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Long-term conservation efforts at flyway scale can halt the population decline in a globally endangered migratory raptor

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Abstract

Many threatened species require ongoing management, which is often funded through short project cycles. Evaluating whether the management is effective in protecting a species is important to inform future management investments. For migratory species, management may affect only part of a species' annual cycle, and reversing a population decline is challenging to achieve and demonstrate. Here, we evaluate whether conservation management projects funded by the European LIFE programme to safeguard a migratory vulture population achieved their major objective of stabilizing the target breeding population. Between 2012 and 2022, an international alliance of conservation organizations implemented multiple actions to reduce poisoning, direct persecution, and electrocution and collision with power lines along the Eastern Mediterranean flyway. We monitored breeding territories of the Balkan population of the globally endangered Egyptian Vulture *Neophron percnopterus* between 2006 and 2022, and tracked 60 young birds with GPS transmitters since 2010. We used these data to examine whether population growth rate and survival probability had increased since project implementation. The mean annual survival probability of adult territorial birds increased by 1.9% since 2014 from 0.937 to 0.955, and the monthly survival probability of wild juvenile birds increased by 9.7% from 0.833 to 0.914 since 2018. The population growth rate across the Balkans increased by 6.9% from 0.939 before 2018 to 1.005 since 2018. This indicates that the Egyptian Vulture population has remained stable for the past 5 years (2018–2022), but at a population size that is only half (105 adult territorial birds in 2022) than at the beginning of the time series (204 in 2006). We caution that ongoing management along the flyway and reinforcement are required to ensure that the Egyptian Vulture population on the Balkans can recover, but we show that flyway-scale collaboration of direct conservation actions can have lasting benefits for migratory species.

Introduction

Many threatened species require active conservation management to prevent human-caused extinction (Bolam *et al*., 2023). Most conservation management actions are supported by relatively short project cycles, and demonstrating whether the management has achieved its objectives can be a difficult task within a given funding cycle (Butchart, Stattersfield, &

Collar, 2006; Baylis *et al.*, 2016; Bolam *et al.*, 2021). Reporting the outcome of any conservation project is however important to adjust and improve management regardless of whether a project was successful (Catalano *et al.*, 2019; Dickson *et al.*, 2023).

One of the key conditions to evaluate management success is the establishment of quantitative and objective indicators such as population size or demographic rates, and a monitoring design that is appropriate to measure these indicators (Stem *et al.*, 2005; Jones *et al.*, 2013). The LIFE Programme is one of the key financial tools in the European Union that facilitates large-scale conservation management to improve the status of species and sites of continental importance (Badia-Boher *et al.*, 2019). Some of the projects funded under this programme aim at halting or reversing the loss of biodiversity in Europe's special protected areas network, and are required to demonstrate the impact of the project via several indicators.

Projects funded under the LIFE programme generally focus on one specific geographic area, but many animals spend time in multiple realms (Giakoumi *et al.*, 2019; Marcacci *et al.*, 2023). Especially migratory species, many of which have been declining in Europe (Berthold *et al.*, 1998; Sanderson *et al.*, 2006; Vickery *et al.*, 2014), can be exposed to threats across different continents, and conservation gains in one country may be negated by persisting threats elsewhere (Dhanjal-Adams *et al.*, 2017; Guilherme *et al.*, 2023; Vickery *et al.*, 2023). Evaluating the effectiveness of regional conservation projects when the target species is migratory and exposed to threats outside the focal project area can be complicated and requires strong international collaboration (Marcacci *et al.*, 2023).

One emblematic species that is threatened by persisting threats along its entire flyway is the Egyptian Vulture, *Neophron percnopterus*, the smallest of the four European vulture species and the only one that performs regular long-distance migrations (Oppel *et al.*, 2022a). A particularly vulnerable population is the migratory population in eastern Europe, which declined from >600 pairs in the 1980s to ~50 pairs across Bulgaria, Greece, North Macedonia and Albania in 2016 (Velevski *et al.*, 2015; Arkumarev *et al.*, 2018). This decline was likely caused by a combination of several known threats such as poisoning, electrocution and collision, direct persecution and changes in livestock farming practices (Angelov, Hashim, & Oppel, 2013; Kret *et al.*, 2018; Ntemiri *et al.*, 2018; Oppel *et al.*, 2021a). From 2012 to 2016, conservation measures were initiated to protect Egyptian Vultures on breeding grounds in the Balkans ('The Return of the Neophron' project – LIFE10 NAT/BG/000152). These measures included nest guarding, supplementary feeding, insulation of dangerous electricity infrastructure and removal of poison baits and carcasses using trained dogs (Kret *et al.*, 2015; Oppel *et al.*, 2016). Regional monitoring showed that breeding success and productivity in the Balkans were comparable to stable populations elsewhere (Dobrev *et al.*, 2016; Arkumarev *et al.*, 2018), but that the annual survival of birds along the flyway was insufficient for population stability (Oppel *et al.*, 2015; Oppel *et al.*, 2016).

Because the active conservation measures concentrated only on the breeding grounds and were by themselves insufficient, the LIFE programme funded a follow-up project (www.lifeneophron.eu; 'Egyptian Vulture New LIFE' project – LIFE16 NAT/BG/000874) to conserve the breeding population of a migratory species in Eastern Europe by addressing threats along its entire flyway, including work beyond European breeding areas in the Middle East and Africa. Following several years of research, the migration routes and wintering areas of Egyptian Vultures were established (Arkumarev *et al.*, 2014; Buechley *et al.*, 2018; Phipps *et al.*, 2019), which facilitated an assessment of threats operating along the species' flyway (Oppel *et al.*, 2021a). From 2017 to 2022, the existing conservation efforts on breeding grounds were therefore expanded to encompass an international alliance of 22 conservation and research organizations in 14 countries along the flyway. This alliance collaborated to reduce threats to migratory soaring birds under this ambitious LIFE-funded project aimed at securing the Balkan breeding population of Egyptian Vultures.

Here, we report on three fundamental outcomes of the long-term conservation management that gradually expanded from regional to intercontinental flyway scales, namely whether the breeding population of Egyptian Vultures in the Balkans has stabilized, and whether the survival of adult and juvenile birds has increased since long-term conservation measures were initiated. We used the long-term monitoring data of breeding territories in the Balkans in a state-space model to estimate population trend, and in a modified binomial mixture model to estimate adult survival probability (Roth & Amrhein, 2010). We further used tracking data in multi-event capture-recapture models to estimate survival of juveniles and immatures, and combined all demographic parameters to update a previous population viability analysis (Oppel *et al.*, 2021b). This population projection allowed us to assess whether the observed change in population trend could have been realized by the estimated improvement in survival probabilities.

Materials and methods

Study area and conservation measures

The flyway of the focal Egyptian Vulture population stretches from the Balkan peninsula through Türkiye and the Middle East (Syria, Lebanon, Jordan, Israel and western parts of Iraq, Saudi Arabia and Yemen) to Africa (Egypt, Eritrea, Djibouti), with wintering areas in Niger, Chad, Sudan, South Sudan and Ethiopia (Phipps *et al.*, 2019; Oppel *et al.*, 2022a). Between 2012 and 2022, we insulated >10 000 hazardous electric poles in Bulgaria, Greece, Albania, North Macedonia, Türkiye, Jordan, Ethiopia and Saudi Arabia to eliminate the electrocution risk along selected dangerous power lines; we guarded most nests in Bulgaria and Greece and provided supplementary food at several vulture restaurants (Oppel *et al.*, 2016); we reduced the availability of vulture products on markets in Niger and Nigeria by 81 and 95%, respectively; we reduced the number of killed birds per hunter in Lebanon by 30%; and we recorded 50% fewer poisoning incidents in the Balkan project areas in 2022 compared to 2018 (Dobrev *et al.*, 2023; Figure S1). In addition, a population reinforcement programme was initiated and three captive-bred young vultures were released in Bulgaria in 2016 and between 3–6 every year between 2018 and 2022 (Oppel *et al.*, 2021b; Arkumarev *et al.*, 2022).

Territory monitoring to estimate population trend and adult survival

Between 2006 and 2022, we monitored a total of 176 Egyptian Vulture territories in four countries to assess the size of the breeding population and the survival of adult territorial birds. A territory was considered occupied by a pair when courtship behaviour, display or nest building were observed (Steenhof & Newton, 2007), and occupied by a single bird if one displaying bird was recorded in the vicinity of a nest or a breeding territory. We further checked suitable neighbouring habitats and cliffs to detect possible breeding in previously unoccupied territories.

Monitoring was initiated each year in late March or early April by searching known territories, and followed by further visits in May, June, July and August to confirm in which territories birds bred and raised fledglings. During each monitoring visit we counted the number of adult birds observed, and recorded the amount of time spent by observers in the territory as an index of observation effort for a particular survey (Olea & Mateo-Tomás, 2011). We used a hierarchical state-space model to describe the population trajectory of Egyptian Vultures between 2006 and 2022 using the annual census data of breeding birds in four countries (Bulgaria, Greece, North Macedonia and Albania; Velevski *et al.*, 2015). To test for an effect of the conservation management, we included two parameters for population trend: up to 2018 prior to the implementation of flyway-scale conservation management, and following 2018. We implemented the state-space model in a Bayesian framework and present the posterior probability density of the population trend estimates. We consider the Balkan population to be 'stable' if the estimate of the most recent population trend estimate (2018–2022) included 1 (=population stability) in its 95% credible interval. Using 2017 or 2019 as a cut-off for the change in trend did not affect our conclusions.

Because only a few of the adult Egyptian Vultures were individually marked, we were unable to estimate adult survival using mark-recapture approaches used for other populations (Lieury *et al.*, 2015; Sanz-Aguilar *et al.*, 2017; Badia-Boher *et al.*, 2019). We therefore used the temporal sequence of territorial observations of 0, 1 or 2 adults per year in a modified binomial mixture modelling framework to estimate the annual survival probability of each territorial bird while accounting for imperfect detection (Roth & Amrhein, 2010; Oppel *et al.*, 2016; Oppel *et al.*, 2021b). This approach assumed that individual breeders would generally be faithful to their breeding territory with no individual replacement of live territorial adult birds (Hernández-Matías, Real, & Pradel, 2011), and that there were no sex differences in survival probability of territorial birds. We consider these assumptions realistic, because other studies of Egyptian Vultures have so far not found sex differences in survival probability (Grande *et al.*, 2009; Lieury *et al.*, 2015; Badia-Boher *et al.*, 2019). We structured our data to assess annual survival of two adults per territory, and allowed for recruitment to occur in years when an adult breeder occupying the territory in a previous year had disappeared. For each year, we recorded the cumulative total survey effort per territory and the maximum number of territorial adults observed, and considered that detection probability would vary with survey effort, as more intensive monitoring would generally result in better detection probability of birds (Olea & Mateo-Tomás, 2011).

Because adult survival requires a longer time period to stabilize and to be estimated than population trend, we tested whether annual adult survival of territorial Egyptian Vultures in the Balkans differed between 2006–2014 (prior to intensive conservation management) and 2014–2022 (when increasingly intensive actions were taken to reduce adult mortality both at regional and flyway scales). An alternative formulation with a linear temporal trend did not improve model fit. We implemented the adult survival model in a Bayesian framework and present the posterior probability density of the survival parameter estimates before and during the LIFE projects, the median and 95% credible intervals, and the proportion of samples in which the survival probability during intensive conservation management was higher than prior to management. We used mostly uninformative priors for this analysis, except for annual survival probability, for which we specified a prior between 0.5 and 1 because annual adult survival was unlikely to be <0.5 (Grande *et al.*, 2009; Lieury *et al.*, 2015; Sanz-Aguilar, De Pablo, & Donázar, 2015).

Satellite tracking to estimate juvenile survival

Project activities were not only intended for adult birds, but were also expected to reduce mortality of juvenile and immature birds. However, the survival of these birds cannot be assessed via territory monitoring. We therefore used satellite telemetry data obtained from 60 juvenile and immature birds tracked since 2010 to assess whether monthly survival probability improved since 2018 when conservation management expanded across the flyway.

Between 2010 and 2022, we equipped 60 juvenile and immature birds with satellite transmitters, of which 29 were wild chicks equipped at the age of 55–65 days, just before fledging, and 31 were captive-bred birds. The captive-bred birds were either released as juveniles via hacking ($n = 8$) or cross-fostering ($n = 4$), or released in spring of their second ($n = 13$) or third ($n = 6$) calendar year in the core breeding population in the Eastern Rhodopes in Bulgaria (Arkumarev *et al.*, 2022). We used solar-powered 45 g GPS transmitters produced by Microwave Telemetry (www.microwavetelemetry.com) or 30 g GPS-GSM transmitters produced by Ornitela (www.ornitela.com) that were fixed to the birds using Teflon ribbons either in a backpack harness (before 2019) or a leg-loop (since 2019) configuration (Anderson *et al.*, 2020). The entire transmitter equipment did not exceed 3% of the bird's body mass and was therefore unlikely to have adversely affected survival (Sergio *et al.*, 2015). The devices recorded the geographic location of the bird several times daily over a period of up to 10 years. When a tag indicated the mortality of a bird (Sergio *et al.*, 2019), a field team searched for the carcass in the area of the last recorded location to establish the fate of the bird where feasible.

To estimate monthly survival probability of satellite-tagged vultures we used a multi-event capture-recapture model (Genovart, Pradel, & Oro, 2012; Kéry & Schaub, 2012; Zúñiga *et al.*, 2017) that included four observable events (functional tags on a moving animal; functional tags that were not moving indicating potential death; bird carcass recovered or other confirmed death; and no transmissions received), as well as three true states (alive with functioning transmitter, alive without functioning transmitter, dead). The probability of an animal to be in any of the three latent true states given that it was observed in one of the four observation events was modelled based on three contributing probabilities: the probability to receive data from an animal; the probability for a tag to fail; and the probability to find a dead animal once it had died (for more details see Oppel *et al.*, 2015; Buechley *et al.*, 2021). We estimated the probability to survive from one month to the next based on the age of the bird (in months), whether the bird migrated in a given month (defined as a cumulative travel distance of >4000 km or a latitudinal or longitudinal displacement of >5 degrees over 1 month; Buechley *et al.*, 2021), whether the bird was wild or captive-bred (Efrat *et al.*, 2022), and the longitude of origin or release for birds during their first autumn, when southbound migration for birds from the western Balkans has a greater probability to include a potentially lethal crossing of the Mediterranean Sea (Oppel *et al.*, 2015; Agostini *et al.*, 2023). We also included a parameter that assumed that survival differed between the time periods before the geographic expansion of conservation management (2010–2017), and under the flyway-scale management (2018–2022) – if this parameter was different from 0 it would provide evidence that survival was indeed different between those two time periods. We implemented the known-fate survival model in a Bayesian framework and present the median estimate for the flyway-scale management parameter on monthly survival, and the median monthly survival estimates (and 95% credible intervals) for juveniles over their first year of life for the period before 2018 and after 2018. We also present projected annual survival probabilities calculated as the product of the 12 monthly survival probabilities over the first year to facilitate comparisons with other studies. Because juvenile survival depended on longitude, we present those annual survival estimates for the Eastern Rhodopes (longitude 25.5°E), from where most of our recent data were acquired. We used mostly uninformative priors for this analysis, except for monthly survival probability, for which we specified a prior between 0.9 and 1 because a monthly survival probability <0.9 would result in annual survival probabilities lower than what has been recorded for juvenile Egyptian Vultures elsewhere (Grande *et al.*, 2009; Lieury *et al.*, 2015; Sanz-Aguilar, De Pablo, & Donázar, 2015).

Population viability analysis

To assess whether the estimated changes in demographic parameters could have resulted in the observed change in population trend, we used an existing population matrix model to simulate future population growth rates with survival estimates obtained in our analyses described above for two scenarios: with and without intensive conservation management. We used annual juvenile survival estimates for birds from the geographical midpoint of the population (longitude 24.3°E) to avoid biasing the estimated growth rate for the population towards the Eastern Rhodopes, and present the estimated population growth rates with and without intensive conservation management. More information on the structure and assumptions of the population model are available elsewhere (Oppel, 2020; Oppel *et al.*, 2021b).

We fitted all four models (population trend, adult survival, juvenile survival, population model) in JAGS (Plummer 2012) called from R 4.1.3 (R Core Team, 2023) via the package 'runjags' (Denwood, 2016), with an appropriate number of iterations for each model to achieve mixing and convergence. We tested for convergence using the Gelman-Rubin diagnostic (Brooks & Gelman, 1998) and confirmed that R-hat was <1.01 for all parameters. We implemented posterior predictive checks to assess the goodness-of-fit for the population trend and adult survival models (Gelman, Meng, & Stern, 1996; Conn *et al.*, 2018; Schaub & Kéry, 2021), and present the Bayesian *P*-values as the proportion of replicated data that were smaller than the observed data. Code and data to replicate these analyses are available online (Oppel, 2023).

Results

Population trend

From 2006 to 2022, we monitored the occupancy of 176 Egyptian Vulture territories in four countries during 4585 territory surveys on 1031 unique days. The number of territorial adult birds decreased from 204 in 2006 to a stable value around 100 (range: 99–105) between 2018 and 2022 (Fig. 1a). Our trend model indicated that the population growth rate between 2006 and 2018 was negative (mean: 0.940, 95% credible interval: 0.909–0.971), but subsequently increased by 6.9% to 1.005 (0.936–1.08; Fig. 1b). There was no evidence for a lack of fit ($P = 0.53$).

Adult and juvenile survival

To estimate annual survival probability of territorial adult birds, we used the same territory survey data as for estimating population trend, but only from 89 breeding territories that were surveyed several times every year in all years between 2006 and 2022. Annual survival probability

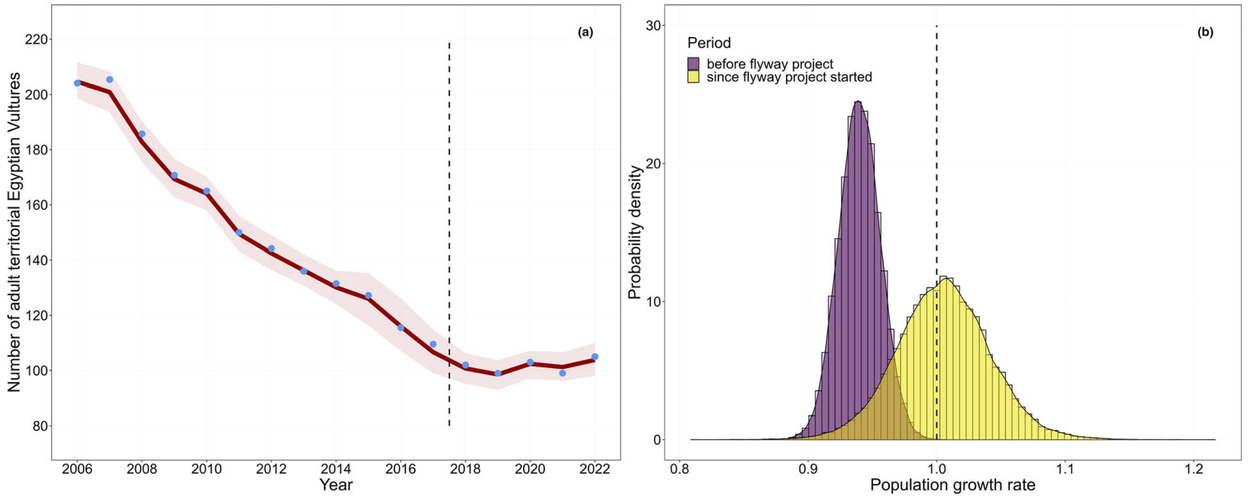

Figure 1 Population trend of the Egyptian Vulture breeding population in four countries (Albania, Bulgaria, Greece, North Macedonia) of the Balkan Peninsula from 2006 to 2022. (a) estimated number of adult territorial birds with 95% credible intervals, and the start time of flyway-scale conservation management as dashed vertical line; (b) posterior probability density for the population growth rate for the time period before flyway-scale conservation management (up to 2018, purple) and since conservation management was expanded across the flyway (since 2018, yellow) estimated through a state-space model based on territory observations.

increased marginally from a mean of 0.935 (95% credible interval: 0.915–0.957) between 2006 and 2014 to a mean of 0.955 (0.939–0.971) since 2014 when first conservation measures came into effect (Fig. 2), and there was no evidence for a lack of fit (P = 0.57). The mean difference was 1.94% (95% credible interval: −0.82% to 4.85%), with 92% of posterior samples indicating a higher survival once conservation measures had come into effect (Fig. 2).

Of the 60 tracked juvenile and immature vultures, 14 were still alive at the time of analysis (February 2023), while 42 had died, one bird was recaptured and retained in captivity, and the fate of three birds was unknown. Of the 42 birds with confirmed mortality, 20 (48%) likely died from natural causes, while 9 (21%) suffered human-caused mortality (electrocution, persecution), and the cause of death for 13 birds (31%) remained unknown. The average monthly survival probability of wild juvenile Egyptian Vultures during their first year increased by 9.7% from 0.833 to 0.914 (Fig. 3) due to the effect of the LIFE-project parameter (median estimate: 0.766, 95% credible interval: −0.087 to 1.632, Figure S2). The average monthly survival probability for captive-raised birds during their first year after release was marginally lower than for wild birds of the same age, but increased by 9.8% from 0.817 to 0.898. The annual survival probability of wild juvenile Egyptian Vultures from the Eastern Rhodopes during their first year of life therefore increased from 0.377 (0.186–0.592) to 0.615 (0.344–0.826) since 2018. For captive-raised birds released in the Eastern Rhodopes, the model predicted an increase in annual survival from 0.166 (0.018–0.451) to 0.394 (0.236–0.559).

Projecting the future population trend using a population model indicated that with the survival estimates from the period of intensive conservation the future population growth rate was 1.005 (0.964–1.07) compared to 0.961 (0.937–0.986) with survival estimates before conservation management (Figure S3). This mathematical projection based on the estimated increase in survival is close to the observed change in population growth rate (Fig. 1) and confirms that the improvement in survival may have been sufficient to result in the observed change in population growth rate of the Balkan population.

Discussion

Population changes in long-lived animals with delayed maturity may take decades, and demonstrating the benefit of any conservation management is therefore extremely challenging (Badia-Boher *et al.*, 2019). Our data show that the Egyptian Vulture population in the Balkans has stabilized at around 100 territorial adult birds since 2018. We also show that the survival of both adults and juvenile birds appears to have increased since conservation measures have been implemented, which constitutes a major success for this population given that low survival probability has been the key limitation to a stable population growth rate over the past decades (Oppel *et al.*, 2021b). However, the intensity of management increased gradually in both scale and scope, and multiple management actions were carried out in several countries simultaneously. Because no counterfactual population exists, we are not able to infer a causal relationship between any given management and the stabilization of the population.

Annual adult survival probability is a key demographic parameter that determines the population trajectory of many long-lived animals (Saether & Bakke, 2000). In a previous assessment we estimated that a 6% improvement in survival would be necessary to achieve population stability (Oppel *et al.*, 2021b), but the improvement we estimate here for adults (Fig. 2) appears to be below this threshold, while for young

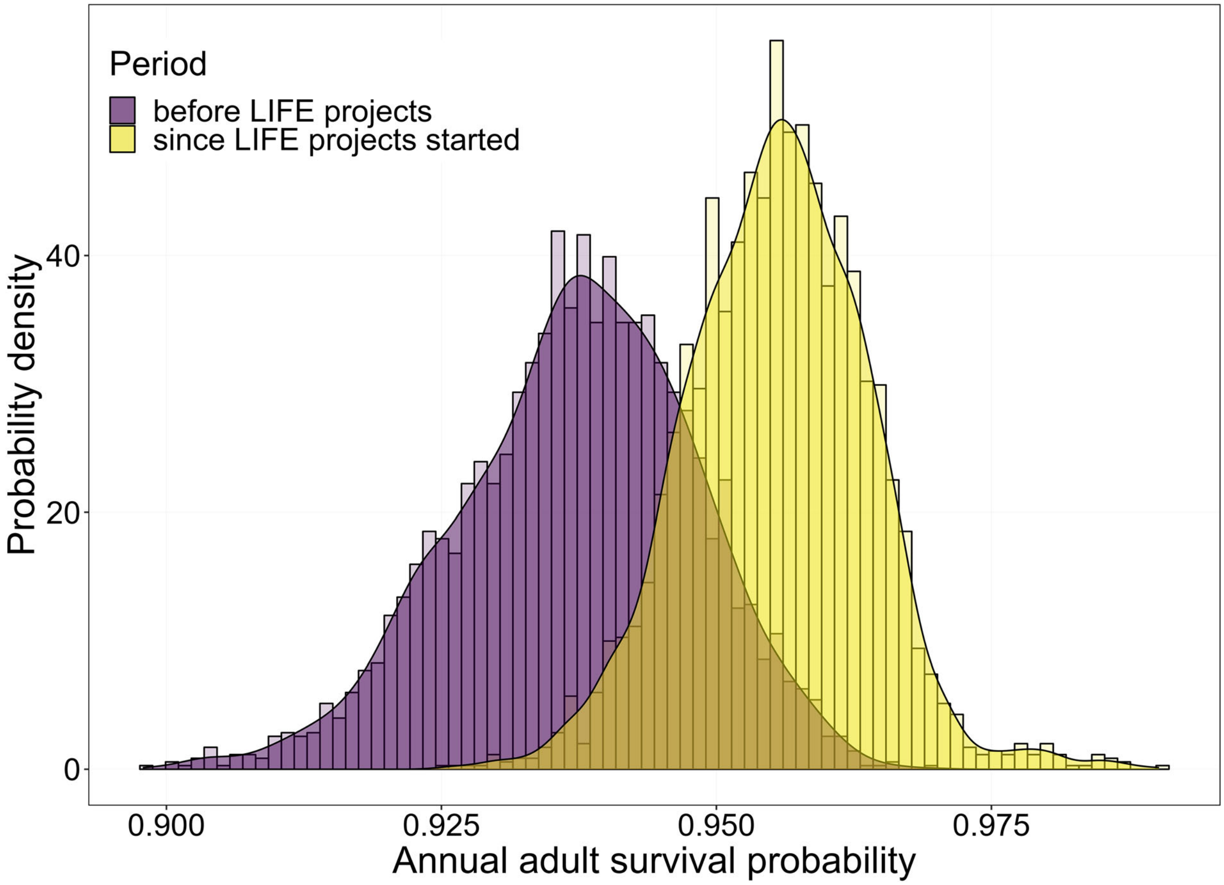

Figure 2 Posterior probability density for the apparent annual survival probability of adult territorial Egyptian Vultures in the Balkan Peninsula before intensive conservation management started (up to 2014, purple) and since intensive conservation management actions were fully implemented on breeding grounds (since 2014, yellow).

birds it was slightly higher. However, adult survival is difficult to estimate in long-lived species and will require future monitoring to increase precision of the estimates and certainty in the effect of conservation management (Lieury *et al.*, 2017; Badia-Boher *et al.*, 2019). Although our estimates are surrounded by considerable uncertainty, the sensitivity of population growth rate to adult survival is very high in long-lived animals (Saether & Bakke, 2000). Our population projection indicates that even the small improvement that we estimated would have been sufficient to stabilize the population trend (Figure S3), but insufficient for a faster recovery of the species (Oppel *et al.*, 2021b). In addition, our estimates of adult survival for Egyptian Vultures in the Balkans with intensive conservation management are similar to the survival probability of adult birds from stable populations in Spain (Sanz-Aguilar, De Pablo, & Donázar, 2015; Badia-Boher *et al.*, 2019; Buechley *et al.*, 2021) and France (Lieury *et al.*, 2015), and we therefore conclude that the population could gradually recover if those demographic rates can be maintained.

Climatic changes can have complex effects on different demographic parameters of raptors (Wichmann *et al.*, 2005; Herfindal *et al.*, 2015; Martínez-Ruiz *et al.*, 2023), including effects on survival (Jonker, Chakarov, & Krüger, 2014; Millon *et al.*, 2019). We cannot exclude that our moderate increase in survival probability may have been caused by certain weather conditions on either breeding or overwintering grounds. However, there are no obvious anomalies in African rainfall since 2006 that could easily explain the pattern we found in our data (Biasutti, 2019; Wainwright *et al.*, 2021), and we therefore remain cautiously optimistic that conservation management may have contributed to the moderate increase in survival that we detected.

The survival of juvenile Egyptian Vultures generally increases with age (Grande *et al.*, 2009; Buechley *et al.*, 2021; Efrat *et al.*, 2022), and the first southward migration for juveniles from the Balkan population poses a particular mortality risk (Oppel *et al.*, 2015). During the conservation management since 2018, we not only improved conditions along the flyway but also modified the way in which captive-raised birds were released into the wild to limit the mortality on the first southward migration (Arkumarev *et al.*, 2022; Efrat *et al.*, 2022). During the project, three different release methods were employed: ‘hacking’ (where captive-bred juveniles were released into the wild at a natural age of fledging in August), ‘cross-fostering’ (where captive-bred juveniles were inserted into a wild nest and

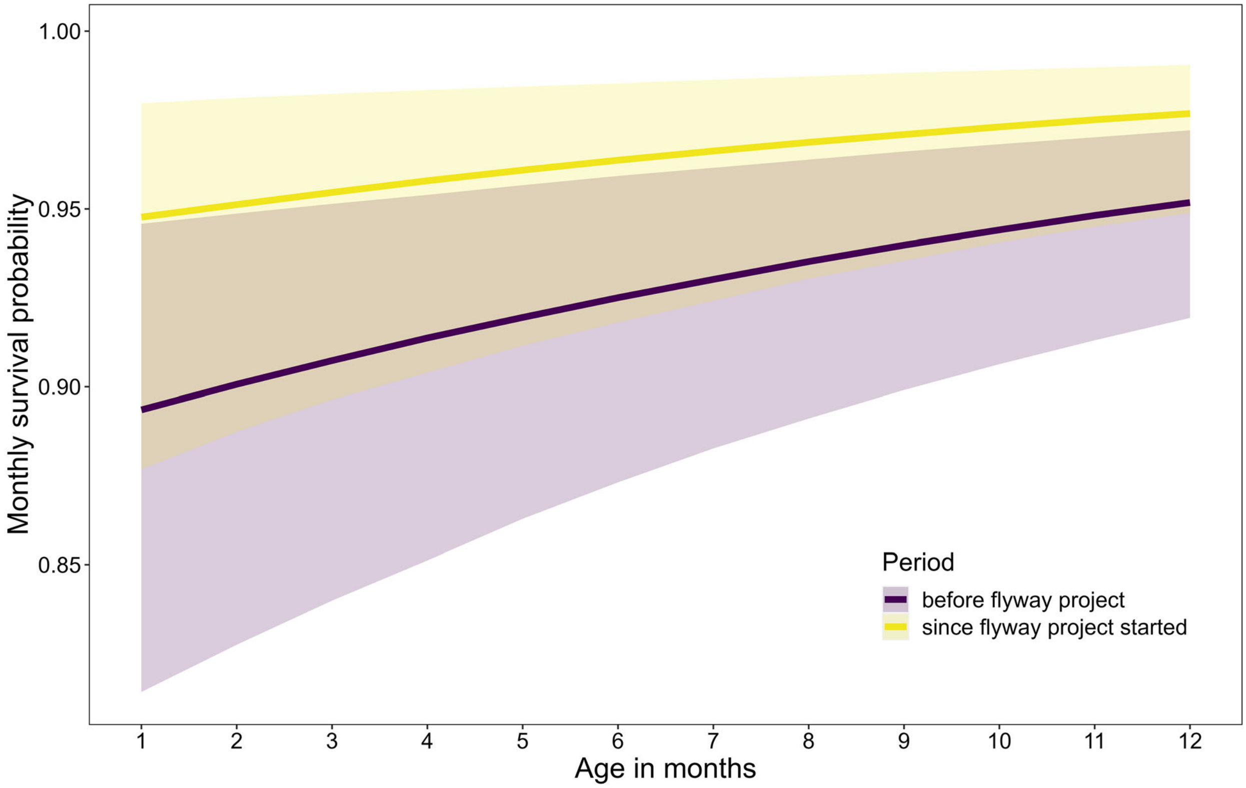

Figure 3 Estimates (mean and 95% credible interval) of the monthly survival probability of wild juvenile Egyptian Vultures tracked with GPS transmitters from the eastern Rhodopes (Bulgaria) during their first year based on a known-fate model and shown for periods before (2010–2018, purple) and since conservation management was expanded across the flyway (2018–2022, yellow).

fledged naturally) and 'delayed release' (where juveniles were retained in captivity until May of the following year, and were therefore released at an older age and with more preparation time in the wild prior to their first migration). Although we controlled for the origin of the birds in our analysis, our findings showing an improvement in juvenile survival probability may be a consequence of both management along the flyway and differences in the numbers and release strategies of captive-bred birds in later years. Since 2019, we released young birds primarily with the most effective 'delayed-release' strategy (Efrat *et al.*, 2022) in the Eastern Balkans, from where migration is less convoluted (Oppel *et al.*, 2015). Nonetheless, we estimated a 9% increase in monthly survival even in wild juveniles after analytically accounting for their longitude of origin, indicating that the improvement in juvenile survival was not solely due to the selection and refinement of the release strategy or the tagging location (Arkumarev *et al.*, 2022).

Despite the improvements in survival and the apparently stable breeding population in the Balkans, the Egyptian Vulture population cannot yet be considered as secure or in a favourable conservation status (BirdLife International, 2021). At present, ongoing management includes supplementary feeding and nest guarding, reduces poisoning and electrocution, provides reinforcement with captive-reared juveniles and increases the public profile of Egyptian Vultures through many outreach activities. All these ongoing activities likely benefit the Balkan population, and it is unknown whether the population would be stable without these diverse management activities. In addition, many threats remain on breeding grounds and along the flyway (Shobrak *et al.*, 2020; Oppel *et al.*, 2021a, 2022b): in the final project year alone, four individually marked birds from this project were killed through persecution in Bulgaria, electrocution in Türkiye, and suspected poisoning in Chad. We therefore caution that the success of the current conservation work depends on ongoing management and cannot be expected to persist if funding for this management does not continue (Drenske *et al.*, 2023). The mid-term review of the Egyptian Vulture Flyway Action Plan (Nikolov *et al.*, 2016) demonstrated that the progress of the action plan implementation was much higher in countries associated with LIFE-programme funding compared to other range states where funding or capacity was insufficient to implement conservation actions.

Wide-ranging migratory species that cross many countries and ecosystems during their regular migrations often suffer from the 'death by a thousand cuts' syndrome, where no single threat in a single location is solely responsible for the decline of a population (Runge *et al.*, 2014; Oppel *et al.*, 2021a; Vickery *et al.*, 2023). This poses a challenge for conservation, as many activities along an entire flyway are often necessary to make the incremental improvements that will collectively lead to population stabilization (Guilherme *et al*., 2023; Marcacci *et al*., 2023). Our work shows that with collective and coordinated conservation management along a flyway it is possible to reverse the fortunes of a long-distance migratory species, but it is not possible for us to identify the key activity that resulted in population change. All activities that reduced mortality through poisoning, persecution, collision and electrocution, as well as the activities to reinforce the population on breeding grounds will have contributed an unknown amount and are therefore important to maintain or expand in the future. Another important conservation management with less tangible benefits is the raising of public awareness of biodiversity loss and threats to biodiversity. During our project several outreach activities reached >2 million people, ranging from international officials to schoolchildren and rural livestock herders. Although we consider such activities essential to ultimately garner political support for conservation (Montana & Mlambo, 2019; Buxton *et al*., 2021), the effect of these activities on the status of populations is impossible to quantify.

Despite the difficulty to quantify the contribution of each conservation action, we encourage similar flyway initiatives to conserve other globally threatened migratory species such as shorebirds (Szabo *et al*., 2016; Pain *et al*., 2018; Chan *et al*., 2019; Donald *et al*., 2021; Smith *et al*., 2023), raptors (McClure *et al*., 2018; Panuccio, Mellone, & Agostini, 2021; Shobrak *et al*., 2022), and many seabirds (Dias *et al*., 2019; Beal *et al*., 2021; Clark *et al*., 2023). Another globally threatened migratory species, the Northern Bald Ibis *Geronticus eremita*, has benefitted from a similar approach of concerted reinforcement and conservation management along the flyway, albeit on a smaller geographic scale (Fritz, Unsöld, & Völkl, 2019; Fritz, 2021). Although this population still suffers from high mortality due to persecution and electrocution, and is not yet self-sustainable (Drenske *et al*., 2023), this project confirms the utility and feasibility of conservation projects at flyway scales. The LIFE programme permits main beneficiaries within the European Union to act as coordinators and use European funds to address and mitigate threats to European breeding populations of priority species along a species' flyway, and the LIFE programme was critical for both the Egyptian Vulture and Northern Bald Ibis conservation management. This programme is therefore a suitable financial instrument to initiate flyway-scale conservation initiatives (Giakoumi *et al*., 2019; Hermoso *et al*., 2022), and similar funding bodies are required for other major flyways around the world.

In summary, we conclude that the intensive conservation management along the flyway has likely benefitted the Egyptian Vulture population in the Balkans. We recommend that the existing management is maintained and expanded to reduce human-caused mortality further, particularly through activities that reduce poisoning, persecution and the electrocution of birds in all countries along the entire flyway (Oppel *et al*., 2021a). On breeding grounds, the maintenance of vulture feeding areas that facilitate pre-migratory gatherings and allow juveniles to associate with adult birds during the preparation for autumn migration will be important, and we encourage ongoing nest guarding and monitoring to be able to quantify further effects of the conservation work in the future. Continued involvement of the governments of the countries along the flyway is a necessary precondition for the persistence of positive population effects after funded project activities. Similar initiatives focussing on different species and populations are urgently needed along the major migration flyways of the world to safeguard the phenomenon of migratory species (Marcacci *et al*., 2023).

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Author contributions

SO, VD, VS, AB, VA, SS and SCN conceived the ideas and designed methodology; VS, AB, VA, EK, VD, DD, PK, TS, MV, NP, TB, MT, IK and SCN collected the data; SO analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

All data and code to replicate the analyses can be downloaded from 10.5281/zenodo.7728232 (Oppel, 2023).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Locations where conservation and monitoring activities were carried out during the lifetime of the LIFE project 'Egyptian Vulture New LIFE' (LIFE16 NAT/BG/000874, www.LifeNeophron.eu). All data used in this paper were collected during the breeding season in the Balkans (shown in red).

Figure S2. Parameter estimates (mean and 95% credible intervals on logit scale) of the factors affecting monthly survival probability of juvenile Egyptian Vultures based on a known-fate model. 'LIFE' represents the parameter distinguishing between the before flyway-scale management period (2010–2018), 'migration' reflects whether a bird migrated in a given month (=travelled >4000 km or moved >5 degree latitude or longitude), 'origin' denotes whether birds came from captive origin, and 'longitude' is the parameter that adjusts survival during the first autumn in the wild based on the longitude of origin (for wild) or release (for captive) birds.

Figure S3. Future population projection of the Egyptian Vulture population in the Balkans using a simple population matrix model and survival estimates from either with intensive conservation management (purple) or from before management (yellow). Please note that the upper credible limit for years beyond 2040 is truncated at 400 individuals to improve the readability of the plot.

Data S1. Supporting information.