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RESEARCH ARTICLE

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Population reinforcement and demographic changes needed to stabilise the population of a migratory vulture

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Abstract

1. One approach to stabilise small and declining populations is to breed individuals in captivity and release them into the wild to reinforce existing populations while working to reduce threats. Population reinforcement programmes require long-term commitments to be successful and can divert limited resources from other conservation measures. A rigorous evaluation whether reinforcement can stabilise a population is therefore essential to justify investments.
2. Many migratory species incur high mortality during their first migration, and releasing captive-bred birds at an older age may therefore benefit reinforcement programmes for migratory birds. We examine whether a small and declining population of a long-distance migratory raptor—the Egyptian Vulture *Neophron percnopterus*—can be stabilised using population reinforcement that reduces mortality during the first migration. We used an integrated population model to evaluate realistic reinforcement and survival improvement scenarios to estimate how many captive-bred birds would need to be released to stabilise the population.
3. Survival probability of wild juveniles during their first year (0.296; 95% CI 0.234–0.384) was too low for a stable population (population growth rate 0.949; 95% CI 0.940–0.956), but captive-bred juveniles released in their second calendar year had improved survival (0.566; 95% CI 0.265–0.862) during their first year in the wild.
4. Reinforcement of 15 birds per year for 30 years was insufficient to achieve a neutral or positive population growth rate. However, reinforcement reduced the probability of extinction by 2049 from 48% without reinforcement to <1% if 12 or more birds were released every year for 30 years. A 6% increase in annual survival probability would likely lead to a stable population without any reinforcement.
5. *Synthesis and applications*. Although releasing captive-bred birds can reduce high juvenile mortality during first migration and assist in postponing local extinction,

further improvements of survival in the wild are required to safeguard a migratory population where threats in the wild will persist for decades despite management.

KEYWORDS

Balkan peninsula, Bayesian population analysis, captive breeding, captive release, extinction, population viability analysis, reintroduction, translocation

1 | INTRODUCTION

Ongoing increases in the number of species threatened with extinction require management strategies to halt or reverse population declines. One approach to rescue or stabilise small and declining populations is to breed threatened animals in captivity and release them into the wild to reinforce existing populations (Seddon et al., 2007, 2014). Reinforcement has been used successfully to improve the conservation status of several populations, but reinforcement programmes require long-term commitments to be successful (Brichieri-Colombi & Moehrenschlager, 2016; Bubac et al., 2019). Because the financial costs for such long-term programmes can be considerable, investing in a reinforcement programme may divert funding from other conservation measures, and should therefore be scientifically justified with population projections (Balmford et al., 1995; Dolman et al., 2015).

Population reinforcements have primarily focused on sedentary species after the threats to them have been eliminated in their native range. Many migratory species are also declining, often because they are exposed to a broad range of different threats across several continents (Kirby et al., 2008; Vickery et al., 2014). Because eliminating sufficient threats along an entire flyway may take longer than a threatened migratory population can survive, the local reinforcement of a breeding population may offer conservation managers an opportunity to postpone the extinction of a population until threats have been sufficiently reduced along the flyway (Bretagnolle & Inchausti, 2005; Pain et al., 2018). Several long-lived bird species have been assisted by conservation translocations following human-induced population collapses, and population assessments have guided the number of captive-released birds that were needed to stabilise populations (Bretagnolle & Inchausti, 2005; Evans et al., 1999; Schaub et al., 2009). However, so far such assessments have not considered long-distance migratory species that are exposed to threats across a large geographic area (but see Villers et al., 2010). Many migratory species incur high mortality of juvenile birds during their first migration (McIntyre et al., 2006; Rotics et al., 2016; Sergio et al., 2014), a problem that could potentially be reduced by releasing captive-bred birds at an older age in a different season (Campbell-Thompson et al., 2012; Hameau & Millon, 2019; Murn & Hunt, 2008). To decide whether population reinforcement would be a sensible investment for a long-distance migrant, wildlife managers need to understand how extensive the captive-breeding efforts need to be and what other improvements to demographic parameters must occur (Canessa et al., 2014; Helmstedt & Possingham, 2017).

Here we examine whether the declining population of a globally threatened migratory bird can be stabilised by the release of captive-bred birds on breeding grounds and other conservation measures along the flyway. The Egyptian Vulture *Neophron percnopterus* is the only long-distance migratory vulture in the Palaearctic, and exposed to a variety of threats that occur along the flyway (Angelov et al., 2013; Brochet et al., 2016; Ogada et al., 2015). Partly because of these threats, the Balkan population in eastern Europe is declining and becoming fragmented and prone to stochastic extinction (Velevski et al., 2015). Because conservation management on breeding grounds has so far not stabilised this population (Arkumarev et al., 2018; Oppel et al., 2016), the potential reinforcement of the population may buy managers time to reduce the various threats that will result in demographic improvements sufficient for population recovery (Badia-Boher et al., 2019; Safford et al., 2019; Sanz-Aguilar, Sánchez-Zapata, et al., 2015). One particular aspect of this population is the high juvenile mortality during the first autumn migration (Oppel et al., 2015), which could potentially be reduced by releasing captive-bred birds in a different season at an older age (Campbell-Thompson et al., 2012; Hameau & Millon, 2019; Murn & Hunt, 2008). However, so far it is unclear whether this reinforcement alone would be sufficient to stabilise a migratory population.

We used an integrated population model based on territory monitoring and satellite telemetry data to estimate demographic parameters and simulate future trajectories of the Egyptian Vulture population under different scenarios including the release of captive-bred birds, and the improvement of survival probability through various conservation actions. Integrated population models have become a standard tool for the evaluation of population trajectories (Plard et al., 2019; Saunders et al., 2018), but they frequently rely on extensive mark–recapture datasets to estimate adult survival. Estimating adult survival with individually marked birds can be logistically or financially prohibitive (Lieury et al., 2017). We used territory monitoring data to estimate adult survival (Hernández-Matías et al., 2011), which allowed us to use an integrated population model without long-term mark–recapture data to address two key questions of management interest.

We used this modelling framework specifically to assess (a) whether the release of captive-bred birds alone could stabilise the Balkan population; and (b) by how much survival probability would have to improve to stabilise the population with or without supplementary releases of captive-bred birds. This work provides a critical assessment of the feasibility and potential success of a reinforcement programme to stabilise a declining population of a globally threatened migratory species.

2 | MATERIALS AND METHODS

2.1 | Study area and conservation measures

The Balkan peninsula in eastern Europe harbours an Egyptian Vulture population that declined from >600 pairs in the 1980s to ~50 pairs across Bulgaria, Greece, North Macedonia and Albania in 2020 (Arkumarev et al., 2018; Velevski et al., 2015). This decline has likely been caused by a combination of several known threats such as poisoning, electrocution and collision, direct persecution and changes in livestock farming practices (Angelov et al., 2013; Kret et al., 2018; Ntemiri et al., 2018). Since 2009, active conservation measures have been performed to protect Egyptian Vultures on breeding grounds in the Balkans, such as supplementary feeding, insulation of dangerous electricity infrastructure and removal of poison baits and carcasses using trained dogs (Kret et al., 2015; Skartsi et al., 2010). Because these measures have so far not been sufficient to revert the population decline (Arkumarev et al., 2018; Oppel et al., 2016; Velevski et al., 2015), conservation efforts were expanded along the migratory flyway of Egyptian Vultures in 2017 to reduce threats in important migration (Buechley et al., 2018) and wintering areas (Arkumarev et al., 2014) by insulating dangerous electricity infrastructure, increasing law enforcement and prosecution of illegal persecution, and campaigns to reduce the use of poison against wildlife (www.lifeneophron.eu). The flyway of the Balkan Egyptian Vulture population stretches from the Balkan peninsula through Turkey 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. This flyway therefore encompasses >20 countries with diverse political stability and economic wealth, and reducing threats at a sufficient geographic scale for wide-ranging migratory birds may take decades. Population reinforcement may therefore be a useful temporary solution to reduce extinction probability until threats can be reduced. The Green Balkans Wildlife Breeding Centre in Bulgaria maintains adult breeding birds in collaboration with the European Association of Zoos and Aquaria European Endangered Species Programme (EAZA-EEP). Within this network, Egyptian Vultures that are acquired from zoos or other captive facilities, or rescued and rehabilitated from the wild, can be reared to facilitate a reinforcement programme of the Egyptian Vulture population in the Balkans. This facility and collaborating institutions within the EAZA-EEP network could potentially supply up to 15 captive-bred birds every year, which are released at the age of 11 months in their second calendar year to improve their survival prospects in the wild (Campbell-Thompson et al., 2012; Murn & Hunt, 2008). Because Egyptian Vultures suffer high mortality during their first migration in autumn (Oppel et al., 2015), the release of birds at an older age and in a different season can potentially reduce the demographic impact of the first migration (Hameau & Millon, 2019).

2.2 | Territory monitoring for population size, adult survival and fecundity

Between 2006 and 2019, we monitored a total of 145 Egyptian Vulture territories to assess the size of the breeding population and annual productivity (Bulgaria: 53, Greece: 40, Albania: 28, North Macedonia: 24). Of these 145 territories, 94 were monitored annually to provide population abundance data, 87 were monitored with several repeated visits per season to provide observation data to estimate adult survival, and 77 were monitored until the end of the breeding season in each year to assess reproductive output (for more details see Arkumarev et al., 2018; Saravia et al., 2019). Nests were discovered in April by searching known territories, and during these monitoring visits, we counted the number of adult birds observed, and recorded the amount of time spent by an observer in the territory as an index of observation effort for a particular survey (Olea & Mateo-Tomás, 2011). At the end of the breeding season (August), we counted the number of fledglings produced by observing dependent young being fed by adults in the vicinity of the nest.

2.3 | Satellite tracking for juvenile survival

Between 2010 and 2019, we equipped 23 wild juveniles with satellite transmitters at the age of 55–65 days just before fledging, and a further 3 birds in their second calendar year on wintering areas in Ethiopia. Although these three birds were not of Balkan origin, many Egyptian Vultures from the Balkans spend their immature life in Ethiopia (Oppel et al., 2015), and we therefore consider these birds as representative for immatures from the Balkan. In addition, we released seven captive-bred birds in their second calendar year in 2018 and 2019 with satellite transmitters in the core breeding population in the Eastern Rhodopes in Bulgaria. 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' backs using a Teflon ribbon backpack harness (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 7 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.

2.4 | Estimating demographic parameters in an integrated population model

We used an integrated population model developed by Lieury et al. (2015) for Egyptian Vultures to combine the different datasets and account for uncertainty in demographic parameters in population projections. An integrated population model provides a joint analytical framework to estimate both annual abundance data and demographic parameters simultaneously in a single model, which generally leads to more precise parameter estimates (Abadi et al., 2010; Schaub et al., 2007). Briefly, we used a hierarchical state-space model to describe the population trajectory of Egyptian Vultures between 2006 and 2019 using the annual census data of breeding birds in four countries (Bulgaria, Greece, North Macedonia and Albania; Velevski et al., 2015), which comprise >95% of the Balkan Egyptian Vulture population. Because complete census data were not available from Albania and North Macedonia in every year, we assumed that the proportion of the Balkan population breeding in these two countries (Albania 13%, North Macedonia 28%) was similar every year to link observed count data to the overall population size at the Balkan scale. By analysing the population at the Balkan scale, we also implicitly assumed that demographic parameters would be similar across the Balkans. This assumption is justifiable because the Balkan population used to be a single homogenous population until it fragmented (Velevski et al., 2015), and the data informing our demographic parameter estimates were collected in all four countries and therefore incorporated geographic variability.

The annual abundance of Egyptian Vultures depends on the productivity and survival of juveniles, immatures and adults. To estimate productivity, we used the annual number of fledglings corrected for the annual number of observed pairs with a Poisson error distribution (Lieury et al., 2015). Although fecundity may decrease at higher population size due to density-dependent effects (Carrete et al., 2006; Ferrer & Donazar, 1996), the population size of Egyptian Vultures in the Balkans was too low during our study period for such effects (Arkumarev et al., 2018; Velevski et al., 2015) and we did not incorporate density dependence in our model.

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 (Badia-Boher et al., 2019; Lieury et al., 2015; Sanz-Aguilar, De Pablo, et al., 2015). 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 (Oppel et al., 2016; Roth & Amrhein, 2010). This approach assumed that individual breeders would generally be faithful to their breeding territory with no individual replacement of live territorial adults, and that there were no sex differences in survival probability of territorial birds (Hernández-Matías et al., 2011). We consider these assumptions realistic, because in our declining population the pool of potential floaters to outcompete and replace territorial adults is very small, and other studies of Egyptian Vultures have so far not found sex differences in survival probability (Badia-Boher et al., 2019; Grande et al., 2009; Lieury et al., 2015). 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 died. 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 detectability of birds (Olea & Mateo-Tomás, 2011). To incorporate temporal variation in adult survival due to stochastic environmental influences and ongoing conservation work, we allowed two separate values for adult survival for 'good' and for 'poor' years similar to standard mixture models in survival estimation (Pledger et al., 2003). Because of the initiation of conservation measures in 2010, 'poor' years were more frequent up to 2010, and 'good' years were more frequent after 2010.

To estimate annual survival probability of satellite-tagged juveniles between fledging and four years of age, we used a multi-event capture–recapture model (Genovart et al., 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 or 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 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 died (for more details see Buechley et al., 2021; Oppel et al., 2015). 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, and whether the bird was captive bred. Annual survival was estimated by multiplying the respective monthly survival estimates over the first, second and third year of life for juveniles, accounting for the different time when the first autumn migration occurred in wild and captive-bred individuals (Buechley et al., 2021). Captive-bred birds were released in May of the year after they hatched, at an age of 11 months, and therefore performed their first migration at the age of 15–16 months rather than at the age of 4 months for wild juveniles. Because the first autumn migration incurs a major survival cost (Buechley et al., 2021; Oppel et al., 2015), the second-year survival probability for captive-bred birds included migration, while wild birds remained on African non-breeding grounds during that time period.

The population model was based on an age-structured matrix model with six different age classes, which assumed an equal sex ratio at hatching and that all adult birds (6 years and older) would attempt to reproduce every year (Lieury et al., 2015). Based on previous research, we also assumed that 2.4% of 4-year-old birds and 12.4% of 5-year-old birds would hold a territory and breed (Lieury et al., 2015). The number of birds in each age class was estimated for each year by random binomial draws with the survival probability of birds from the previous year. Although immigration can be an important driver of population dynamics in small populations (Lieury et al., 2015; Schaub & Ullrich, 2021; Soriano-Redondo et al., 2019), and has been shown for other raptors in the Balkans (Demerdzhiev et al., 2015), we did not include an immigration component in our

TABLE 1 Demographic parameter estimates of the Egyptian Vulture population in the Balkans estimated with an integrated population model based on territory monitoring and telemetry data from 2006 to 2019. Note that the annual survival during the 'first year' of captive-bred birds refers to their first year in the wild, at the age of 11–23 months due to delayed release in their second calendar year

Parameter	Median	Lower 95% credible limit	Upper 95% credible limit
Fecundity	1.005	0.914	1.109
Annual survival first year (captive bred)	0.566	0.265	0.862
Annual survival first year (wild)	0.296	0.234	0.384
Annual survival second year (wild)	0.484	0.405	0.566
Annual survival third year	0.580	0.450	0.700
Annual survival adult (good year)	0.932	0.913	0.953
Annual survival adult (poor year)	0.913	0.887	0.937
Population growth rate	0.949	0.940	0.956

population model. The Egyptian Vulture population in the Balkans is small and fragmented (Velevski et al., 2015), and >500 km from the nearest healthy source population that could provide a significant number of immigrants (Balaban & Yamac, 2018; Katzenberger et al., 2019). Although it is not impossible that birds from other populations might recruit into the Balkan population, the number of immigrants is likely a negligible source of the population trajectory in the Balkans.

We used a Bayesian framework for inference and parameter estimation because it provided more flexibility and allowed for the incorporation of existing information to inform prior distributions for demographic parameters (Schaub et al., 2007). Specifically, we used diffuse priors (0–1) for the poorly known survival probabilities during the first 3 years of life, but curtailed priors of annual survival probabilities of territorial individuals to values >0.75 consistent with previous studies (Badia-Boher et al., 2019; Grande et al., 2009; Lieury et al., 2015). The prior for fecundity was set to values between 0 and 2 as Egyptian Vultures generally do not raise >2 fledglings per year (Arkumarev et al., 2018). We fitted the integrated population model in JAGS (Plummer, 2012) called from R 3.5.1 (R Core Team, 2019) via the package JAGSUI (Kellner, 2016). We ran four Markov chains each with 50,000 iterations and discarded the first 10,000 iterations. We tested for convergence using the Gelman–Rubin diagnostic (Brooks & Gelman, 1998) and confirmed that R-hat was <1.01 for all parameters. We present posterior estimates of parameters with 95% credible intervals. Code and data to replicate these analyses are available online (Oppel, 2020).

2.5 | Population projections under different scenarios of reinforcement and conservation impact

To examine whether releases of captive-bred birds would result in a stable or increasing population trend, we projected the population size estimated by the integrated population model 30 years into the future while accounting for the uncertainty in demographic parameters (Kéry & Schaub, 2012; Oppel et al., 2014; Schaub & Abadi, 2011). We used the survival probabilities for each age class and the mean fecundity to project population growth into the future, and incorporated different realistic scenarios of the number of captive-bred birds released every year, and the improvements in survival that could result from conservation action. We did not simulate any management to improve productivity, as the productivity in the Balkans is similar to that in stable populations in Europe due to past and ongoing management (Arkumarev et al., 2018).

The Green Balkans Wildlife Breeding Centre in Bulgaria and collaborating institutions within the EAZA-EEP network have the plausible capacity to release up to 15 young Egyptian Vultures every year. We therefore assessed future population size assuming a total of 46 reinforcement scenarios that simulated that from 2020 onwards captive-bred birds would be released every year for a period of either 10, 20 or 30 years, with the number of released birds varying from 0 (baseline scenario) to 15 in every year when releases were simulated.

Due to ongoing efforts to remove poison baits and carcasses from breeding grounds (Kret et al., 2015; Ntemiri et al., 2018), reduce direct persecution, insulate dangerous electricity infrastructure (Badia-Boher et al., 2019) and improve survival of immature birds through food provisioning (Oppel et al., 2016), we simulated scenarios in which annual survival probability of all age classes of Egyptian Vultures increased either not at all (baseline scenario) or by 2% (i.e. a change from Φ to $1.02 \times \Phi$), 4%, 6% or 8% compared to the average baseline from 2006 to 2019. Birds of all age classes share the same flyway and wintering grounds (Phipps et al., 2019), and we therefore assumed that the removal of threats would equally affect all age classes. Because these survival improvements are unlikely to materialise instantaneously, we gradually increased survival over the first 10 years of the future projection until the final simulated increment had been attained.

For each scenario of reinforcement and survival improvement—including a 'do nothing' scenario of no reinforcement and no survival improvement—we projected the population 30 years into the future and calculated the future population growth rate as the geometric mean population growth rate from 2019 to 2049. We present this population growth rate to assess at which combination of reinforcement and survival improvement the population would stabilise (growth rate ≥1). We also present the probability of extinction calculated as the proportion of population simulations under each scenario where the total number of birds of breeding age was <25 in the year 2049 (Brink et al., 2020; Hilbers et al., 2016).

3 | RESULTS

3.1 | Estimation of population trend and demographic parameters

The monitored Egyptian Vulture population in the Balkans declined by 5.1% per year from 204 adult territorial birds in 2006 to 97 territorial birds in 2019, most prominently due to low survival probability of young birds (Table 1). Of the 23 satellite-tracked wild juveniles, 16 (70%) died within the first 8 months, and only one bird out of 21 (4.8%) tagged sufficiently long ago survived to the age of 5 years. Of the seven captive-bred birds released in their second calendar year, two (29%) died within the first 8 months after their release, one disappeared after 17 months, another one died after 24 months and three birds (43%) were still alive at the time of analysis (at ages of 2–3 years respectively).

The integrated population model was able to replicate the declining trend, and predicted a further decline at a mean rate of 2.5%–5% per year for the next 30 years without any reinforcements or improvements in survival (Figure 1). Based on this projection the probability of extinction in 2049 was 48% (Figure 2).

3.2 | Population projection under conservation management scenarios

Releasing up to 15 captive-bred birds every year for 30 years did not yield a median population growth rate >1 which would stabilise the population (Figure 3). However, the probability of extinction in 2049 was reduced from 48% without any reinforcement to 24% if 15 captive-bred birds were released every year for 10 years, to 4% if 15 birds were released for 20 years, and to <1% if 15 birds were released for 30 years (Figure 2). The negligible extinction risk of <1% could also be achieved if only 12 birds were released every year for 30 years. Alternatively, a 4% improvement in survival combined with the release of six birds per year for 30 years would also lead to a median population growth rate >1 (Figure 3). Our projections are surrounded by considerable uncertainty and for most scenarios the credible limits of our projected population growth rate included both increasing and declining populations.

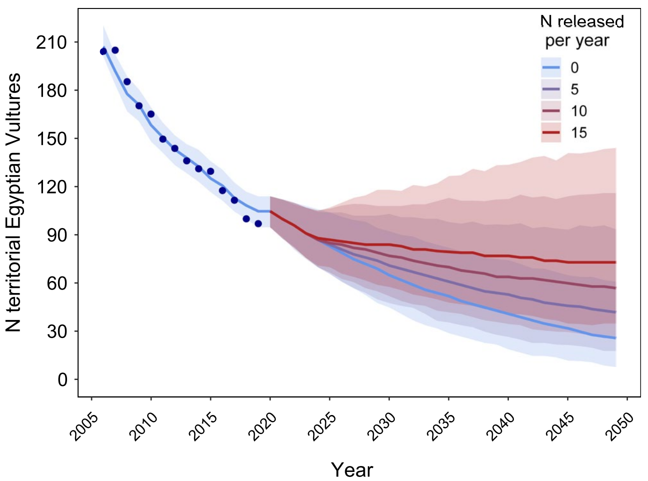

FIGURE 1 Median (and 95% credible interval) realised and projected population trend of the Egyptian Vulture population in the Balkans estimated with an integrated population model for four different scenarios of reinforcement (number of captive-bred birds released every year for the entire 30-year projection period) and assuming that no improvement in survival would occur between 2020 and 2050. Solid points represent count data from 2006 to 2019

Without any improvement in survival, no scenario of reinforcement resulted in a median population growth rate >1, but with a 6% improvement in survival no reinforcement was necessary for the population to achieve a median population growth rate >1 (Figure 3). The main benefit of population reinforcement was therefore to reduce the immediate extinction risk and the survival improvement necessary to achieve a median population growth rate >1 in the medium term: a 2% improvement in survival would be sufficient if the population could be reinforced with 15 captive-bred birds every year, or a 4% improvement in survival if the population could be reinforced with 6 captive-bred birds every year (Figure 3).

4 | DISCUSSION

Our study demonstrates that population reinforcement can reduce the risk of extinction in the medium term, but is insufficient to stabilise a population threatened by low survival probability in the wild. The Egyptian Vulture population in the Balkans is declining, and our estimates suggest that annual survival probability, especially for juveniles, is lower than in stable populations elsewhere in Europe (Badia-Boher et al., 2019; Grande et al., 2009; Lieury et al., 2015). Thus, without improving the survival of birds in the wild, any population reinforcement will only postpone eventual extinction. However, population reinforcement can slow the rate of population decline and thereby afford conservation managers more time to achieve the survival improvements in the wild that will be necessary to stabilise the population over the long term without ongoing reinforcement.

Releasing birds into the wild is generally only recommended once the threats that led to the decline or disappearance of a population have been removed (Bubac et al., 2019; IUCN, 2017). However, in cases of extreme extinction risk, population reinforcement can be considered despite persisting threats to bridge the temporal delay before conservation measures take effect (Bretagnolle & Inchausti, 2005; Seddon et al., 2012). Major anthropogenic threats to Egyptian Vultures breeding in the Balkans are poisoning from a variety of sources (Murn & Botha, 2018; Ntemiri et al., 2018; Ogada et al., 2015), electrocution at poorly designed electrical infrastructure (Angelov et al., 2013; Demerdzhiev, 2014; Serra et al., 2015) and direct persecution (Brochet et al., 2016; Buij et al., 2016). Reducing these threats across Europe, the Middle East and Africa to increase survival of a wide-ranging migratory bird species is technically possible, but will take time (Safford et al., 2019). Population reinforcement can therefore be a valid strategy to reduce extinction risk of the threatened Balkan population in the medium term. However, a recent review of conservation translocations found that the causes leading to programme failures are often different from the original causes of population decline (Bubac et al., 2019), and complicating factors that may undermine the success of a reinforcement programme must be considered (Villers et al., 2010).

A major reason for the failure of reinforcement programmes is the lack of long-term funding and management (Brichieri-Colombi & Moehrenschlager, 2016; Bubac et al., 2019). Although reinforcement can reduce extinction risk, funding for such a programme for at least 10–30 years would be necessary. Our model suggests that at least six birds need to be released every year for the next 30 years to reduce extinction probability to <10% by 2049 (Figure 2), and while the costs for such a programme are challenging to estimate, the existing facility in Bulgaria and affiliated zoos and institutions within the EAZA-EEP network would likely require several million Euros to maintain and expand their current capacity. Whether such a population reinforcement programme is cost-effective would require estimates of the financial resources necessary to improve survival in the wild (Converse et al., 2013; Dolman et al., 2015). While improving survival in the wild is the demographically more effective strategy to stabilise the population, it is logistically impossible to coarsely extrapolate the cost required to achieve the necessary survival improvement given the broad dispersion of Egyptian Vultures outside the breeding season (Buechley et al., 2018; Oppel et al., 2015; Phipps et al., 2019). Conservation investments in countries with poor governance are often ineffective, and even large financial investments along the flyway of Egyptian Vultures may only lead to negligible improvements in survival. Improving survival only on breeding grounds may be more easily achievable, but will require further investigations whether improvement in seasonal survival (rather than annual survival) will be sufficient (Buechley et al., 2021). The cost of a captive breeding facility in a European country may therefore be a more reliable investment even if reinforcement is demographically less effective.

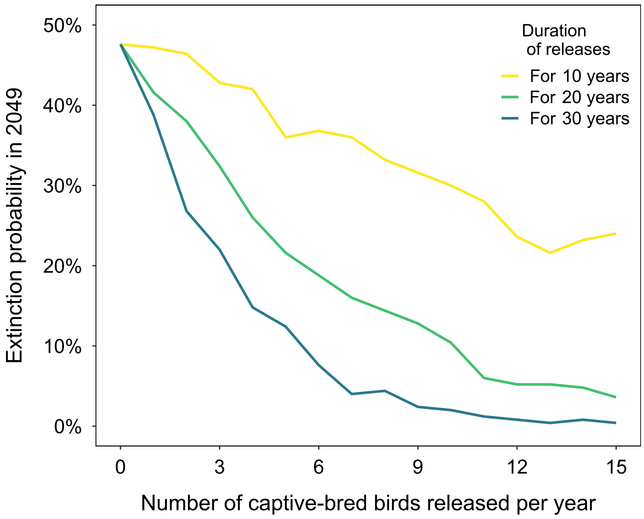

FIGURE 2 Probability of 'extinction' (defined as the proportion of 40,000 stochastic simulations with <25 adult breeders remaining) of the Egyptian Vulture population in the Balkans by 2049 estimated with an integrated population model under different scenarios of population reinforcement without any improvement in survival probability of wild birds

The cost of the reinforcement programme could potentially be reduced if the released birds were not bred in captivity but taken from the wild. Our assessment demonstrates that captive-bred birds released in their second calendar year had higher survival probability than wild juvenile birds (Table 1), while mortality in captivity occurred primarily within the first month after hatching (Hameau & Millon, 2019). Therefore, wild chicks could—in theory—be collected from nests at an age just prior to fledging, maintained in a

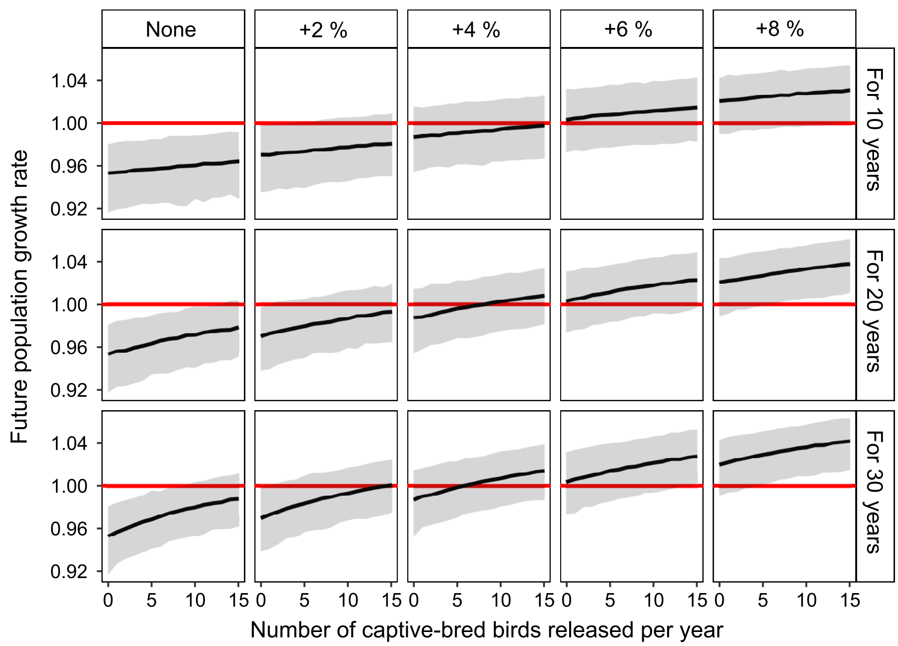

FIGURE 3 Median (and 95% credible interval) future population growth rate (2019–2049) of the Egyptian Vulture population in the Balkans estimated with an integrated population model under several scenarios of population reinforcement (0–15 captive-bred birds released each year for 10, 20 or 30 years) and increase in annual survival probability (none to 8% increase) for all age classes along the flyway. Red horizontal line indicates population stability (growth rate = 1)

captive-breeding facility for 9 months and released in their second calendar year to overcome the critical mortality 'bottleneck' of the first autumn migration at an early age (Buechley et al., 2021). Such 'head-starting' management has been successfully applied to endangered migratory animals (Burke, 2015; Pain et al., 2018). However, the costs and trade-offs of such an approach will require careful evaluation for the Balkan population of Egyptian Vultures: costs to foster wild fledglings for 9 months may not be significantly lower than breeding birds in captivity, and releasing captive-reared birds in western parts of the Balkans may incur higher mortality during the first autumn migration than our experimental data to date suggest (Buechley et al., 2021; Oppel et al., 2015). We therefore encourage a discussion among stakeholders about the logistical and socio-economic implications of any potential head-starting programme that would consider taking chicks from wild nests.

Such a discussion may be informed by additional data provided by ongoing trial releases of captive-reared birds. Captive releases of Egyptian Vultures in the Balkans started in 2016, and no data are therefore available on recruitment success and where captive-reared birds would establish to breed. Although Egyptian Vultures are generally philopatric (Elorriaga et al., 2009), it is unclear whether captive-reared birds can be used to re-populate former subpopulations in the western Balkans that may not have a sufficiently large breeding population to attract first-time breeders (Velevski et al., 2015). There is also no information yet on whether captive-bred birds would ultimately achieve the same fecundity as wild birds, but a reintroduced vulture population in the Alps achieved fecundity similar to wild conspecifics (Schaub et al., 2009). Ongoing trial releases of captive-reared birds will increase the sample size and confidence in population projections that rely on a reinforcement programme.

In summary, we caution that population reinforcement alone is unlikely to stabilise a population of a long-lived species that is threatened by low survival probabilities of birds in the wild. However, there are many logistical, political and financial hurdles to reduce all threats affecting a widely dispersing migratory species and to effectively improve its survival probability in the wild. A reinforcement programme that can release 10 birds every year may considerably reduce extinction probability and thus gain the necessary time to reduce threats and improve survival in the wild.

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CONFLICT OF INTEREST

The authors declared no conflict of interest.

AUTHORS' CONTRIBUTIONS

S.O., V.S., A.B., V.A., S.S. and S.C.N. conceived the ideas and designed methodology; V.S., A.B., V.A., E.K., V.D., D.D., P.K., T.S., M.V., N.P., T.B., M.T., I.K. and S.C.N. collected the data; S.O. analysed the data; S.O., V.S. and A.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Egyptian Vulture tracking data can be downloaded from Movebank (https://www.movebank.org/) via the Movebank ID 15869951. Data available via Zenodo http://doi.org/10.5281/zenodo.4320549 (Oppel, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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