compete for breeding sites (Krüger et al. 2002, Sillett et al. 2004, Katzenberger et al. 2021), which delays the onset of their reproductive life. Lower recruitment rates also result in an increase in the non-breeding proportion of the population and thereby a change of the population structure. Similar delays in the onset of territory acquisition and reproduction have been recorded in recovering peregrine falcon and urban Cooper's hawk *Accipiter cooperii* populations (Tordoff and Redig 1997, Stout and Rosenfield 2010), and also in mammalian predators (Wikenros et al. 2021) and non-predatory birds (Cooper et al. 2009).

Finnish white-tailed eagles are continuing to expand their range, with the Baltic Sea population moving inland in southern areas and the Lapland population expanding southward, where many potentially suitable areas with large lakes currently remain unoccupied. This suggests that habitat availability may not yet be a limiting factor. Nevertheless, recruitment appears to delay as population size increases. An explanation is that white-tailed eagles exhibit strong natal site fidelity (Penttinen et al. 2024) and recent research indicates that many young eagles might be socially attracted to established breeding areas (Penttinen et al. 2024, Canal et al. 2025) or show a preference for natal-like habitats (Penttinen et al. 2026), leading them to delay breeding until a territory becomes available. This queuing behaviour may result in a surplus of floaters and generate density-dependent recruitment, even when suitable but unoccupied habitat exists elsewhere. However, as the true extent of unoccupied suitable habitat and habitat preferences have not been studied, it is difficult to determine whether habitat saturation is being approached or whether social constraints primarily limit expansion. For the Baltic Sea population, it is further important to note that the main waterfowl prey, the eider duck, has seen a decline in population size in recent years (Öst et al. 2022), potentially contributing to the habitat saturation process.

It is interesting to note that adult survival is not affected by negative density-dependence, although both territory acquisition and defending a territory are often associated with intense and sometimes lethal fights (Tordoff and Redig 1997, Gahbauer et al. 2015, Caballero et al. 2016). One possibility is that density-related mortality from territorial conflicts is offset by concurrent positive influences on survival, such as the long-term decline in environmental contaminants and other improving environmental conditions, which may help maintain high adult survival even at increasing population densities. Although this pattern may appear counterintuitive, density dependence acting more strongly on subadult or non-breeding cohorts than through adult survival has been observed in other long-lived species (Ferrer et al. 2004,

Bonenfant et al. 2009, Katzenberger et al. 2021). However, negative density dependence in adult survival has also been documented in some systems (Fowler 1987, Frederiksen and Bregnballe 2000, Lieske et al. 2000, Owen-Smith 2006), particularly at high population densities or under strong resource limitation (Frederiksen and Bregnballe 2000), suggesting that the balance among regulatory pathways is context dependent. Large non-breeding cohorts are key buffers in recovering populations of territorial vertebrates (Barraquand et al. 2014, Katzenberger et al. 2021, Sergio et al. 2021), dampening short-term demographic stochasticity but potentially obscuring early warning signals of decline.

The increase in reproductive success with increasing population size is unlikely due to true positive density-dependence but general time- and environment-related effects, e.g. due to a reduction of environmental contaminants in the Baltic Sea environment (Sun et al. 2020, HELCOM 2022).

Comparison to other populations and implications for demographic constraints on recovery

First reproduction in the white-tailed eagle is typically assumed to occur at five years of age (Struwe-Juhl and Grünkorn 2007, Evans et al. 2009), which coincides with eagles obtaining the full adult breeding plumage. However, consistently across time and for both populations, our results indicate later onset of reproduction at age nine. Besides that, both populations exhibit demographic rates similar to those reported elsewhere in the species' range (Evans et al. 2009) or in related species (Elliott et al. 2011). Furthermore, adult survival falls well within the expected range for large birds of prey (Newton et al. 2016). This suggests that adult survival and breeding performance are neither exceptionally high nor strongly constrained by local conditions. Thus, population recovery is unlikely to be driven by unusually favourable conditions, but rather by the accumulation and persistence of individuals in the population. However, the reproductive rates continue to remain below pre-collapsed levels, which are 1.64 (brood size) and 0.59 (reproductive success) (HELCOM 2022), implying that recovery potential is currently maintained by demographic buffering rather than by high productivity.

Implications for conservation

The recovery of the white-tailed eagle highlights the success of conservation efforts (Stjernberg et al. 2007, Nebel et al. 2025), yet caution is warranted as existing and emerging threats pose risks (Isomursu et al. 2018, Nebel et al. 2024). While lead poisoning is the leading cause of death in white-tailed eagles (Isomursu et al. 2018), in particular the impact of wind power infrastructure, which was shown to decrease adult survival (Nebel et al. 2024) and reproductive success (Balotari-Chiebao et al. 2016) is an increasing cause of concern. Because the two populations rely on different demographic mechanisms to sustain growth, they are likely to differ in their sensitivity to emerging threats. While the relatively large proportion of floaters in the Baltic Sea population likely buffers against additional losses of breeding adults to some degree (Katzenberger et al. 2021, Sergio et al. 2021), this effect may only delay rather than prevent long-term population declines. In contrast, the Lapland population, with fewer individuals and also fewer floaters available, may be more vulnerable to increasing mortality pressures. The IPM developed here provides a tool for future studies to examine how different environmental stressors and changes can influence the populations in the future.

Broader implications

More broadly, our results show how recovery dynamics in long-lived, territorial species may be shaped by context-dependent constraints acting on different life stages. Similar growth rates can mask substantial differences in demographic structure, density dependence, and buffering capacity, with important consequences for resilience to threats. IPMs provide a powerful framework to uncover these hidden mechanisms, particularly in recovering populations where transient dynamics, delayed recruitment, and non-breeding cohorts play a disproportionate role.

Limitations

Our IPM includes a few limitations that may affect the precision of parameter estimates. First, the model treats both sexes equally, although sex-specific differences in survival and dispersal behaviour are likely (Penttinen et al. 2024), and brood sex ratios appear slightly male-biased in our data (unpublished data, but Nebel et al. 2025 for basic data on nestling sexes). Second, age structure of survival is simplified into three categories, potentially masking variation in demographic rates. Third, identifying the demographic pathway of density dependence is challenging, as the largely steady population growth with minimal fluctuations makes it difficult to distinguish density effects from gradual environmental changes (discussion on reproductive success above). Detecting mechanisms of density-dependence might become easier in the future when the populations approach carrying-capacity. Finally, we need to note that while the aim of the population monitoring has been total census of the breeding population, it is clear that in each year some nests have been missed and that achieving a total census becomes more challenging as the population increases and spreads. The observed and estimated numbers are therefore a minimum while the real population size can be larger. However, we see no reason to assume that those unknown nests would change any of the demographic parameters of the population except the population size.

Conclusion

The two white-tailed eagle populations investigated in this study showed a remarkable comeback in last ca 50 years, with annual population growth rates of 8.7–8.8%. The IPM shows that both populations have high demographic rates, particularly high adult survival, which may have contributed to species' recovery – alongside reduced threats – even though reproductive rates remain below pre-collapse levels (HELCOM 2022). Although the two populations

experienced similar levels of population growth, there were differences in demographic rates, most notably in terms of adult and subadult survival. The opposing patterns in subadult versus adult survival suggest partial demographic compensation between life stages, whereby limitations acting on one stage are offset by enhanced performance in another. Such compensation may explain how similar growth rates are maintained despite divergent environmental constraints. It is unclear how these differences arise but might be associated with different environmental conditions that the populations experience along the latitudinal gradient and in different habitats. More generally, these results highlight that populations exhibiting similar growth rates may nonetheless require different monitoring and management strategies, depending on the demographic pathways underlying recovery.

There were also differences with implication for future population developments and the susceptibility to long-term success of the species. The large floater population in the Baltic Sea population is likely providing a buffer against future threats (Sergio et al. 2021), but the inland Lapland population might be more susceptible. This study improves our understanding of white-tailed eagle recovery and offers insights into the potential resilience of large predators. By identifying key demographic drivers, it informs future projections and can guide conservation efforts for raptor populations in our changing world. Our findings underscore that successful recovery in long-lived predators does not imply uniform demographic processes and highlight the importance of understanding underlying mechanisms when assessing population resilience and guiding conservation strategies.

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Author contributions

Carina Nebel: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Toni Laaksonen:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Torsten Stjernberg:** Data curation (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Heikki Lokki:** Data curation (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Michael Schaub:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the figshare Repository: https://doi.org/10.6084/m9.figshare.31926960 (Nebel et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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