Corresponding author:
Ülo Väli;
Email: ulo.vali@emu.ee

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Low juvenile survival threatens the Black Stork *Ciconia nigra* in northern Europe

Ülo Väli[1] ⬤, Māris Strazds[2], Katrin Kaldma[1] and Rimgaudas Treinys[3]

[1]Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, 51006 Tartu, Estonia; [2]Laboratory of Ornithology, Institute of Biology, University of Latvia, LV–1004 Rīga, Latvia and [3]Nature Research Centre, Akademijos 2, LT- 08412 Vilnius, Lithuania

Summary

Detecting factors causing the decline of wildlife populations provides essential knowledge for their effective conservation. Populations of Black Stork *Ciconia nigra* are decreasing in northern Europe; however, there are no detailed analyses of its survival, which frequently is a key demographic parameter affecting population dynamics in long-lived species. We used long-term data from re-sighted colour-ringed birds and satellite-tracked birds to estimate age- and sex-specific survival in a rapidly declining Black Stork population in the Baltic region at the northern end of the European range. Apparent survival (0.89) among colour-ringed birds older than one year was not significantly different from the previously reported estimates in Central Europe and the estimated real survival of GPS-tracked birds (0.77). However, the apparent survival of first-year (1y) birds was only 0.04, which is remarkably lower than earlier estimates in Central Europe. The real survival of GPS-tracked 1y birds was somewhat higher (0.11), but still much lower than estimates in other long-lived species. Apparent survival was three times lower in 1y females (0.013) than 1y males (0.045); this could be explained in part by a higher mean natal dispersal of females (189.1 km), compared with that of males (72.0 km), as well as by sex-specific mortality due to poor foraging conditions. There were no significant differences in apparent survival between the male and female storks older than one year. To better address the population decline, further research is needed to determine the factors causing low survival in young Black Storks, including the roles of food availability and climate change.

Introduction

Detecting factors causing declines in wildlife populations provides essential knowledge for the development of effective conservation strategies (Salafsky et al. 2002; Faaborg et al. 2010). Variation in demographic parameters, which is frequently age specific, guides the management of wildlife populations (Sandercock 2006). Among demographic parameters, survival is often thought to have the greatest impact on population dynamics, especially among long-lived species (Doherty et al. 2004; Schorcht et al. 2009; Sandercock 2020). However, in wild populations, separating survival from dispersal is challenging because it is often impossible to distinguish between the death and emigration of an animal. Although various statistical models have been developed to distinguish between the two parameters, real data are often insufficient for the application of these models (Sandercock 2020). Therefore, "apparent survival", defined as the product of real survival and site fidelity, is often estimated (Lebreton et al. 1992).

The centre–periphery hypothesis assumes that environmental conditions are more favourable for populations located near the centre of the range and harsher at the periphery (Brown 1984). Both biotic and abiotic factors determine species distributions (Brown et al. 1996), and in parallel, influence population size and demographic processes across the range (Pironon et al. 2016). For example, bird species tend to decrease in abundance from the centre to the periphery (Väli et al. 2004; Pironon et al. 2016) and show lower demographic rates in populations located at the margins of distributions (Niedzielski and Bowman 2014; Konovalov et al. 2019), although several studies have failed to detect spatial trend in demographic rates (e.g. Treinys et al. 2017; Martín et al. 2021). These differences in demographic properties along the centre–periphery axis emphasise the importance of spatial analyses of key demographic variables, especially for threatened species or species containing regionally threatened populations.

Black Stork *Ciconia nigra* is a large, long-lived bird species with a breeding distribution across Europe and Asia and in southern Africa. In Europe, it has an unfavourable conservation status and is listed in Annex I of the EU Birds Directive (2009/147/EC). This migratory species is also listed in Annex II of the Berne, Bonn, and Convention on International Trade in Endangered Species of Wild fauna and Flora (CITES) Conventions, and is included in the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA). The Black Stork nearly disappeared from western Europe in the first half of the last century; however, populations have

been recovering in recent decades (Janssen et al. 2004; Cano Alonso and Strazds 2020; European Commission 2020). The opposite pattern has been observed in northern Europe, where the population was once large but has declined since the 1980s (Janssen et al. 2004; Cano Alonso and Strazds 2020; European Commission 2020). Although previously reported abundances may be somewhat biased, the declining trends are obvious and alarming. For example, the Estonian population decreased by more than three times in 1991–2020 (Väli et al. 2021b). In Latvia, the numbers declined by 55% between the early 1990s and early 2000s (Strazds 2011). In Lithuania, the decrease between the 1980s and mid-2000s was at least 20% (Treinys et al. 2008), with a continuous decline thereafter (Treinys 2021). A two-fold decline was recorded in north-eastern Poland in 1989–2019 (Zawadzki et al. 2022). Owing to severe declines and/or small population sizes, the Black Stork is considered endangered and strictly protected in the above-mentioned countries.

The secretive habits of this woodland-nesting species have hindered studies of its biology (Strazds 2011), and analyses of its survival are limited. Re-sightings of colour-ringed birds have been thoroughly analysed only in Hungary (Central Europe), where apparent survival was low in the first year of life (0.16), but much higher later (0.83; Tamás 2011). A preliminary study in Estonia (northern Europe) reported a two-fold lower estimate for first-year (1y) birds (0.08), but a similar survival rate for older birds (0.84; Väli et al. 2021b). Väli et al. (2021b) also compared the two sexes and noticed a remarkably lower apparent survival rate among females. Although the analysis was based on a limited sample, this difference between sexes would explain the high proportion of unpaired birds, low reproductive success, and population decline in Estonia (Konovalov et al. 2019). Uncovering the factors contributing to the rapidly decreasing population in northern Europe is an urgent aim requiring more extensive analyses of species demography.

In the current study, we used long-term data from re-sighted colour-ringed birds to estimate age- and sex-specific apparent survival in a declining Black Stork population in a region located east of the Baltic Sea (Estonia, Latvia, and Lithuania, hereafter the Baltic region). Assuming that the demographic patterns of the Black Stork population follow the centre–periphery hypothesis, we expected that (H1) survival rates are lower in the declining Baltic population than in an increasing Hungarian population (European Commission 2020), and also hypothesised that (H2) survival decreases northwards within the Baltic region (northern part of the range) due to the increase in migration distance and severity of environmental conditions. We also expected that (H3) females have a lower survival rate than that of males, similar to most birds (e.g. Donald 2007; Newton et al. 2016). Finally, we hypothesised that (H4) survival rates in the Baltic Black Stork population decreased over time along with the declining abundance. For most analyses, we used a large sample of colour-ringed birds. In addition, we estimated the survival of satellite-tracked birds, enabling us to exclude the effect of dispersal and providing estimates of real survival.

Methods

Study area and species

The study was conducted in the Baltic region (including Estonia, Latvia, and Lithuania), northern Europe, on the northern limit of the European distribution of the species (Figure 1). Baltic storks are
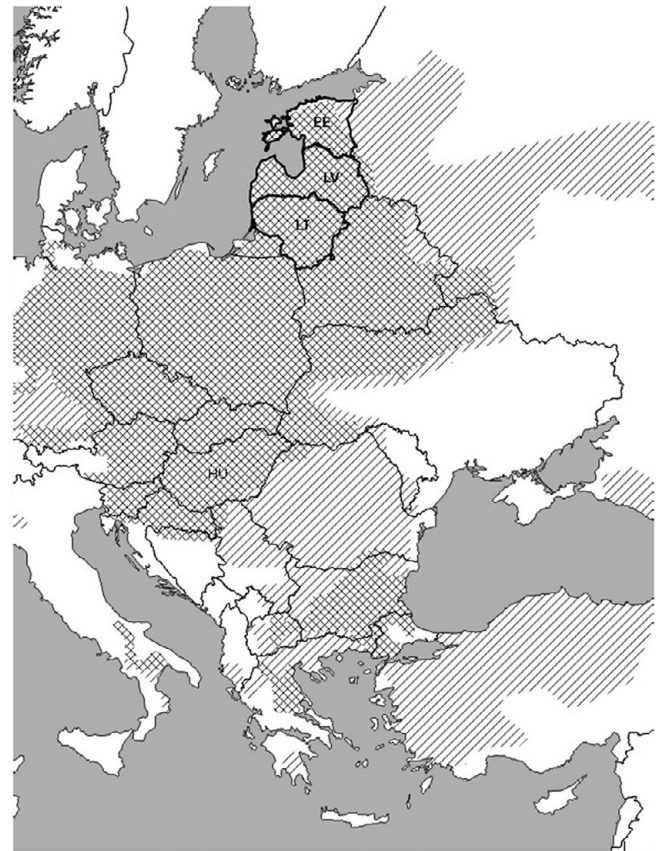

Figure 1. Distribution of the Black Stork *Ciconia nigra* in central and eastern parts of Europe. Crosshatching indicates permanent breeding sites (according to Cano Alonso and Strazds 2020), simple hatching indicates scattered or irregular breeding sites. The study area is indicated with bold borders (EE: Estonia, LV: Latvia, LT: Lithuania); HU denotes Hungary, where survival was studied earlier.

long-distance migrants, covering some 6,000 km to reach their wintering grounds in eastern sub-Saharan Africa and the Middle East; they arrive at breeding grounds in late March or early April and depart in late August or early September (Sellis 2012; Elliott et al. 2014, our data). The nests are located in woodlands on large trees, and storks forage primarily on fish in forest streams and other aquatic habitats. Typically, the same nest is used for many years: accordingly, re-sighting efforts can be focused on nest sites, which facilitates research on demographic processes in the breeding population.

Regular monitoring of Black Stork nests in the Baltic region started in Latvia in 1978 (Strazds 2011), followed by Estonia in 1991 (Väli et al. 2021b), and Lithuania since the early 2000s (Treinys et al. 2008). Nests are usually inspected from late May until the end of July; however, nestlings are usually ringed in late June or early July when they are at least three weeks old (Strazds et al. 2006). In the course of monitoring, all nestlings are ringed with scientific (metal) rings. Since 1990 (Latvia), 1994 (Estonia), and 2006 (Lithuania), plastic colour rings with unique alphanumeric codes have been added to the tibiotarsus of the other leg. This facilitates the re-sighting of live individuals without the need for trapping. Over the study period, only three losses of colour rings were recorded. Therefore, similarly to analogous studies of other species (e.g. Wahl and Barbraud 2014; Väli et al. 2021a), these were considered very rare events and our mark–re-sighting analyses did not account for ring losses.

Data collection

Prior to 2010, data for re-sightings were obtained from field observations (mostly photographs). Later, data were largely collected using camera traps (trail cameras) installed at nests in Estonia and Latvia (15–25 in 2010–2015, 30–50 in 2016–2022), and additional data were obtained from five webcams set up at nests. Cameras were mounted on the branch of the nesting tree, or on the neighbouring tree, 1–5 m (usually 2–3 m) from the nest. Cameras were installed in the second half of March, before storks returned from wintering grounds to their nest sites, or during the ringing of nestlings in late June or early July (see further methodological details in Konovalov et al. 2019). Few ringed birds were recorded by camera traps installed at foraging sites (streams and rivulets, usually supplied with additional food to attract and trap storks) and one was recorded by a hunter's camera trap. No camera traps or webcams have been used in Lithuania.

The data set was composed of encounter histories of 3,304 nestlings (539 from Estonia, 1,881 from Latvia, and 825 from Lithuania) marked with colour rings in 1990–2020; re-sightings were collected up to 2022. A total of 91 storks (12 from Estonia, 60 from Latvia, and 19 from Lithuania) were re-sighted at least once in subsequent years alive in the Baltic region. A subsample of 175 birds from Estonia and Latvia were sexed by DNA analysis (Fridolfsson and Ellegren 1999). This subsample (79 females and 96 males), supplemented with marked but unsexed and later unseen birds (assuming an equal sex ratio in the Baltic region; Konovalov et al. 2015), was used for detecting sex-specific biases in survival.

Finally, real survival was estimated for birds tagged with GPS transmitters in 2005–2021 (https://birdmap.5dvision.ee/, M. Strazds et al., unpublished data), including 45 juveniles (27 females, 5 males, and 13 of unknown sex; 28 from Latvia, 17 from Estonia) and 26 adults (17 males, 7 females, 2 of unknown sex; 23 from Estonia, 3 from Latvia). Each of these birds was equipped with a 30–50 g (<3% of the body mass) solar-powered GPS tag (Microwave Telemetry Inc., Ecotone Telemetry, Ornitela UAB, E-OBS GmbH), as a backpack, using full Teflon harnesses. Thirty-six GPS transmitters were collected in the field after the suspected death of the bird and in all cases mortality was confirmed; there were no known losses of GPS loggers nor confirmed failures over the years.

We also evaluated natal dispersal as the distance and direction between the nest of hatching (and ringing) and the nest of the first known breeding (only birds ringed as nestlings in Latvia were included in this analysis). Long-lived Black Storks do not breed every year. When storks are not breeding, they may explore several nests in the area. In subsequent years, breeding of the previously exploring individual is recorded in one of the explored nests (both sexes do so, as verified by repeated re-sightings and GPS tracking; unpublished data of authors). Therefore, to increase sample size, we supplemented the verified breeding records with observations at nests even when the bird was not breeding there. Although this approach may cause some bias in the results, the bias is not likely to be large and is equal for both sexes; hence the comparison between sexes is not affected.

Data analysis

Data were analysed using R.4.0.0 (R Core Team 2023). Analyses only included re-sightings in the Baltic region (breeding grounds). Probabilities of re-sighting (encounter; p) and apparent survival (Φ) were estimated using RMark 2.2.7 (Laake 2013), an R-package for model building in MARK (White and Burnham 1999). The real survival of GPS-tracked birds was also estimated by RMark, with the probability of re-sighting fixed at 1. According to White and Burnham (1999), we initially generated a fully time-dependent Cormack–Jolly–Seber model with "sex" and/or "country" as groups. The goodness-of-fit test (release.gof function in RMark) indicated a poor fit of this model (Test 2: $P < 0.97$, Test 3: $P < 0.001$), suggesting a hidden structure within our sample in which survival patterns differed among groups of birds. This was consistent with earlier results of Tamás (2011), who distinguished two age classes with differences in survival: (1) birds during their first year of life (1y birds) and (2) older birds. Therefore, we assumed the same structure to test our first hypothesis (H1) that apparent survival is lower in the declining Baltic population than in a previously observed stable population (Tamás 2011). Additionally, we were aware of changes in observation effort over time and incorporated time-dependent re-sighting probability in the model. Thus, our initial model was $\Phi_{a2} p_t$. For comparison, we evaluated mean re-sighting probabilities for the two groups using the simplified model $\Phi_{a2} p_2$. To evaluate the hypotheses of survival differences between the three Baltic countries (H2) and two sexes (H3), country and sex, respectively, were included in the model ($\Phi_{a2g} p_t$; $\Phi_{a2s} p_t$). Finally, we included time dependence to evaluate whether survival decreased over time along with declining abundance ($\Phi_t p_t$; H4). In this analysis, groups were not considered owing to a low sample size. The models were compared using Akaike's information criterion corrected for small samples (AICc). Following Cooch and White (2016), we evaluated the fit of all models using the Fletcher variance inflation factor ĉ (Fletcher 2012), which is more appropriate for data sets involving a large number of capture histories with sparse data and low expected re-sighting frequencies than other overdispersion parameters (Cooch and White 2016). The models fitted to the data well (Fletcher ĉ = 1.00). To study sex-specific differences in natal dispersal distances and directions, the nonparametric Wilcoxon rank-sum test and Watson–Wheeler test (package Circular; Agostinelli and Lund 2023), respectively, were used.

Results

Apparent survival in the Baltic population (H1; model $\Phi_{a2} p_t$) was 0.043 ± 0.005 (SE; 95% confidence interval [CI] = 0.034–0.054) among 1y birds and 0.886 ± 0.016 (0.850–0.914) among older birds. Given the substantial increase in study effort after the mid-2000s, we additionally estimated apparent survival using the subset of data from 2007–2022. The survival estimates for 1y birds (0.042 ± 0.006; 0.032–0.055) and older birds (0.865 ± 0.025; 0.809–0.907) were similar to those estimated from the full data set. The estimated real survival of GPS-tracked 1y birds was also very low (0.11 ± 0.05; 0.05–0.24), yet higher than that of the colour-ringed birds. Real survival of GPS-tracked older (adult) birds from Estonia and Latvia was slightly lower (0.77 ± 0.04; 0.68–0.85) than the estimated apparent survival.

To evaluate the possibility that different re-sighting probabilities account for the low survival estimate among 1y birds, we fitted the data in the simplified model including only two age classes ($\Phi_{a2} p_t$). The re-sighting probability was lower among 1y birds (0.09 ± 0.03) than that among older birds (0.23 ± 0.02), while the estimates of survival were similar to those provided by time-dependent models (0.04 ± 0.01 and 0.91 ± 0.02, respectively).

To evaluate spatial variation in apparent survival within the Baltic region (H2), we added the categorical variable "country" to

Table 1. Probabilities (± SE, 95% confidence intervals in brackets) of re-sighting and survival of Black Storks *Ciconia nigra* fledged in the three Baltic States during the first year and at a later age

Age	Country	Apparent survival
First–year birds	Estonia	0.046 ± 0.014 (0.025–0.083)
	Latvia	0.054 ± 0.008 (0.041–0.071)
	Lithuania	0.028 ± 0.007 (0.017–0.047)
Older birds	Estonia	0.863 ± 0.040 (0.765–0.924)
	Latvia	0.884 ± 0.020 (0.840–0.917)
	Lithuania	0.884 ± 0.038 (0.785–0.941)

Figure 2. Apparent survival probabilities for male and female colour-ringed Black Storks *Ciconia nigra* during their first year (A) and later (B). Note the different scales on the *y*-axes.

the initial model. The more complex model indicated similar survival probabilities for older birds in all three countries and some variation in survival probabilities among countries for young birds (Table 1). However, this model ($\Phi_{a2g}\,p_t$ AICc = 1,811.2) was less well supported by the data compared with the initial model ($\Phi_{a2}\,p_t$ AICc = 1,809.8), suggesting a lack of significant variation in survival within the Baltic population.

To study sex-specific differences in survival (H3), the variable "sex" was included. The model with sex ($\Phi_{a2s}\,p_t$) had higher support (AICc = 680.1) than the model without this parameter ($\Phi_{a2}\,p_t$ AICc = 688.6; note that the lower sample size resulted in lower AICc values than those presented above). There was a three-fold difference in apparent survival in 1y females (0.013 ± 0.006; 0.006–0.030) compared with that for 1y males (0.045 ± 0.010; 0.029–0.070); the CIs were nearly exclusive (Figure 2). In older birds, we did not detect a significant difference in apparent survival between males (0.821 ± 0.035; 0.742–0.879) and females (0.784 ± 0.073; 0.609–0.894). Estimated real survival of GPS-tracked adult males was 0.80 ± 0.05 (0.69–0.88) and that among females was 0.70 ± 0.10 (0.47–0.85); however, the CIs overlapped extensively, indicating a non-significant difference between the sexes. Unfortunately, our data were too limited to obtain sex-specific estimates for young birds. Natal dispersal distances were significantly longer in females (189.1 ± 193.9 km, mean ± SD, *n* = 17) than that in males (72.0 ± 53.7 km, *n* = 27; *W* = 372, *P* <0.001). However, there was no difference between dispersal directions (females: 238.2 ± 79.0 degrees, males: 184.6 ± 107.6 degrees; *W* = 3.56, *P* <0.168) as both sexes generally dispersed southwards, on average.

To evaluate whether survival declined along with the declining abundance (H4), we compared model $\Phi_t\,p_t$ with the constant model $\Phi.p.$ and the model with the constant survival and time-dependent re-sighting probability $\Phi.p_t$. The model with the time-dependent probability ($\Phi_t\,p_t$) received higher support (AICc = 1,182.8) than those of the other two models (AICc = 1,414.0 and AICc = 1,268.1). Annual estimates fluctuated during the first half of the study period, when the re-sighting probability was low; however, we noticed a steady decrease in apparent survival after the early 2000s (Figure 3). The trend between 2001 and 2020 was negative, although it did not exceed the significance threshold (β = −0.016 ± 0.009, *P* = 0.1).

Discussion

Re-sightings of colour-ringed birds provided data on apparent survival in the Black Stork population east of the Baltic Sea and GPS-tracking provided comparative data for estimating real survival. Contrary to our first two hypotheses (H1 and H2), we did not
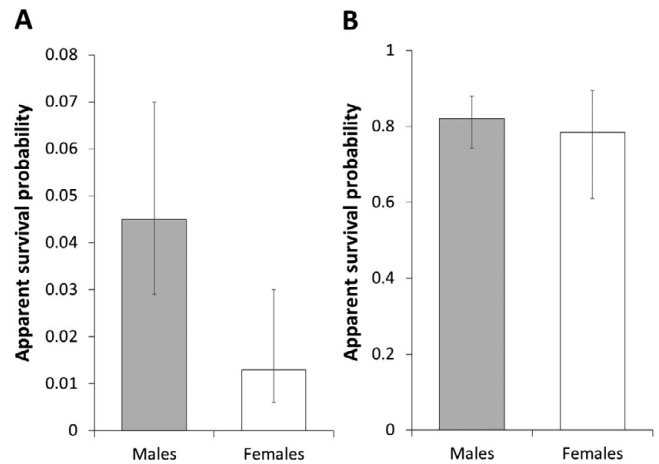
detect significant differences in the apparent survival of older birds along the north–south axis. However, apparent survival of 1y birds was much lower than that of older birds and remarkably lower than an earlier estimate in Hungary (Tamás 2011). Consistent with our third hypothesis (H3), female survival was slightly lower than male survival, with no significant differences between older males and females; however, apparent survival of 1y females was three times lower than that of 1y males. Consistent with our fourth hypothesis (H4), we detected a negative trend over time in apparent survival; however, the differences were only close to the significance threshold.

We did not find spatial differences in apparent survival along the north–south axis of c.700 km as would be expected according to the centre–periphery hypothesis (Brown 1984). Moreover, apparent survival estimates of storks older than one year in the three Baltic countries (0.86–0.88) were similar to those obtained for a Hungarian population (0.83) located more than 600 km south in Central Europe (Tamás 2011). These findings suggest that the apparent survival of older birds is not related to the position of the population in the distribution range, despite the fact that previously studied demographic variables (long-term population trends and breeding success) show continuous declines towards the northern edge of the range (Treinys et al. 2008; Strazds 2011; Väli et al. 2021b; Treinys 2021). Yet, our findings for Black Stork are not unique because several studies similarly have reported the lack of spatial trend in demographic rates (Carbonell et al. 2003; Pironon et al. 2016; Treinys et al. 2017; Martín et al. 2021). Hence, the apparent survival of adult Black Storks in the Baltic region is probably not influenced by variation in: (1) the length of the migration route, which differs up to c.10% within the region; (2) local environmental conditions, including climatic and habitat factors; (3) biotic interactions, such as competition or predation (Niedzielkski and Bowman 2014); (4) anthropogenic disturbance. Instead, equal apparent survival rates in breeding grounds across geographical locations support the relative importance of environmental conditions in the wintering grounds on survival, which has been earlier observed both in Black Stork and White Stork *Ciconia ciconia* (Schaub et al. 2005; Cano et al. 2013; Martín et al. 2021).

Apparent survival estimates for older colour-ringed Black Storks (0.86–0.88) were somewhat higher than real survival (0.77),
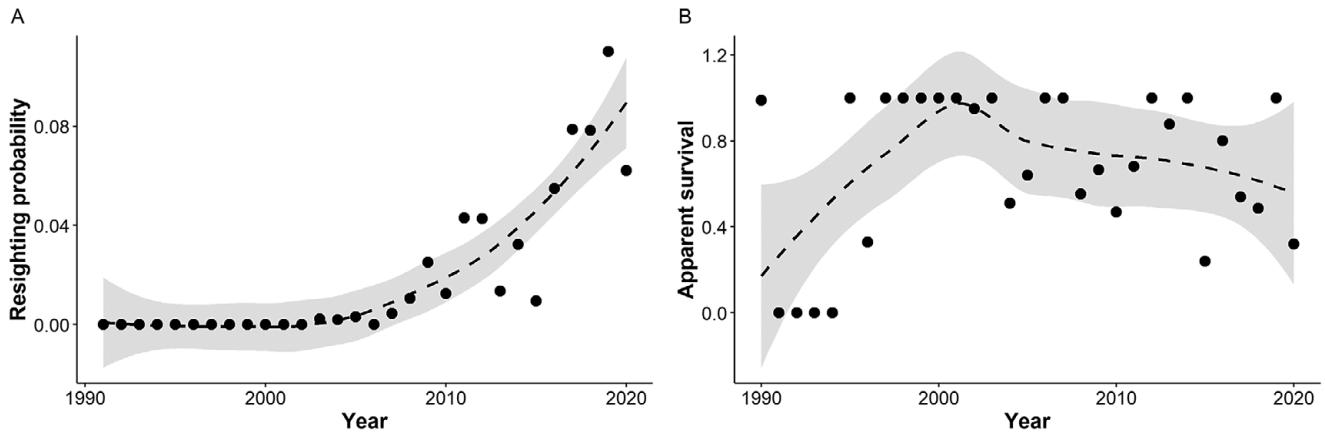
Figure 3. Temporal dynamics of the re-sighting probability (A) and apparent survival (B) of Black Stork in the Baltic region in 1991–2020.

estimated by GPS telemetry. However, the difference between results based on ring re-sightings and GPS tracking was not significant as the CIs overlapped. Considering the similar estimates of survival, we conclude that adult survival rate cannot explain the decline in the Baltic population.

However, re-sightings of colour-ringed birds suggested that apparent survival is significantly lower (0.03–0.05) in Baltic 1y birds. These figures are several times lower than those estimated in Hungary using a similar method (0.16; Tamás 2011). The real survival estimate was somewhat higher in our study (0.11). This difference highlights the necessity to complement the analysis of ring recoveries by less biased techniques such as GPS tracking. Furthermore, for long-lived species with a long maturation period, nest monitoring could be complemented with other types of monitoring (e.g. monitoring known feeding sites) to increase the re-sighting probability of young individuals and thus improve the reliability of survival estimates. However, both obtained figures were exceptionally low in comparison with those for other long-lived birds (Newton et al. 2016). As an example, only four out of 27 GPS-tracked juveniles reached the age of one year, and only one of them reached breeding age (and started breeding; M. Strazds, unpublished data). Hence, our results indicate the exceptionally high mortality rates of young Black Storks.

There are several potential explanations for the particularly low survival of Baltic Black Storks during their first year. Deaths seem to start during the late nestling period but not in the earlier phases because the clutch size in the Baltic States is similar to those in other regions (Janssen et al. 2004), and a peak in mortality is not detected during the first weeks after hatching in Black Stork (Väli et al. 2021b; M. Strazds, unpublished data), whereas it is found in White Stork (Kosicki 2012). Instead, survival likely decreases later. For instance, Väli et al. (2021b) confirmed the death of eight of 14 Black Stork nestlings during the late nestling period and first days of migration and a high mortality shortly after fledging has been recorded in Latvia (M. Strazds et al., unpublished data).

There are several mutually non-exclusive explanations for the low survival of 1y birds. First, the condition of large nestlings and fledglings may be poor due to a food shortage. We suspect that this may be the result of forest drainage, which affects biodiversity in watercourses (Rosenvald et al. 2014) and reduces the abundance of Black Stork prey. This may have acted in concert with climate change, particularly increased temperatures and decreased precipitation in July and August, the hottest summer months in northern Europe, when young storks fledge. Secondly, Baltic Black Storks are

affected by recent DDT contamination, which has likely increased mortality among nestlings and fledglings (Strazds et al. 2015). Thirdly, Black Stork nestlings and fledglings may suffer from predation. Although Konovalov et al. (2019) did not detect any significant impact of predation, recent records from webcams and camera traps suggest that pressure by avian predators on young Black Storks is increasing (authors' pers. obs., see also Langgemach and Henne 2001; Zawadski et al. 2022).

Among 1yr birds, apparent survival was significantly lower in females than in males. This could be explained in part by a higher natal dispersal of females, a characteristic pattern in many long-lived birds (Faccio 2013; Murphy et al. 2018; Morandini et al. 2019; Väli et al. 2021a), and also detected in the current study. Similarly, White Stork females settle at significantly longer distances from natal sites than corresponding estimates for males (Chernetsov et al. 2006). Furthermore, birds migrating through regions with suitable nest sites and potential partners may settle down *en route* instead of continuing migration (Chernetsov et al. 2006; see also Itonaga et al. 2010). Indeed, the studied Black Storks generally dispersed southwards. Hence, natal dispersal may explain the low rates of female apparent survival and eventually disproportionately reduce populations in the northern part of the range.

However, we believe that sex-dependent mortality also shaped the sex difference detected in the apparent survival of young Black Storks. Kenward et al. (1999) reported markedly lower survival rates for 1y males (smaller sex) than 1y females (larger sex) in Eurasian Goshawk *Accipiter gentilis*. Among various explanations for this pattern, the authors proposed that the small size of males may have provided lower body reserves than those of larger females for survival during periods of food shortage. We supposed that a food shortage is the main cause of the low survival of young Black Storks in the Baltic States (see above), in which case we could also predict that survival rates will be lower in the smaller sex. Indeed, the body mass of fledgling females is lower than that of males (2.7 kg vs 3.2 kg at 50 days of age, respectively, $n = 158$, M. Strazds, unpublished data), corresponding to the apparent dimorphism in adulthood (males are slightly larger than females; Cramp and Simmons 1977). This size difference could be particularly important during the first migration of inexperienced Black Stork juveniles. In long-lived species, distances travelled and time spent at stop-overs are longer for juveniles than adults (Sergio et al. 2014), consistent with observations of Black Storks, in which juveniles were observed in stop-over sites in Israel significantly later in the autumn compared with observations of adults (ringing data from

Lithuania; R. Treinys, unpublished). Irrespective of the reason for the relatively low apparent survival in young female Baltic Black Storks, this may skew the adult sex ratio in the population. Higher female mortality is observed in many bird species but is more pronounced in threatened species or populations (Donald 2007). At the northern margin of the range, an increasing lack of partners is an important threat for Black Stork and probably an essential driver of the population decline (Konovalov et al. 2019; Väli et al. 2021b).

We noticed a declining (although not significant) trend in apparent survival in Black Stork. Unfortunately, our sample sizes were not sufficient for analysing temporal trends separately in the two age classes. However, in White Stork, declines in survival in both age classes have been detected (Martín et al. 2021). Even a non-significant trend is alarming in declining populations, as survival often has a great impact on population dynamics, especially in long-lived species (Doherty et al. 2004; Schorcht et al. 2009; Sandercock 2020), emphasising the need for further monitoring and conservation measures.

Conclusions

The most important finding of the current study was the alarmingly low apparent survival of Baltic Black Storks during their first year of life, especially among females. This, along with the declining population numbers, strongly questions the viability of the population. The most plausible explanation is a shortage of food, along with freshwater contamination with environmental pollutants, predation, and climate change. Therefore, further research should evaluate the causal relationship between these potential factors and the survival of young Black Storks in the Baltic region. If a food shortage is a key factor in explaining the low survival of young birds, then supplementary feeding could be considered as an additional conservation measure in the short term, as this approach has been successful in restoring threatened populations (Janssen et al. 2004; Jones 2004). However, this measure is labour-intensive, influences only a fraction of the population, and can also have negative consequences (e.g. Carrete et al. 2006). In the medium term, the building of water reservoirs in drainage systems can improve the survival of prey during the summer when drainage ditches are dried up. In the long term, the environmental quality of managed forests should be recovered by restoring damaged watercourses (brooks and streams).

References

Agostinelli C. and Lund U. (2023). R Package 'Circular': Circular Statistics (version 0.5-0). Available at https://r-forge.r-project.org/projects/circular/.

Brown J.H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist* **124**, 255–279.

Brown J.H., George C.S. and Kaufman D.M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* **27**, 597–623.

Cano L.S., Franco C., Doval G., Tores A., Carbonell I. and Tellería J.L. (2013). Conservation of Iberian Black Storks *Ciconia nigra* outside breeding areas: distribution, movements and mortality. *Bird Conservation International* **23**, 463–468.

Cano Alonso L.S. and Strazds M. (2020). *Ciconia nigra* Black Stork. In Keller V., Herrando S., Voříšek P., Franch M., Kipson M., Milanesi P. et al., *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. Barcelona: European Bird Census Council/Lynx Edicions.

Carbonell R., Pérez-Tris J. and Tellería J.L. (2003). Effects of habitat heterogeneity and local adaptation on the body condition of a forest passerine at the edge of its distributional range. *Biological Journal of the Linnean Society* **78**, 479–488.

Carrete M., Donázar J.A. and Margalida A. (2006). Density-dependent productivity depression in Pyrenean bearded vultures: Implications for conservation. *Ecological Applications* **16**, 1674–1682.

Chernetsov N., Chromik W., Dolata P.T., Profus P. and Tryjanowski P. (2006). Sex-related natal dispersal of White Storks (*Ciconia ciconia*) in Poland: How far and where to? *The Auk* **123**, 1103–1109.

Cooch E.G. and White G.C. (2016). *Program MARK. A Gentle Introduction*, 14th Edn. Available at http://www.phidot.org/software/mark/docs/book/ (accessed 6 February 2021).

Cramp S. and Simmons K.E.L. (1977). *The Birds of the Western Palearctic*. Vol. **I**: *Ostrich to Ducks*. Oxford: Oxford University Press.

Doherty Jr P.F., Schreiber E.A., Nichols J.D., Hines J.E., Link W.A., Schenk G.A. et al. (2004). Testing life history predictions in a long-lived seabird: a population matrix approach with improved parameter estimation. *Oikos* **105**, 606–618.

Donald P.F. (2007). Adult sex ratios in wild bird populations. *Ibis* **149**, 671–692.

Elliott A., Christie D.A., Garcia E.F.J. and Boesman P. (2014). Black Stork (*Ciconia nigra*). In del Hoyo J., Elliott A., Sargatal J., Christie D.A. and de Juana E. (eds), *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions.

European Commission (2020). Article 12 Web Tool on Population Status and Trends of Birds under Article 12 of the Birds Directive. Available at https://nature-art12.eionet.europa.eu/article12/ (accessed 7 May 2023).

Faaborg J., Holmes R.T., Anders A.D., Bildstein K.L., Dugger K.M., Gauthreaux Jr S.A. et al. (2010). Conserving migratory land birds in the New World: Do we know enough? *Ecological Applications* **20**, 398–418.

Faccio S.D. (2013). Movement patterns, natal dispersal, and survival of Peregrine Falcons banded in New England. *Journal of Raptor Research* **47**, 246–261.

Fletcher D. (2012). Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika* **99**, 230–237.

Fridolfsson A.K. and Ellegren H. (1999). A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30**, 116–121.

Itonaga N., Köppen U., Plath M. and Wallschläger D. (2010). Breeding dispersal directions in the white stork (*Ciconia ciconia*) are affected by spring migration routes. *Journal of Ethology* **28**, 393–397.

Janssen G., Hormann M. and Rohde C. (2004). *Der Schwarzstorch*. Hohenwarsleben: Westarp Wissenschaften.

Jones C.G. (2004). Conservation management of endangered birds. In Sutherland W.J., Newton I. and Green R., *Bird Ecology and Conservation: A Handbook of Techniques*. Oxford: Oxford University Press, pp. 269–302.

Kenward R.E., Marcström V. and Karlbom M. (1999). Demographic estimates from radio-tagging: models of age-specific survival and breeding in the goshawk. *Journal of Animal Ecology* **68**, 1020–1033.

Konovalov A., Kaldma K., Bokotey A., Brossault P., Chapalain F., Dmitrenok M. et al. (2015). Spatio-temporal variation in nestling sex ratio among the Black Stork *Ciconia nigra* populations across Europe. *Journal of Ornithology* **156**, 381–387.

Konovalov A., Nellis R., Nellis R., Nurmla A., Sellis U. and Väli Ü. (2019). Solitude at periphery: lack of partners limits reproduction of the Black Stork (*Ciconia nigra*) at the margin of the distribution range. *Ornis Fennica* **96**, 13–23.

Kosicki J.Z. (2012). Effect of weather conditions on nestling survival in the White Stork *Ciconia ciconia* population. *Ethology Ecology & Evolution* **24**, 140–148.

Laake J.L. (2013). RMark: An R Interface for Analysis of Capture-recapture Data with MARK. Available at https://CRAN.R-project.org/package=RMark (accessed 1 February 2021).

Langgemach T. and Henne E. (2001). Störche *Ciconia ciconia*, *C. nigra* und Kraniche *Grus grus* im Beutespektrum des Seeadlers *Haliaeetus albicilla*. *Vogelwelt* **122**, 81–87.

Lebreton J.D., Burnham K.P., Clobert J. and Anderson D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118.

Martín B., Onrubia A. and Ferrer M. (2021). Climate change and the spatio-temporal variation in survival of a long-distance migrant (White Stork, *Ciconia ciconia*) across Western Europe. *Birds* **2**, 362–380.

Morandini V., Muriel R., Newton I. and Ferrer M. (2019). Skewed sex ratios in a newly established osprey population. *Journal of Ornithology* **160**, 1025–1033.

Murphy R.K., Stahlecker D.W., Millsap B.A., Jacobson K.V., Johnson A., Smith C.S. et al. (2018). Natal dispersal distance of golden eagles in the southwestern United States. *Journal of Fish and Wildlife Management* **10**, 213–218.

Newton I., McGrady M.J. and Oli M.K. (2016). A review of survival estimates for raptors and owls. *Ibis* **158**, 227–248.

Niedzielski B. and Bowman J. (2014). Survival and cause-specific mortality of the female eastern wild turkey at its northern range edge. *Wildlife Research* **41**, 454–551.

Pironon S., Papug, G., Villellas J., Angert A.L., García M.B. and Tompson J.D. (2016). Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. *Biological Reviews* **92**, 1877–1909.

R Core Team (2023). *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing. Available at https://www.R-project.org/ (accessed 4 September 2020).

Rosenvald R., Järvekülg R. and Lõhmus A. (2014). Fish assemblages in forest drainage ditches: Degraded small streams or novel habitats? *Limnologica* **46**, 37–44.

Salafsky N., Margoluis R., Redford K.H. and Robinson J.G. (2002). Improving the practice of conservation: A conceptual framework and research agenda for conservation science. *Conservation Biology* **16**, 1469–1479.

Sandercock B.K. (2006). Estimation of demographic parameters from live-encounter data: a summary review. *The Journal of Wildlife Management* **70**, 1504–1520.

Sandercock B.K. (2020). Mark-recapture models for estimation of demographic parameters. In Murray D. and Sandercock B.K. (eds), *Population Ecology in Practice*. Hoboken: Wiley-Blackwell,. pp. 157–190.

Schaub M., Kania W. and Köppen U. (2005). Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *Journal of Animal Ecology* **74**, 656–666.

Schorcht W., Bontadina F. and Schaub M. (2009). Variation of adult survival drives population dynamics in a migrating forest bat. *Journal of Animal Ecology* **78**, 1182–1190.

Sellis U. (2012). Migration and wintering based on tracking data of the Estonian black stork population. In *Abstracts of the 6th International Black Stork Symposium, Châlons-en-Champagne*, France, p. 17

Sergio F., Tanferna A., De Stephanis R., Jiménez L.L., Blas J., Tavecchia G. et al. (2014). Individual improvements and selective mortality shape lifelong migratory performance. *Nature* **515**, 410–413.

Strazds M. (2011). *Conservation Ecology of the Black Stork in Latvia.* PhD dissertation, University of Latvia, Riga.

Strazds M., Bauer H.G., Väli Ü., Kukāre A. and Bartkevičs V. (2015). Recent impact of DDT contamination on Black Stork eggs. *Journal of Ornithology* **156**, 187–198.

Strazds M., Ķuze J. and Reine S. (2006). Evaluation of Black Stork *Ciconia nigra* nest inspections in Latvia in 2003–2005. *Biota* **7**, 93–101.

Tamás E.A. (2011). Longevity and survival of the black stork *Ciconia nigra* based on ring recoveries. *Biologia* **66**, 912–915.

Treinys R. (2021). Juodasis gandras *Ciconia nigra* (Linnaeus, 1758). In Rašomavičius, V. (ed.), *Red Data Book of Lithuania. Animals, Plants, Fungi*. Vilnius: Aplinkos ministerija, p. 222.

Treinys R., Lõhmus A., Stončius D., Skuja S., Drobelis E., Šablevičius B. et al. (2008). At the border of ecological change: status and nest sites of the Lithuanian Black Stork *Ciconia nigra* population 2000–2006 versus 1976–1992. *Journal of Ornithology* **149**, 75–81.

Treinys R., Väli Ü. and Berganis U. (2017). Strong territoriality and weak density-dependent reproduction in Lesser Spotted Eagles *Clanga pomarina*. *Ibis* **159**, 343–351.

Väli Ü., Kalvāns A. and Tuvi J. (2021a). Apparent survival and dispersal in a recovered Osprey population: effects of age, sex and social status. *Journal of Ornithology* **162**, 1025–1034.

Väli Ü., Nellis R., Kaldma K., Vainu O. and Sellis U. (2021b). The abundance, reproductive success and apparent survival of the Estonian black stork population in 1991–2020. *Hirundo* **34**, 20–39.

Väli Ü., Treinys R. and Lõhmus A. (2004). Geographical variation in macro-habitat use and preferences of the Lesser Spotted Eagle *Aquila pomarina*. *Ibis* **146**, 661–671.

Wahl R. and Barbraud C. (2014). The demography of a newly established Osprey *Pandion haliaetus* population in France. *Ibis* **156**, 84–96.

White G.C. and Burnham K.P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139.

Zawadzki G., Zawadzki J., Drozdowski S. and Zawadzka D. (2022). The avoidance of living in the vicinity of a top predator: the coexistence of the black stork and the white-tailed eagle in NE Poland. *The European Zoological Journal* **89**, 1223–1237.