Bewick’s swans in a changing world

Species responses and the need for dynamic nature conservation

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Publication date
2020

Document Version
Other version

License
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Chapter 2

Apparent breeding success drives long-term population dynamics of a migratory swan

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Abstract

Success or failure of adaptation is ultimately reflected in a species’ vital rates, i.e. survival and reproduction success of individuals, that together determine a population trend. Population trends are commonly monitored using counts of a species’ abundance. Rapid changes or fluctuations in this abundance can be a reason for concern, and call for research into the underlying demographics and causes. In the case of the NW European flyway population of Bewick’s swan (Cygnus columbianus bewickii) an interesting population trend has been observed in five decades of monitoring. The total number of birds increased to a maximum of c. 30,000 individuals in 1995 and subsequently decreased to about 18,000 individuals in 2010, after which the population appears to be stabilizing. Such fluctuations in population numbers are rare in long-lived species and understanding the drivers behind these changes is crucial for species management and conservation. By using the integrated population model (IPM) framework we analysed three demographic datasets jointly: population counts, capture-mark-resightings and proportion of juveniles. We modelled age-class specific survival, reproduction and resulting population numbers over a period of ~50 years (1970-2015). We found no consistent trend in adult and yearling survival, an increasing trend in juvenile survival, and higher apparent breeding success rates in the years when the population had a positive growth rate compared to years with a negative growth rate. A transient life table response experiment showed that apparent breeding success and adult survival contributed most to the variation in population growth rate. We explored possible explanatory variables for the different demographic rates and found a significant association between juvenile survival and the water level in lakes during autumn migration and the temperature in summer. Such associations are important for understanding the population dynamics of species with fluctuating population sizes, and to inform management and conservation decisions.

Submitted manuscript
**Introduction**

In the rapidly changing world we currently live in, species constantly need to adapt to changing environments (Chen et al., 2011; Hoffmann and Sgrò, 2011; Williams et al., 2008). Especially in migratory species, the changing environment poses a challenge because of the lack of correlation between the (rates of) change in different geographical areas (Bairlein, 2016; Visser et al., 2009). Success or failure of adaptation is ultimately reflected in a species’ vital rates, i.e., survival and reproduction success of individuals, which are reflected in a population growth rate. Understanding how species respond and how population trends differ under varying environmental conditions therefore is of great interest, both from a scientific and a conservation perspective (Oppel et al., 2014).

Population counts often form the basis for conservation and management strategies in an attempt to conserve or control, either positively or negatively, species’ numbers. However, in many species the actual status remains uncertain, despite large-scale and labour-intensive monitoring programmes (Tempel et al., 2014). This can be due to the elusiveness of the species, or to slow life-history traits (Cardillo et al., 2005), both of which make it difficult to monitor properly and thus to assess the species’ status. Looking at the underlying demographic rates of the population of interest can in such cases give further insights (Besbeas et al., 2002; Katzner et al., 2006; Lebreton and Clobert, 1991), although fully understanding population dynamics can be very challenging (Robinson et al., 2014). Identifying the main demographic processes steering population dynamics can also help in defining where and at what spatial scale conservation strategies need to be implemented, especially when species are migratory (Schaub et al., 2012).

Integrated population models (IPMs) were initially developed to exploit the fact that census data contain information on the survival of individuals and vice versa (Besbeas et al., 2002; Schaub and Abadi, 2011) and are increasingly used for conservation science (Zipkin and Saunders, 2018). Rather than analysing census data and demographic data separately (such as survival analysis based on mark-recapture data), integrating them based on a joint likelihood allows for information flow among demographic processes, accounting for imprecision of data and correlation between estimators (Besbeas et al., 2002; Schaub and Abadi, 2011). The method improves the accuracy of parameter estimation and allows for estimation of parameters for which no explicit data are available (Altwegg et al., 2014; Schaub and Abadi, 2011; Tavecchia et al., 2009). IPMs in the Bayesian framework are based on a state-space model (Brooks et al., 2004): time-series models in which the latent state process (i.e. the true population size) is linked to population counts via an observation process, thus accounting for observation error (Brooks et al., 2004).

In long-lived species, it is generally the case that adult survival is the main contributor to population growth rates (Sæther and Bakke, 2000) and this relative contribution increases with generation time (Koons et al., 2014). At the same time, it is often found that there is little variation in the particular traits that make the largest contribution to the rate of population growth (Pfister 1998, Gaillard et al. 2000, Sæther and Bakke 2000, Koons et al. 2014, but see Morris and Doak 2004, Jongejans et al. 2010). In turn, the realized population growth rate of species with slow life histories (e.g., long life span and generation time, and high adult survival rates) are more sensitive to changes in their stable age distribution (Koons et al., 2014).
The Bewick’s swan (*Cygnus columbianus bewickii*) is a large, long-lived migratory bird species (Rees 2006). The flyway population breeding in the European tundra and wintering in NW Europe has shown a fluctuating population trend. Between 1970 and 1995 the population increased rapidly from c.15,000 to about 30,000 birds (Beekman et al., 2019). Such population trends were also observed for many European goose species and other swan species, and were attributed to increased use of agricultural land by the birds and reduced mortality as a result of hunting bans (Fox et al., 2010; Rees & Beekman, 2010; Van Eerden et al., 2005). However, in contrast to many waterfowl species, Bewick’s swan numbers decreased again, to 21,500 birds in 2005 and 18,000 in 2010 (Beekman et al., 2019; Rees & Beekman, 2010). The most recent international count indicated an increase in population size with around 20,500 birds in 2015, but results of the January 2020 census are required to confirm the population trajectory (Beekman et al., 2019). The causes of these population trends and the mechanisms underlying the population dynamics remain unclear, though the population is thought to be sensitive to climate and habitat changes, and illegal or accidental shooting (Nagy et al., 2012; Newth et al., 2011).

Given its small population size and recent declining population trend, the NW European population of Bewick’s swans is now considered endangered and listed as such on the European Red List for bird species of conservation concern (Birdlife International, 2015; Rees et al., 2019). The species is also listed as a target within the Natura 2000 framework (Annex I Birds Directive 2009/147/EC of the European Parliament). In response to the decline, experts on the species from across the flyway met to discuss and develop a species action plan (SAP) for the population; the resulting SAP was adopted by the AEWA in 2012, with the overall aim of halting the ongoing decline in the short-term and maintaining the population minimally at its 2000 level (23,000 birds) in the long-term (Nagy et al., 2012). Several hypotheses for the decline are postulated in the SAP, and the plan also calls for continued international collaborative monitoring and research into demographic parameters and population change, in order to understand and thus address the causes of the decline.

Previous efforts to study the population dynamics of the NW European population of Bewick’s swan found no trends in breeding success (neither in the percentage of juveniles in the population nor in brood size) over the period 1964-2015 (Wood et al., 2016). However, fewer young were observed in winters following a colder summer or a higher abundance of Arctic fox in the breeding area (Wood et al., 2016). Similarly, no consistent temporal trend was found in survival over the years 1970-2015 (Wood et al., 2018). Survival rates over the study period did show differences between decades, with mean survival rates being highest in the 1980s and lowest in the 2010s (Wood et al., 2018), which is somewhat in accordance with the population trend based on the counts. Neither of these two studies explained the population trend satisfactorily.

In this study, we developed an integrated population model (Abadi et al., 2010; Kéry and Schaub, 2011) to study the population dynamics and underlying vital rates of Bewick’s swans. By combining three different long-term datasets we aimed to get precise estimates of the demographic rates of this species during periods of positive and negative population growth. In addition, we performed a transient life table response experiment to assess which changes
in the age distribution and vital rates contributed most to the variation in population growth. We also explored which environmental variables might explain the estimated vital rates.

**Methods**

**Data collection**
Three different types of data sources were used in this analysis: census data, capture-mark-resighting data and juvenile proportions.

*Census data*
Internationally coordinated Bewick’s swan counts have been carried out since the early 1970s, in conjunction with the International Waterbird Censuses coordinated by Wetlands International in 1973, 1976, 1979 and as special surveys focussing on Bewick’s swans in 1984 and 1987 (Dirksen & Beekman, 1991; Rees, 2006; Nagy et al., 2012). From 1990 onwards, the Wetlands International/IUCN SSC Swan Specialist Group has organized an International Swan Census (for Bewick’s swans in 1990; also including the NW Mainland European Whooper swans since 1995) every 5 years in mid-January (Beekman et al., 2019; Laubek et al., 2019). To estimate vital rates annually in the IPM, the population counts in-between census years were imputed. Imputed values were drawn from a normal distribution with mean and standard deviation based on counts in the nearest two census years to mimic natural fluctuations in population size (Zhao et al., 2019).

*Capture-mark-resighting data*
Data from two different ringing schemes were used in this study. One originates from the Wildfowl & Wetlands Trust (WWT) in the United Kingdom. In this scheme, which started in the 1960s, Bewick’s swans are ringed with a plastic leg-ring with a unique alphanumeric code (Ogilvie, 1972). The second scheme was initiated by TH (in 1989) and continued by the Netherlands Institute of Ecology (NIOO-KNAW) (since 2005). In this scheme, Bewick’s swans are ringed with both a neck-band and leg-ring with identical alphanumeric codes. The WWT dataset used in this study (1969-2015) consists of 830 individuals marked as juveniles, 529 marked as yearlings and 1833 marked as adults. The NIOO dataset (1989-2015) contained 79 individuals marked as juveniles, 33 as yearlings and 432 as adults. Ringed birds have been reported by volunteer bird-watchers from across NW-Europe. Including maximally one resighting per individual per winter, running from December through February, this resulted in 13,358 resightings of the leg-ringed birds and 2,201 resightings of the neck-banded birds. Resighting probabilities were modelled for leg-rings ($p_l$) and neck-bands ($p_n$) separately, as it is known the former has a lower resighting probability (Wood et al., 2018; S1 and S2).

*Winter reproduction data*
Long-term reproduction data from the breeding grounds is not available for Bewick’s swans. Therefore, we used winter brood size (i.e., the average number of juveniles per successful breeding pair) and proportion of juveniles in the population, recorded in winter, as a proxy for productivity. Both variables were monitored annually in the UK (Wood et al., 2016) and in the Netherlands (Hornman et al., 2020; Poorter, 1991) in late November/early December. Bewick’s swans in these two countries amount to 60-90% of the whole population, and no consistent geographical trend in juvenile proportions was detected (Beekman et al., 2019). Therefore, we took the annual averages from these countries for each of these two variables to represent the
whole population in this study. We used the annual proportion of juveniles to create age-structured counts to which the model was fitted. Winter brood size was used to create an informative prior for the estimate of apparent breeding success $\kappa$ (see below).

**Integrated population modelling**

We developed a female-based, age-structured population model with three age classes (i.e., juvenile, yearling, and adult). We modelled (female) apparent breeding success $\kappa$ as a latent parameter, because reproduction data from the breeding grounds were lacking. $\kappa$ Reflects breeding propensity, breeding success and post-fledging survival until winter, all in one parameter.

The CMR data were analysed as individual encounter histories and modelled with a Cormack-Jolly-Seber (CJS) model (Lebreton et al., 1992). Apparent survival from year $t$ to $t+1$ was modelled on the logit scale as a function of age class and time. Resighting probability in year $t$ was modelled on the logit scale as a function of marker type and time. In both rates (survival and resighting probability), environmental stochasticity was accounted for by considering time as a random year effect.

The census data were analysed using a state-space model (Brooks et al., 2004). The state-space model consists of a state process and an observation process. The state process describes the true but unknown population trajectory and accounts for demographic stochasticity by describing the number of juveniles via a Poisson distribution and the number of yearlings and adults via a binomial distribution. The observation process describes the link between the true and the observed population size (De Valpine and Hastings, 2002). Using the data on the proportion of juveniles, we divided the counts into juveniles and older individuals. Assuming an even sex ratio, we halved counts before implementation in the female-based model.

The population transition matrix of the female-based, age-structured population model is the following:

\[
W_{t+1} = \begin{bmatrix} W_j \\ W_y \\ W_a \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & \kappa \phi_a \\ \phi_j & 0 & 0 \\ 0 & \phi_y & \phi_a \end{bmatrix} \begin{bmatrix} W_j \\ W_y \\ W_a \end{bmatrix}_t \tag{2.1}
\]

where $W_j$, $W_y$ and $W_a$ are the number of juvenile, yearling and adult females in winter, respectively, $\phi_x$ is the annual survival rate between year $t$ and $t+1$ for individuals in age class $x$, and $\kappa$ is the apparent breeding success in year $t$: the average number of female fledglings per successful breeding female, that survived until winter.

To estimate age class-specific numbers and demographic parameters, the joint likelihood is composed of the likelihood of the state-space model for the population census data and the CJS model for the individual encounter histories. The IPM is analysed in the Bayesian
framework, which combines the joint likelihood with prior probability distributions to obtain posterior distributions of the parameters. We specified non-informative priors for all parameters but apparent breeding success. The prior for apparent breeding success was a uniform distribution between 0 and 2 (i.e., the average winter brood size (Wood et al., 2016) that is set to be the upper limit of $\kappa$). Markov chain Monte Carlo (MCMC) methods were used to simulate observations from the posterior distributions with JAGS version 4.3.0 (Plummer, 2003) run from R with jagsUI version 1.5.1 (Kellner 2019). We ran 3 chains of 200,000 iterations with a burn-in of 100,000 and a thinning rate of 50, resulting in a total of 6,000 posterior samples. Convergence of the MCMC chains was evaluated by ensuring that the Brooks-Rubin-Gelman diagnostic $\hat{R}$ for each parameter was below 1.1 (Brooks & Gelman, 1998).

A more detailed description of the IPM, including likelihoods and priors, can be found in S1. R and JAGS code of the IPM can be found in S2.

**Retrospective perturbation analysis**

Retrospective perturbation analyses aim to decompose the effects of observed variation in demographic parameters on past population dynamics (Caswell, 2000). Traditionally, the focus has been placed on identifying the demographic rate with the strongest influence on the asymptotic growth rate $\lambda$ (Koons et al., 2016). These analyses, however, ignore the feedback between population structure and demographic rates (Tuljapurkar, 1990) and short-term transient dynamics (Stott et al., 2011) that are common for many contemporary populations (Koons et al., 2016). Here, we performed a transient life table response experiment (LTRE) (Koons et al., 2017, 2016) to determine the contributions of changing vital rates and population structure to the variation in the realized population growth rate, $\lambda_r = W_{t+1}/W_t$. A more detailed description of the transient LTRE can be found in S3.

**Explanatory variables**

We collated data on several potential explanatory variables for the variation in vital rates based on previous research on Arctic-nesting waterfowl (e.g., Morrissette et al., 2010; Skinner et al., 1998; Trinder et al., 2009). In order to prevent collinearity, we condensed variables wherever possible (e.g. Morrissette et al. 2010). Weather-related variables included were the cumulative negative degree days (ndd, °C) in Naryan-Mar (Russia, i.e. the breeding range) in late spring (1 May - 30 June, corresponding to the nesting and incubation period; Rees 2006), cumulative degree days (cdd, °C) in Naryan-Mar during summer and autumn (1 July – 31 October, corresponding to the period between hatching and fledging and set to include the frost days in autumn; Rees, 2006), and average tailwind (calculated from north-south and east-west winds combined, using a heading of 225°) in the Baltic region (58°N, 23°E) in autumn (18 September - 31 October, corresponding to the autumn migration period; Rees 2006). Temperature data were acquired from the NOAA Global Summary of the Day dataset (NOAA National Climatic Data Centre 2019) and wind data from the NOAA NCEP/NCAR reanalysis project (Kalnay et al., 1996). Ndd and cdd comprised of the summed mean daily negative and positive air temperatures, respectively, in the specified time windows. Tailwind was calculated based on the average windspeed multiplied with the cosines of the heading in degrees (225°).

Furthermore, we included the whooper swan population count in NW Europe from the International Waterbird Census over the study period, as it was hypothesized that competition with this species might be of influence on the declining population trend of the Bewick’s swan since 1995 (Nagy et al., 2012). The Lake Peipsi (Estonian-Russian border, 58.5°N, 27.5°E)
water levels for each year of the study (average September - October), measured by the Estonian Meteorological and Hydrological Institute, were also included, as water levels determine the availability of macrophytes in this key stop-over site and other lakes in the region for Bewick’s swans arriving from the Russian Arctic during autumn migration (Luigjõe et al., 1996). We ran a series of generalized linear models (GLMs) with the posterior means of the IPM output parameters (adult, yearling and juvenile survival, apparent breeding success) as response variables, and the explanatory variables as predictors. We included year as a predictor variable in the analysis to cover all environmental variables that changed monotonically over time but that we were unable to capture in data. None of the predictor variables were correlated (Pearson correlation coefficient $r < 0.3$), apart from year and whooper swan count, that were highly correlated ($r = 0.96$). We therefore ran all models twice: once with year and whooper swan count detrended, and once with only whooper swan count. All variables were centered and scaled to a mean of 0 and sd of 1 before running the model. We compared the AIC of the models to choose the most parsimonious one (lowest AIC). All analyses were run in R version 3.6.2 (R Core Team 2019).

**Results**

**Age class-specific demographic rates**

The mean apparent juvenile survival was 0.908 (95% credible interval: 0.891, 0.926; Fig. 2.1a), with lower values at the start of the study period. Apparent yearling survival (0.936; 0.917, 0.954; Fig. 2.1b) was higher and more constant through time than apparent adult survival (0.873; 0.869, 0.877; Figure 1c). Apparent breeding success $k$, defined as the average number of female fledglings per successful breeding female, that survived until winter (overall mean: 0.189; 95% credible interval 0.184, 0.194), showed a clear shift from 0.224 (0.216, 0.232) in the period of population increase (period 1, 1970-1994) to 0.145 (0.138, 0.151) in the period of population decrease (period 2, 1995-2015) ($P(k_{\text{period 1}} > k_{\text{period 2}}) = 1.0$), and closely followed (Pearson’s $r$: 0.88) the fluctuations of the proportion of juveniles in the population as observed in winter (Fig. 2.1d and 2.1e).
Figure 2.1: Estimates from the integrated population model of NW European population of Bewick’s swans. (a, b, c) Annual apparent survival for (a) juveniles ($\varphi_{j,t}$), (b) yearlings ($\varphi_{y,t}$), and (c) adults ($\varphi_{a,t}$). (d) Annual apparent breeding success ($\kappa_t$; black points) and proportion of juveniles in the population as observed in winter (grey points). (e) Annual winter proportion of juveniles as estimated by the model (black points) and as observed in winter (grey points). (f) Annual winter abundance as estimated by the model (black points), with actual (solid grey points) and imputed (open grey points) population counts. Estimates are represented by posterior means and 95% credible intervals.

Contributions to variation in population growth rate
The mean realized population growth rate in period 1 was 1.035 (±0.052 SD) and in period 2 0.983 (±0.041 SD). The two demographic rates that contributed most to between-year variation in realized population growth rate $\lambda_t$ (var($\lambda_t$): 0.003), were apparent breeding success $\kappa$ and adult survival $\varphi_a$ (Fig. 2.2). The contribution of juvenile survival $\varphi_j$ and yearling survival $\varphi_y$ to variation in $\lambda_t$ was positive but small, whilst the effect of the population structure components were negative and also small (Fig. 2.2). Based on non-overlap of the posterior means with zero, all variables contributed significantly to the variation in realized population growth rate, except for $\varphi_i$ and $\varphi_y$. Vital rates contributed 94.6% of the total contribution. See Table S2.2 for numerical estimates.
Figure 2.2: Contributions of the demographic rates (i.e., apparent breeding success $\kappa$, apparent survival for juveniles $\varphi_J$, yearlings $\varphi_Y$, and adults $\varphi_A$) and normalised components of the population structure (i.e., winter abundance for juveniles $w_J$, yearlings $w_Y$, and adults $w_A$) to the variation in realized population growth rate, $\text{var}(\lambda_t)$, determined through a transient life table response experiment (LTRE).

**Explanatory variables**
Comparing the model outputs of the two different sets of GLMs (Table 2.1 and Table S2.4) based on their AIC values (Burnham and Anderson, 2002), showed that the model including year was the most parsimonious (AIC of 100.41 as compared to an AIC of 103.7 for the model without year). In this model, we found no significant effects of any of the predictor variables on adult and yearling survival. Year, the water level in Lake Peipsi and ndd showed a significant positive association with juvenile survival (higher juvenile survival in more recent years, with higher water levels in autumn and with colder summers). Apparent breeding success was negatively associated with year (Table 2.1).
Table 2.1: Model output of GLM with demographic parameters estimated by the IPM as response variables (adult, yearling and juvenile survival, and apparent breeding success) and the explanatory variables as predictors (year, whooper swan count, tailwind in the Baltic sea in autumn, water level in Lake Peipsi in autumn, negative degree days in Naryan-Mar in spring, cumulative degree days in Naryan-Mar in summer and autumn combined). Because year and whooper swan count correlate strongly, we only included one of them in the model. The model including year was the most parsimonious and is presented here (model with whooper swan count in S4). In the models with year, whooper swan count was detrended (indicated by Dt).

<table>
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<th>Juvenile survival</th>
<th>Apparent breeding success</th>
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<td>SE</td>
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<td>P</td>
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<td>cdd Naryan-Mar</td>
<td>-0.160</td>
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</table>
Discussion

By integrating three long-term datasets available for the NW European Bewick’s swan population (census data, capture-mark-resighting data and proportion of juveniles) we were able to get precise estimates for the survival rates for the different age classes (Abadi et al., 2010). In addition, we used the possibility of the IPM framework to estimate parameters for which no specific data were available (Abadi et al., 2010; Altwegg et al., 2014): annual apparent breeding success $\kappa$, a variable reflecting breeding propensity, breeding success and post-fledging survival (until winter) combined. We show that adult survival and $\kappa$ were the vital rates that contributed most to the variation in the population growth rate as observed over the last five decades (Fig. 2.2).

Although population growth rates of long-lived species are in theory particularly sensitive to changes in adult survival, this vital rate is often fairly stable over time. Other demographic rates are more sensitive to environmental influences and thus in effect contribute more to the realized population growth rate based on a higher variability over time (Koons et al., 2014). In our species we indeed find a high contribution to variation in population growth rate of, but little variation in, adult survival. This is in line with the Demographic Buffering Hypothesis (Boyce et al., 2006), although no proof for this hypothesis was found in a comparative study among waterfowl species (Koons et al., 2014). More between-year variation was visible in the juvenile survival and $\kappa$ estimates, for the latter especially between the two periods with contrasting growth rates, i.e. population growth and population decline (Fig. 2.1a and 2.1d). The same pattern (i.e. high contribution of adult survival to the population growth rate but low variation in this parameter, and more variation in the fecundity-related parameters such as nest success and juvenile survival) was also found for other waterfowl species (Bentzen and Powell, 2012; Cooch et al., 2001; Hoekman et al., 2002; Wilson et al., 2012).

On regarding potential explanatory variables for the variation in demographic rates, we found that juvenile survival was significantly increasing over time (year). This means that juvenile survival is increasing over time. The year variable can be seen as a proxy for all environmental variables that changed over the years without being captured in our set of variables. This includes for example the migration distance of the NW European Bewick’s swan population, that was found to have gradually decreased over time (Nuijten et al. in press). Other variables that might have changed gradually over time, such as predation in the Arctic (Béty et al., 2002; Nolet et al., 2013; Smith et al., 2010), could also play a role. The increase in juvenile survival follows the time that Bewick’s swans switched from feeding on aquatic resources to agricultural resources (Merne, 1972; Mullié and Poorter, 1977). Juveniles have lower intake rates than adults when feeding on below-ground part of aquatic macrophytes, and hence are thought to benefit from this switch, more so than adult birds (Nolet et al., 2014). The overall increasing pattern in juvenile survival was a surprising finding, as the overall population is known to show a decreasing population trend since 1995.

One factor that we know has changed over time is whooper swan abundance (see results Table S2.4). Whooper swans have been steadily increasing in the past decades (Laubek et al., 2019). Being larger, the whooper swan is likely to win competitive encounters about food or nesting places from Bewick’s swans. Competition for food outside the breeding season may lead to a lower breeding success, by influencing body condition prior to the breeding season.
It has been found that food abundance in the wintering area is not limiting, even when competition is present (Wood et al., 2019), but food limitation is more likely at migratory sites where swans concentrate and food depletion has been shown previously (Nolet & Drent, 1998). We know from previous research that spring staging areas in Estonia often overlap between the two species (Luigujõe et al., 2002). Aerial surveys done between 1980 and 2000 in the Pechora Delta, considered as the main breeding area of the Bewick’s swan (Rees, 2006), showed an increase in territorial whooper swan breeding pairs while the number of Bewick’s swan pairs was stable in the northern part of the delta (Shchadilov, 2002). Further studies are needed to investigate effects of potential interspecific competition.

In addition both the water level in Lake Peipsi in autumn and nedd (both continuous variables) were significantly and positively associated with annual estimates of juvenile survival. Lake Peipsi comprises an important stop-over site for Bewick’s swans in autumn (Luigujõe et al., 1996). To be able to reach the belowground parts of macrophytes in the substrate of the lake, the water level must not be too high (Luigujõe and Kuresoo, 2007). Observations in 2005 and 2006, years with a very high and very low water table respectively, convincingly showed the strong relationship of Bewick’s swan numbers with water tables: in 2005 smaller groups visited far fewer sites in autumn, while in 2006 the total autumn count reached up to 3000 on both sides of the lake (Luigujõe and Kuresoo, 2007). Autumn water levels are heavily dependent on rainfall, and high water levels in Lake Peipsi are likely to be representative for high water levels in surrounding lakes; hence, aquatic foraging conditions are poor in the whole region when water levels are high, leading to slower autumn migration of Bewick’s swans (Beekman et al., 2002). Based on this we expected to find, if any, a negative relationship of water level with (juvenile) survival, but supposedly our preconception that slower migration is detrimental is wrong. Our satellite tracking in an autumn with extremely high water levels in Peipsi (1998) revealed that the Bewick’s swans visited many alternative foraging sites like fish ponds before continuing their migration. This might thus be beneficial for juveniles, supposedly due to less intraspecific competition at a specific site. A similar reasoning could be true for the effect of nedd: in years with low summer temperatures, apparent breeding success might be lower resulting in less interspecific competition for the hatchlings, leading to higher juvenile survival rates the following year. Another plausible explanation for the positive association of juvenile survival with nedd, is that in harsh autumns many fledglings die (e.g. Wood et al. 2016), leaving only the stronger individuals in the juvenile phase. However, we did not find a negative association between apparent breeding success and nedd to substantiate these possible explanations (Table 2.1).

In previous research it was found that Bewick’s swans seem to profit from favourable wind conditions during spring migration (Klaassen et al., 2004). In line with this, we expected headwinds during autumn migration to have negative effects on (juvenile) survival, but little research has been done to substantiate this. However, no long-term trends in headwinds were detected (S4), so it remains to be seen whether this factor affects the longer-term population dynamics of Bewick’s swans.

Negative density dependence (NDD) is regarded as an important driver of population growth rates (Koons et al. 2014). If influential, NDD can have both negative and positive effects on the demographic rates when population numbers are high or low, respectively (Turchin, 1995) and effects can vary for different age classes (Layton-Matthews et al., 2019). Results from the
LTRE however, show only a small negative effect of components of the population size on the variation in population growth rate over the study period, of which only the effect of adults $w_a$ was significant (Fig. 2.2). This is in line with previous results where it was found that density-dependence performed poorly as a predictor of survival estimates in Bewick’s swans (Wood et al., 2018).

An assumption of the IPM framework is the independence of the underlying datasets (Kéry and Schaub, 2011). Although it is possible that this study violates this assumption because every dataset originates from the same population in the wintering grounds and individuals can appear in multiple datasets, we argue that this assumption is valid for our input datasets. The international censuses are conducted on a 5-year basis, in one weekend in January, the juvenile proportions are determined separately and on an annual basis in December, and the resightings of marked individuals are collected by individual observers throughout the winter season on any location. Besides, it has been shown that violation of this assumption has little effect on estimation of parameters (Abadi et al., 2010; Schaub and Fletcher, 2015), in particular when the number of individually marked birds is a small proportion of the studied population (Weegman et al., 2016).

As part of the IPM, we ran a CJS model to obtain survival estimates from the encounter histories. In traditional survival analysis, usually a goodness-of-fit test is conducted. We currently know of no solution on how to do this in the IPM framework that we were able to implement (Kéry and Schaub 2011; but see (Besbeas and Morgan, 2014). In a previous, traditional survival analysis based on the same data a goodness-of-fit test revealed evidence for both trap-dependence (trap-happiness) and transience (Wood et al. 2018). However, the $\hat{c}$ value (2.5; calculated in U-Care, Choquet et al. 2009) below the maximum $\hat{c}$ value of 3.0 recommended for reliable survival modelling (Lebreton et al., 1992). In addition, Abadi et al. (2013) showed that capture heterogeneity did not have a large effect on the resulting estimates.

In the model, all individuals in the adult age class are capable of breeding, with a certain breeding propensity (included in $\kappa$). We know from observations (individuals that returned to the wintering grounds with juveniles) that although birds of 3 years old do reproduce, most individuals start reproduction later in life (4-5 years of age; (Rees, 2006)). This artefact in the model means that $\kappa$ underestimates the apparent breeding success of potential breeders (i.e. $\geq$ 4-year-olds), while still providing a useful estimate for the whole population of $\geq$ 3-year-olds. We do not know whether the distribution of age of first breeding has changed over time, something one might expect due to density-dependence (Koons et al., 2014). In contrast to most population modelling studies, we derived a value for apparent breeding success, $\kappa$, instead of using a direct measure for breeding success, because we have no structural data available from the breeding grounds. Reproduction data were available only from the wintering grounds, in the form of brood size and proportion of juveniles in the population. We think that $\kappa$, that was modelled without explicit input data by the IPM, is more representative for the actual breeding success as it is based on the summer population of potentially breeding females instead (S3). This can explain why we do find a significant decline of reproductive success over the years while previous efforts using the winter measurements have not (Wood et al., 2016).
In conclusion, we found that declining reproductive success in this long-lived migratory species drives the observed population decline in north-western Europe. In addition, we found an increase in juvenile survival over time, associated with the water level in important foraging sites in autumn. Our study highlights the importance of considering all information available on the population level to estimate precise demographic rates which can in turn be used to accurately assess the influence of potential explanatory variables on population growth rates. Such analyses are important in understanding the population dynamics of species with fluctuating population sizes, and to inform management and conservation decisions.

Acknowledgements -
We thank all the people involved in the ringing schemes and the volunteers for counting and reporting their resightings. We thank Michael Schaub and Marc Kéry for introducing us to IPM and providing useful modelling suggestions. RJMN was supported by NWO-NPP grant 866.15.206 awarded to BAN.

The first and second author contributed equally to this paper.
1
Detailed description of the integrated population model

I. Population model
We developed a female-based, age-structured integrated population model (IPM) of three age classes (i.e., juvenile, yearling, and adult) and a pre-breeding census (Fig. S2.1).

![Figure S2.1: Age-structured life cycle of the Bewick’s swan with juvenile, yearling and adult age classes. $\varphi_x$ is the annual survival rate between year $t$ and $t+1$ for individuals in age class $x$, and $\kappa$ is the apparent breeding success: the average number of female fledglings, per successful breeding female, that survived until first winter.](image)

In the IPM, apparent survival was modelled for juveniles ($\varphi_j$), yearlings ($\varphi_y$) and adults ($\varphi_a$). Resighting probabilities were modelled for leg rings ($p_l$) and neck bands ($p_n$) separately, as they are known to have different resighting probabilities (Wood et al., 2018). Because reproduction data from the breeding grounds were lacking, breeding success was modelled through a latent parameter $\kappa$. Modelling the age-specific abundances in the IPM with bi-annual time step allowed us to explicitly estimate the actual number of breeding females, and their apparent breeding success, in addition to the number of females in winter. The resulting population transition matrices are as follows:

$$W_{t+1} = \begin{bmatrix} W_j \\ W_y \\ W_a \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & \kappa \sqrt{\varphi_a} \\ \varphi_j & 0 & 0 \\ 0 & \varphi_y & \varphi_a \end{bmatrix} \begin{bmatrix} W_j \\ W_y \\ W_a \end{bmatrix}_t$$

(S2.1)

which can be separated in the transition from the start of the breeding season to winter,

$$W_t = \begin{bmatrix} W_j \\ W_y \\ W_a \end{bmatrix}_t = \begin{bmatrix} 0 & 0 & \kappa \\ \sqrt{\varphi_j} & 0 & 0 \\ 0 & \sqrt{\varphi_y} & \sqrt{\varphi_a} \end{bmatrix} \begin{bmatrix} B_j \\ B_y \\ B_a \end{bmatrix}_t$$

(S2.2)
and from winter to the start of the breeding season,

\[
\mathbf{B}_{t+1} = \begin{bmatrix} B_j \\ B_y \\ B_a \end{bmatrix}_{t+1} = \begin{bmatrix} \sqrt{\varphi_j} & 0 & 0 \\ 0 & \sqrt{\varphi_y} & 0 \\ 0 & 0 & \sqrt{\varphi_a} \end{bmatrix} \begin{bmatrix} W_j \\ W_y \\ W_a \end{bmatrix}_t
\]

(S2.3)

where \(B_{jt}, B_{yt}, B_{at}\) are the number of juveniles, yearlings and adults at the start of the breeding season in year \(t\), respectively, \(W_{jt}, W_{yt}, W_{at}\) are the number of juveniles, yearlings and adults in winter in year \(t\), respectively, \(\varphi_{xt}\) is the annual survival probability between \(t\) and \(t+1\) for individuals in age class \(x\), and \(\kappa_t\) is apparent breeding success, i.e., the average number of female fledglings produced per successful breeding female that survived until first winter in year \(t\).

This model was extended to account for demographic stochasticity, by using binomial and Poisson distributions to link between age-specific numbers in year \(t\) and \(t+1\), and environmental stochasticity, by allowing annual variation in all demographic rates. The projection matrix translates to the following relationships:

\[
\begin{align*}
W_{jt} &\sim \text{Poisson}(B_{at}, \kappa_t) \\
W_{yt} &\sim \text{Binomial}(\sqrt{\varphi_{jt}}, B_{jt}) \\
W_{at} &\sim \text{Binomial}(\sqrt{\varphi_{yt}}, B_{yt}) + \text{Binomial}(\sqrt{\varphi_{at}}, B_{at}) \\
B_{jt+1} &\sim \text{Binomial}(\sqrt{\varphi_{jt}}, W_{jt}) \\
B_{yt+1} &\sim \text{Binomial}(\sqrt{\varphi_{yt}}, W_{yt}) \\
B_{at+1} &\sim \text{Binomial}(\sqrt{\varphi_{at}}, W_{at})
\end{align*}
\]

(S2.4)

II. Likelihoods of the single datasets

Combining the data on the proportion of juveniles (\(j\)) and the census data (\(c\)), we separated the counts for juveniles (\(c_j = j \cdot c\)) and older individuals (\(c_{ya} = [1 - j]c\)). These two counts were modelled using state-space models (Brooks et al., 2004). The state-space model consists of a state process and an observation process. The state process describes the true but unknown population trajectory under the population model. The observation process describes the link between the true and the observed population size (De Valpine and Hastings, 2002). The state process models were described in the previous section. For the observation process models we assumed that the observation error was different between juveniles and older individuals, to account for the incorporation of the data on the proportion of juveniles, normally distributed on the log scale and constant over time.
\[
\log(C_{j,t}) \sim \text{Normal}(W_{j,t}, \sigma_{j,\text{obs}}^2)
\]
\[
\log(C_{ya,t}) \sim \text{Normal}(W_{y,t} + W_{a,t}, \sigma_{ya,\text{obs}}^2)
\]

(S2.5)

The likelihood of the state-space model was composed of the likelihood of the observation processes and the state processes (Kéry and Schaub, 2011).

Capture-mark-resighting data were modelled using a Cormack-Jolly-Seber model (Lebreton et al., 1992). We defined the latent variable \(z_{i,t}\) as the true state of individual \(i\) at time \(t\), which takes value 1 if individual \(i\) is alive at time \(t\), and value 0 if individual \(i\) is dead at time \(t\). Because only events after first capture are modelled in the CJS model, we also defined vector \(f_{i}\), which denotes the occasion at which individual \(i\) was first captured and marked. The state of individual \(i\) at first capture \((z_{i,f_i})\) is 1 with probability 1. The subsequent occasions are modelled as Bernoulli trials. Conditional on being alive at time \(t\), individual \(i\) may survive to time \(t+1\) with probability \(q_{i,t}\), resulting in the following state process model:

\[
z_{i,t+1} \mid z_{i,t} \sim \text{Bernoulli}(z_{i,t} \varphi_{i,t})
\]

(S2.6)

If individual \(i\) is alive at time \(t\), it may be recaptured/resighted with a probability \(p_{i,t}\). With Bernoulli trials, the true state \(z_{i,t}\) can be linked to the observation \(y_{i,t}\), resulting in the following observation process model:

\[
y_{i,t} \mid z_{i,t} \sim \text{Bernoulli}(z_{i,t} p_{i,t})
\]

(S2.7)

The probabilities of apparent survival and resighting were modelled with random year effects:

\[
\logit(\theta_i) = \bar{\theta} + \varepsilon_{\theta,i}
\]

(S2.8)

where \(\bar{\theta}\) was the mean demographic rate over time on the logit scale and \(\varepsilon_{\theta,i}\) the temporal component of the demographic rate with mean 0 and variance \(\sigma_{\theta}^2\):

\[
\varepsilon_{\theta,i} \sim \text{Normal}(0, \sigma_{\theta}^2)
\]

(S2.9)

III. Joint likelihood

The joint likelihood of the IPM is the product of the individual likelihoods of the different datasets, assuming independence between them (Kéry and Schaub, 2011). Individuals can appear in multiple datasets included in this study, so the assumption is violated to some degree. However, violation of this assumption has been shown to have little effect on estimation of parameters (Abadi et al., 2010; Schaub and Fletcher, 2015), in particular when
the number of marked birds is a small proportion of the studied population (Weegman et al., 2016). The joint likelihood is as follows:

\[
L_{IPM}\left(C, j, y \mid W_x, B_x, \phi_x, \kappa, p_m, \sigma_{obs}^2, \sigma_{ya,obs}^2 \right) = \\
L_O\left(C, j \mid W_x, \sigma_{obs}^2, \sigma_{ya,obs}^2 \right) \\
\times L_S\left(W_x, B_x \mid \phi_x, \kappa \right) \\
\times L_{CJS}\left(y \mid \phi_x, p_m \right)
\]

where \(L_O\) is the likelihood of the census observation process model, \(L_S\) the likelihood of the census state process model, \(L_{CJS}\) the likelihood of the CJS model, \(x\) age class (i.e., juvenile, yearling, adult) and \(m\) mark type (i.e., leg ring, neck band). A graphical representation of this model is shown in Fig. S2.2.

**Figure S2.2:** Directed acyclic graph of the integrated population model. Estimated parameters are represented by circles, data by rectangles. Arrows represent dependencies between nodes. \(C\) population census data, \(j\) proportion of juveniles, \(y\) capture-mark-resighting data, \(W_x\) is abundance of age class \(x\) (i.e., juvenile, yearling, adult) in winter, \(B_x\) is abundance of age class \(x\) in the breeding season, \(\phi_x\) is the survival probability of age class \(x\), \(p_m\) is the resighting probability of mark type \(m\) (i.e., leg ring, neck band), and \(\kappa\) is the latent parameter apparent breeding success.
IV. Computation

To estimate the parameters, we analysed the joint likelihood combined with prior distributions to obtain posterior distributions. For all but apparent breeding success, which prior was informed by the winter brood size, we specified non-informative priors (Table S2.1). Markov chain Monte Carlo (MCMC) methods were used to simulate observations from the posterior distributions with JAGS version 4.3.0 (Plummer, 2003) run from R with jagsUI version 1.5.1 (Kellner 2019). We ran 3 chains of 200,000 iterations with a burn-in of 100,000, thinning every 50th iteration, resulting in a total of 6,000 posterior samples. Convergence of the MCMC chains was evaluated by ensuring that the Brooks-Rubin-Gelman diagnostic \( \hat{R} \) (Brooks and Gelman, 1998) for each parameter was below 1.1. R and JAGS code of the IPM can be found in S2.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Prior distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean survival</td>
<td>( \bar{\phi}_{j,t} \sim \text{Normal}(0,100)T(-5,5) )</td>
</tr>
<tr>
<td></td>
<td>( \bar{\phi}_{y,t} \sim \text{Normal}(0,100)T(-5,5) )</td>
</tr>
<tr>
<td></td>
<td>( \bar{\phi}_{a,t} \sim \text{Normal}(0,100)T(-5,5) )</td>
</tr>
<tr>
<td>Temporal variability of survival</td>
<td>( \varepsilon_{\phi_j} \sim \text{Normal}(0,\sigma^2_{\phi_j}) )</td>
</tr>
<tr>
<td></td>
<td>( \varepsilon_{\phi_y} \sim \text{Normal}(0,\sigma^2_{\phi_y}) )</td>
</tr>
<tr>
<td></td>
<td>( \varepsilon_{\phi_a} \sim \text{Normal}(0,\sigma^2_{\phi_a}) )</td>
</tr>
<tr>
<td></td>
<td>( \sigma_{\phi_j} \sim \text{Uniform}(0,10) )</td>
</tr>
<tr>
<td></td>
<td>( \sigma_{\phi_y} \sim \text{Uniform}(0,10) )</td>
</tr>
<tr>
<td></td>
<td>( \sigma_{\phi_a} \sim \text{Uniform}(0,10) )</td>
</tr>
<tr>
<td>Mean resighting probabilities</td>
<td>( \bar{p}_{l,t} \sim \text{Normal}(0,100)T(-5,5) )</td>
</tr>
<tr>
<td></td>
<td>( \bar{p}_{n,t} \sim \text{Normal}(0,100)T(-5,5) )</td>
</tr>
<tr>
<td>Temporal variability of resighting probabilities</td>
<td>( \varepsilon_{p_l} \sim \text{Normal}(0,\sigma^2_{p_l}) )</td>
</tr>
<tr>
<td></td>
<td>( \varepsilon_{p_n} \sim \text{Normal}(0,\sigma^2_{p_n}) )</td>
</tr>
<tr>
<td></td>
<td>( \sigma_{p_l} \sim \text{Uniform}(0,10) )</td>
</tr>
<tr>
<td></td>
<td>( \sigma_{p_n} \sim \text{Uniform}(0,10) )</td>
</tr>
<tr>
<td>Apparent breeding success (upper limit informed by average winter brood size (Wood et al., 2016))</td>
<td>( \kappa \sim \text{Uniform}(0,2) )</td>
</tr>
</tbody>
</table>
Observation errors census data

\[ \sigma_{j,\text{obs}} \sim \text{Uniform}(0,100) \]
\[ \sigma_{ya,\text{obs}} \sim \text{Uniform}(0,100) \]

Abundances in the breeding season in the first year.

\[ B_{j,1} \sim \text{Normal}(300,10^4)T(0,) \]
\[ B_{y,1} \sim \text{Normal}(1000,10^4)T(0,) \]
\[ B_{a,1} \sim \text{Normal}(4000,10^4)T(0,) \]

2

R and JAGS code for the integrated population model

```r
# Data objects

# eh: encounter history matrix
# f: vector of first observations
# x: age matrix
# juvper: proportion of juveniles in winter
# counts: population winter counts
# gr: leg ring vs neck band

sink("ipm-season-s3.jags")
cat(""
model {
  #******************************************************************************
  # 1. Define priors and constraints
  #******************************************************************************

  #******************************************************************************
  # 1.1 Initial population sizes
  #******************************************************************************
  b1 ~ dnorm(300, 0.001)T(0,) # Number of 1-year olds in breeding season
  b2 ~ dnorm(1000, 0.001)T(0,) # Number of 2-year olds in breeding season
  b3 ~ dnorm(4000, 0.001)T(0,) # Number of 3-year olds and older in breeding season

  B1[1] <- round(b1)
  B2[1] <- round(b2)
  B3[1] <- round(b3)

  #******************************************************************************
  # 1.2 Observation errors
  #******************************************************************************
  sigma.y ~ dunif(0, 100)
  sigma2.y <- pow(sigma.y, 2)
  tauy <- pow(sigma.y, -2) # Precision counts 1.5-year olds and older
```

sigma.z ~ dunif(0, 100)
sigma2.z <- pow(sigma.z, 2)
tauz <- pow(sigma.z, -2) # Precision counts 0.5-year olds

#******************************************************************************
# 1.3 Survival probabilities (3 age classes)  
#******************************************************************************
for(a in 1:3){
  for(t in 1:(nyears-1)){
    eta.phi[a,t] <- mu.phi[a] + epsilon.phi[a,t]
    epsilon.phi[a,t] ~ dnorm(0, tau.phi[a])T(-15,15)
  } #t
  mu.phi[a] ~ dnorm(0, 0.01)T(-5,5)
  sigma.phi[a] ~ dunif(0, 10)
  tau.phi[a] <- pow(sigma.phi[a], -2)
  sigma2.phi[a] <- pow(sigma.phi[a], 2)
} #a

# Constrain parameters
for(i in 1:nind){
  for(t in f[i]:(nyears-1)){
    logit(phi[i,t]) <- eta.phi[x[i,t],t]
  } #t
} #i

#******************************************************************************
# 1.3 Resighting probabilities (2 classes)  
#******************************************************************************
for(g in 1:2){ # leg rings and neck bands
  for(t in 1:(nyears-1)){
    eta.p[g,t] <- mu.p[g] + epsilon.p[g,t]
    epsilon.p[g,t] ~ dnorm(0, tau.p[g])T(-15,15)
  } #t
  mu.p[g] ~ dnorm(0, 0.01)T(-5,5)
  sigma.p[g] ~ dunif(0, 10)
  tau.p[g] <- pow(sigma.p[g], -2)
  sigma2.p[g] <- pow(sigma.p[g], 2)
} #g

# Constrain parameters
for(i in 1:nind){
  for(t in f[i]:(nyears-1)){
    logit(p[i,t]) <- eta.p[group[i],t]
  } #t
} #i

#******************************************************************************
# 1.4 Apparent breeding success  
#******************************************************************************
for(t in 1:nyears){
  kappa[t] ~ dunif(0, 2) # Informed by winter brood size
} #t
### 1.5 Derived parameters

#### Survival

```r
for(t in 1:(nyears-1)){
  logit(phi.j[t]) <- eta.phi[1,t]
  logit(phi.y[t]) <- eta.phi[2,t]
  logit(phi.a[t]) <- eta.phi[3,t]
}
```

#### Resighting

```r
for(t in 1:(nyears-1)){
  logit(p.l[t]) <- eta.p[1,t]
  logit(p.n[t]) <- eta.p[2,t]
}
```

### 2 Likelihoods of single datasets

#### 2.1 Population count data (state-space model)

```r
# 2.1.1 System process
for (t in 1:(nyears-1)){
  B1[t+1] ~ dbin(phi.j[t]^(1/2), W1[t])
  B2[t+1] ~ dbin(phi.y[t]^(1/2), W2[t])
  B3[t+1] ~ dbin(phi.a[t]^(1/2), W3[t])
}
```

```r
for (t in 1:(nyears-1)){
  mean.w[t] <- B3[t] * kappa[t]
  W1[t] ~ dpois(mean.w[t])
  W2[t] ~ dbin(phi.j[t]^(1/2), B1[t])
  W3a[t] ~ dbin(phi.y[t]^(1/2), B2[t])
  W3b[t] ~ dbin(phi.a[t]^(1/2), B3[t])
  W3[t] <- W3a[t] + W3b[t]
}
```

#### 2.1.2 Observation process

```r
for (t in 1:(nyears-1)){
  cen[t] ~ dnorm(W23[t], tauy)
  cenjuv[t] ~ dnorm(W1[t], tauz)
}
```

### 2.2 Capture-mark-resighting data (CJS model)

```r
# 2.2.1 Observation process
for (t in 1:(nyears-1)){
  cen[t] ~ dnorm(W23[t], tauy)
  cenjuv[t] ~ dnorm(W1[t], tauz)
}
```

```r
for(i in 1:nind){
  # CJS
```
# Define latent state at first capture
z[i,f[i]] <- 1
for (t in (f[i]+1):nyears){
  # State process
  z[i,t] ~ dbern(mu1[i,t])
  mu1[i,t] <- phi[i,t-1] * z[i,t-1]
  # Observation process
  y[i,t] ~ dbern(mu2[i,t])
  mu2[i,t] <- p[i,t-1] * z[i,t]
} #t
} #i

", fill = TRUE)
sink()

# Bundle data
jags.data.season.s3 <-
  list(
    y = eh,
    f = f,
    x = x,
    z = known.state.cjs(eh),
    nind = dim(eh)[1],
    nyears = dim(eh)[2],
    cen = round((1 - juvper/100) * counts/2),
    cenjuv = round(juvper/100 * counts/2),
    group = gr
  )

# Initial values
inits.season.s3 <-
  function() {
    list(
      z = cjs.init.z(eh, f),
      epsilon.phi = array((0), dim = c(3, dim(eh)[2] - 1)),
      epsilon.p = array((0), dim = c(2, dim(eh)[2] - 1)),
      mu.phi = runif(3, 0.01, 1),
      mu.p = runif(2, 0.01, 1),
      kappa = runif(dim(eh)[2] - 1, 0.01, 2),
      sigma.phi = runif(3, 0.1, 10),
      sigma.p = runif(2, 0.1, 10),
      sigma.y = runif(1, 0.1, 10),
      sigma.z = runif(1, 0.1, 10),
      b1 = rpois(1, 300),
      b2 = rpois(1, 2000),
      b3 = rpois(1, 3000)
    )
  }

# Parameters to be monitored
parameters.season.s3 <- c("phi.j", "phi.y", "phi.a", "p.l", "p.n", "kappa",}
3 Transient life table response experiment

To calculate the contributions of demographic parameters and components of the population structure to the population dynamics, we performed a transient life table response experiment (transient LTRE) based on developments by Caswell (2007) and Koons et al. (2016, 2017).

For a time-varying population matrix model $A_t$, the realized population growth rate at any time step can be expressed as:

$$\lambda_t = \frac{\mathbf{n}_{t+1}}{\mathbf{n}_t} = A_t \hat{\mathbf{n}}_t / \hat{\mathbf{n}}_t \quad (S2.11)$$

where $\mathbf{n}_{t+1}$ and $\mathbf{n}_t$ are vectors of structured population abundances at time $t+1$ and $t$, respectively. To decompose the variance in $\lambda_t$ into contributions from the variance in underlying demographic parameters and components of the population structure, we first expanded eq. S3.1 for our age-structured population model:

$$\lambda_t = \sqrt{\varphi_{a,t} \cdot K_t \cdot \hat{\mathbf{w}}_{a,t} + \varphi_{j,t} \cdot \hat{\mathbf{w}}_{j,t} + \varphi_{y,t} \cdot \hat{\mathbf{w}}_{y,t} + \varphi_{a,t} \cdot \hat{\mathbf{w}}_{a,t}}$$

$$\hat{\mathbf{w}}_{j,t} + \hat{\mathbf{w}}_{y,t} + \hat{\mathbf{w}}_{a,t} \quad (S2.12)$$

where $\hat{\mathbf{w}}_{j,t}$, $\hat{\mathbf{w}}_{y,t}$ and $\hat{\mathbf{w}}_{a,t}$ are the number of juveniles, yearlings and adults in winter in year $t$, respectively, $\varphi_{x,t}$ is the annual apparent survival rate between $t$ and $t+1$ for individuals in age class $x$, and $\kappa_t$ is the annual apparent breeding success. Each demographic parameter (i.e., each element of $A_t$) and each component of the population structure (i.e., each element of $\mathbf{w}_t$) is combined in a vector $\Theta_t$. Contrary to Koons et al. (2016), but in line with Layton-Matthews et al. (2019), we used non-normalized values for the components of the population structure.
because actual rather than relative abundances more appropriately represent possible density dependent consequences for the population dynamics. Next, we calculated the sensitivity of $\lambda_t$ to change in each element of $\Theta_t$, which are the first derivatives of $\lambda_t$ with respect to changes in each element of $\Theta_t$

$$\frac{\partial \lambda_t}{\partial \kappa_t} = \frac{\sqrt{\varphi_{a,t} \cdot \hat{w}_{a,t}}}{w_t},$$

$$\frac{\partial \lambda_t}{\partial \varphi_{j,t}} = \hat{w}_{j,t},$$

$$\frac{\partial \lambda_t}{\partial \varphi_{y,t}} = \hat{w}_{y,t},$$

$$\frac{\partial \lambda_t}{\partial \varphi_{a,t}} = \hat{w}_{a,t} \cdot \left(1 + \frac{\kappa_t}{2\sqrt{\varphi_{a,t}}}\right),$$

$$\frac{\partial \lambda_t}{\partial \hat{w}_{j,t}} = \varphi_{j,t} \cdot \frac{w_t - w_{t+1}}{w_t^2},$$

$$\frac{\partial \lambda_t}{\partial \hat{w}_{y,t}} = \varphi_{y,t} \cdot \frac{w_t - w_{t+1}}{w_t^2},$$

$$\frac{\partial \lambda_t}{\partial \hat{w}_{a,t}} = \left(\kappa_t \sqrt{\varphi_{a,t} + \varphi_{r,t}}\right) \cdot \frac{w_t - w_{t+1}}{w_t^2},$$

(S2.13)

where $w_t$ is the denominator of eq. S3.2, i.e., $w_t = \hat{w}_{j,t} + \hat{w}_{y,t} + \hat{w}_{a,t}$, and $w_{t+1}$ the numerator of eq. S1.2, i.e., $w_{t+1} = \sqrt{\varphi_{a,t} \cdot \kappa_t \cdot \hat{w}_{a,t} + \varphi_{j,t} \cdot \hat{w}_{j,t} + \varphi_{y,t} \cdot \hat{w}_{y,t} + \varphi_{r,t} \cdot \hat{w}_{r,t}}$. Sensitivities were evaluated at the mean values of each element in $\Theta_t$ across the time series. These sensitivities were then combined with the covariances among all elements of $\Theta_t$ to achieve the first-order approximation of the variance in $\lambda_t$. The contribution of variation in each element of $\Theta_t$ to $\text{var}(\lambda_t)$ was obtained by summing over the covariances (Horvitz et al., 1997):

$$\text{contribution}_{\text{var}(\lambda)}^{\theta} \approx \sum_j \text{cov}(\theta_{i,t}, \theta_{j,t}) \frac{\partial \lambda_t}{\partial \theta_{i,t}} \frac{\partial \lambda_t}{\partial \theta_{j,t}}$$

(S2.14)

Results of the LTRE are visualized in Fig. 2.2 in the main text and Table S2.2. Relative contribution and relative absolute contribution of vital rates to variation in population growth
rate was 106% and 94%, respectively, whilst the population structure contributed -6% and 6%, respectively.

**Table S2.2:** Estimated variance, sensitivities of realized population growth rate to changes in underlying vital rates and population structure components, transient life table response experiment (LTRE) contributions (eq. S2.14), relative contributions

\[
\left( \frac{\text{contribution}_{\theta_i}^{\text{var}(\lambda)}}{\sum_i \text{contribution}_{\theta_i}^{\text{var}(\lambda)}} \right) \text{ and relative absolute contributions}
\]

\[
\left( \frac{\text{abs(contribution}_{\theta_i}^{\text{var}(\lambda)})}{\sum_i \text{abs(contribution}_{\theta_i}^{\text{var}(\lambda)})} \right)
\]

to variation in realized population growth rates. Estimates are provided as posterior means and 95% credible intervals.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Variance</th>
<th>Sensitivity</th>
<th>LTRE contribution</th>
<th>Relative contribution</th>
<th>Relative absolute contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\kappa$</td>
<td>0.0066</td>
<td>0.7159</td>
<td>0.0034 (0.0029, 0.0038)</td>
<td>0.521 (0.457, 0.592)</td>
<td>0.461 (0.409, 0.516)</td>
</tr>
<tr>
<td>$\varphi_j$</td>
<td>0.0059</td>
<td>0.1225</td>
<td>0.0002 (1.116•10^{-5}, 0.0005)</td>
<td>0.033 (0.002, 0.072)</td>
<td>0.029 (0.003, 0.063)</td>
</tr>
<tr>
<td>$\varphi_y$</td>
<td>0.0004</td>
<td>0.1116</td>
<td>0.0001 (-2.667•10^{-5}, 0.0002)</td>
<td>0.010 (-0.004, 0.033)</td>
<td>0.009 (0.000, 0.029)</td>
</tr>
<tr>
<td>$\varphi_a$</td>
<td>0.0034</td>
<td>0.8417</td>
<td>0.0032 (0.0025, 0.0041)</td>
<td>0.501 (0.437, 0.560)</td>
<td>0.444 (0.381, 0.501)</td>
</tr>
<tr>
<td>$w_j$</td>
<td>1.987•10^{5}</td>
<td>-1.102•10^{-5} (-1.281•10^{-5}, -9.321•10^{-6})</td>
<td>-0.0002 (-0.0003, -0.0002)</td>
<td>-0.032 (-0.040, -0.026)</td>
<td>0.029 (0.023, 0.035)</td>
</tr>
<tr>
<td>$w_y$</td>
<td>2.085•10^{5}</td>
<td>-8.287•10^{-6} (-1.026•10^{-6}, -6.502•10^{-6})</td>
<td>-0.0001 (-0.0001, -0.0001)</td>
<td>-0.012 (-0.017, -0.008)</td>
<td>0.011 (0.007, 0.015)</td>
</tr>
<tr>
<td>$w_a$</td>
<td>5.135•10^{6}</td>
<td>2.972•10^{-6} (2.649•10^{-6}, -3.316•10^{-6})</td>
<td>-0.0001 (-0.0002, -0.0001)</td>
<td>-0.020 (-0.025, -0.016)</td>
<td>0.018 (0.015, 0.022)</td>
</tr>
</tbody>
</table>
4
Explanatory variables

Table S2.3: Pearson correlations between original explanatory variables Year, Whooper swan count, Tailwind, Lake Peipsi water level, negative degree days (ndd) Naryan-Mar and cumulative degree days (cdd) Naryan-Mar.

<table>
<thead>
<tr>
<th></th>
<th>Year</th>
<th>Whooper count</th>
<th>Tailwind</th>
<th>Lake Peipsi</th>
<th>ndd</th>
<th>cdd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>1</td>
<td>0.959</td>
<td>-0.047</td>
<td>-0.132</td>
<td>0.134</td>
<td>0.281</td>
</tr>
<tr>
<td>Whooper count</td>
<td>0.959</td>
<td>1</td>
<td>0.005</td>
<td>-0.165</td>
<td>0.211</td>
<td>0.231</td>
</tr>
<tr>
<td>Tailwind</td>
<td>-0.047</td>
<td>0.005</td>
<td>1</td>
<td>0.080</td>
<td>-0.054</td>
<td>-0.121</td>
</tr>
<tr>
<td>Lake Peipsi</td>
<td>-0.132</td>
<td>-0.165</td>
<td>0.008</td>
<td>1</td>
<td>-0.244</td>
<td>-0.065</td>
</tr>
<tr>
<td>ndd Naryan-Mar</td>
<td>0.134</td>
<td>0.211</td>
<td>-0.054</td>
<td>-0.244</td>
<td>1</td>
<td>0.274</td>
</tr>
<tr>
<td>cdd Naryan-Mar</td>
<td>0.281</td>
<td>0.231</td>
<td>-0.121</td>
<td>-0.065</td>
<td>0.274</td>
<td>1</td>
</tr>
</tbody>
</table>

Table S2.4: Model output of GLM with demographic parameters estimated by the IPM as response variables (adult, yearling and juvenile survival, and apparent breeding success) and the explanatory variables as predictors (Year, Whooper swan count, Tailwind in the Baltic sea in autumn, water level in Lake Peipsi in autumn, negative degree days in Naryan-Mar in spring, cumulative degree days in Naryan-Mar in summer and autumn combined). Because Year and Whooper swan count correlate strongly, we only included one of them in the model. The model including Year was the most parsimonious and is presented in the main text, the model with Whooper swan count is presented here.

<table>
<thead>
<tr>
<th></th>
<th>Adult survival</th>
<th>Yearling survival</th>
<th>Juvenile survival</th>
<th>Apparent breeding success</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Est</td>
<td>SE</td>
<td>t</td>
<td>P</td>
</tr>
<tr>
<td>(Intercept)</td>
<td>-0.144</td>
<td>0.175</td>
<td>-0.827</td>
<td>0.415</td>
</tr>
<tr>
<td>Whooper swan</td>
<td>0.087</td>
<td>0.188</td>
<td>0.463</td>
<td>0.647</td>
</tr>
<tr>
<td>Tailwind</td>
<td>0.144</td>
<td>0.170</td>
<td>0.850</td>
<td>0.402</td>
</tr>
<tr>
<td>Lake Peipsi</td>
<td>0.259</td>
<td>0.174</td>
<td>1.494</td>
<td>0.145</td>
</tr>
<tr>
<td>ndd Naryan-Mar</td>
<td>0.156</td>
<td>0.210</td>
<td>0.745</td>
<td>0.462</td>
</tr>
<tr>
<td>cdd Naryan-Mar</td>
<td>-0.159</td>
<td>0.180</td>
<td>-0.881</td>
<td>0.385</td>
</tr>
</tbody>
</table>