Differential survival throughout the full annual cycle of a migratory bird presents a life-history trade-off

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Long-distance migrations are among the most physically demanding feats animals perform. Understanding the potential costs and benefits of such behaviour is a fundamental question in ecology and evolution. A hypothetical cost of migration should be outweighed by higher productivity and/or higher annual survival, but few studies on migratory species have been able to directly quantify patterns of survival throughout the full annual cycle and across the majority of a species’ range.

Here, we use telemetry data from 220 migratory Egyptian Vultures Neophron percnopterus, tracked for 3,186 bird months and across approximately 70% of the species’ global distribution, to test for differences in survival throughout the annual cycle.

We estimated monthly survival probability relative to migration and latitude using a multi-event capture–recapture model in a Bayesian framework that accounted for age, origin, subpopulation and the uncertainty of classifying fates from tracking data.

We found lower survival during migration compared to stationary periods (β= −0.816; 95% credible interval: −1.290 to −0.318) and higher survival on non-breeding grounds at southern latitudes (<25°N; β= 0.664; 0.076–1.319) compared to on breeding grounds. Survival was also higher for individuals originating from Western Europe (β= 0.664; 0.110–1.330) as compared to further east in Europe and Asia, and improved with age (β= 0.030; 0.020–0.042). Anthropogenic mortalities accounted for half of the mortalities with a known cause and occurred mainly in northern latitudes. Many juveniles drowned in the Mediterranean Sea on their first autumn migration while there were few confirmed mortalities in the Sahara Desert, indicating that migration barriers are likely species-specific.

Our study advances the understanding of important fitness trade-offs associated with long-distance migration. We conclude that there is lower survival associated with migration, but that this may be offset by higher non-breeding survival at lower latitudes. We found more human-caused mortality farther north, and suggest that increasing anthropogenic mortality could disrupt the delicate migration trade-off balance. Research to investigate further potential benefits of migration (e.g. differential productivity across latitudes) could clarify how migration evolved and how migrants may persist in a rapidly changing world.
Peer-reviewed research derived from the abstract:


Reinforcement program for the Egyptian Vulture in the Balkans


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The Egyptian Vulture (EV) Balkan population suffered a sharp decline, most notably in the last four decades. It has become extinct in most Balkan countries and it is estimated that only around 50 pairs survive today in Albania, Bulgaria, North Macedonia and Greece, mostly in small and relatively isolated clusters. An integrated population model shows that reinforcement of the population with captive-bred individuals would reduce the probability of extinction. The model and a Feasibility Study suggest that a
4% improvement in the survival of the wild individuals combined with the release of 9 birds per year for 20 years, or 6 birds per year for 30 years would lead to a stable population while releases continue. However, a 6% improvement in the survival of the wild individuals must be achieved to guarantee that the population will continue to increase when the releases stop. Trial releases of EVs started in Bulgaria in 2016 but the efforts were intensified in the period 2018-2021. Captive-bred EVs were released through three methods – delayed release, fostering and hacking. The aim was to evaluate the success of the methods and to identify the best release technique which to be applied at a larger scale in the frame of the EV reinforcement programme in the Balkans. The survival probabilities of the individuals released through the three methods as well as those of wild juveniles used as controls was calculated for the first six months after fledging/release. This period covers the post-release adaptation and the first south migration and partially the wintering period for some individuals. For this comparison only wild juvenile EVs (n=17) tagged in Bulgaria and northern Greece in the period 2012-2020 were considered. At the end of the 6-month period the survival probability of the wild juveniles was 0.59. The captive-bred individuals released through fostering (n=4) had survival probability of 0.5. The survival of the delayed released individuals (n=13) was the highest – 0.69. Individuals released through hacking had the lowest survival probability – 0.22. The wild individuals completed their first fall migration in $32 \pm 16$ days. Individuals released through hacking and fostering completed their migrations faster – $26 \pm 9$ days and $25 \pm 7$ days respectively. The delayed released individuals needed on average two times longer time to complete their first fall migration than the individuals released through fostering and hacking and the wild juveniles. In 2022 seven of the released EVs returned to Bulgaria – six released through delayed release and one released through hacking. Two individuals formed pairs with wild partners and occupied breeding territories which marked the achievement of a historic milestone of the reinforcement programme.

**First six-months survival probability of the wild juvenile Egyptian Vultures and captive-bred individuals released through fostering, hacking and delayed release methods in Bulgaria.**

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First documented case of Cainism in the Egyptian Vulture

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Brood reduction where sibling aggression is responsible for the loss of the second chick is a widespread phenomenon among raptor species. Cainism can be either obligate or facultative but the outcome is always the same. Two main hypotheses exist that try to explain the obligate sibling killing. The first one is the insurance that the second egg is the substitute if something happens to the first one, and in the second hypothesis, obligate siblicide might be a consequence of an evolutionary process favoring the raising of high-quality offspring. Despite this phenomenon being spread among many raptor species pivotal knowledge is absent for some of them and for others, there were no data that exist. Here, we present the first documented case of cainism in the Egyptian Vulture (EV). The case was documented in a wild nest with an online streaming camera in 2018. The pair laid two eggs that hatched with six days in between hatching. Nevertheless, the aggression became apparent when the younger chick is nine days old. Despite the constant provision of food to both chicks and the attempts of parents to separate both chicks on day 10 and 11 the older chick is constantly pecking the younger and express a high level of aggression. As a result on the next day the younger chick died and later on was eaten by the parents. The same events were never observed before or again in the same nest or any other EV nest in Bulgaria.
First remarks on the environmental imprinting of released captive-born young Egyptian Vultures

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In 1993 a restocking programme of the Egyptian Vulture (EV) started in Italy with the creation of a captive-breeding station in Tuscany. From 2004 to 2015 the CERM Endangered Raptors Centre released in a rocky ravine (Gravina di Laterza, Apulia region) through the hacking method 14 fledglings captive-born at the CERM or in other European centres. Before being released the birds spent 4-5 days acclimatization phase inside a natural cave closed by a net or a hack-box, directly overlooking the canyon. Later on, from 2018 to 2021, 19 more EVs captive-born at the CERM (age classes 0/2 years) were released in the framework of the LIFE Egyptian Vulture project (by the CERM and the ISPRA Italian Institute for Environmental Protection and Research) by using a nest-box installed in a semi-flat area inside a feeding site for raptors in the Murgia Materana Natural Park, in Basilicata region. It was noted that nearly all the young EVs released in the Murgia Materana Natural Park, which had spent the short acclimatization phase in a nest-box far from rocky gorges, chose as diurnal and nocturnal roosts power poles of medium-voltage power lines located in the release area, only rarely using the rock faces about 1 km far away. This habit, which was thought to be temporary, turned out to be permanent for almost all the released individuals. The power lines surrounding the release area are safe for birds and this guaranteed their safety as long as they started to make medium or large-scale movements. The use of GPS tags showed that the birds have been continuing to perch on power poles or pylons of power lines during their wanderings, during migration and wintering in Africa, even in the presence of close rocky gorges. Some individuals have been observed at sunset leaving the rocky faces where they were perched on to move for perching and rest on the poles of the closest power line. Of course, this behaviour has very adverse implications: three of the individuals which were released through this method died electrocuted and the others run the same risk. On the contrary, the young EVs released from 2004 and 2015 in the Gravina di Laterza canyon have always been observed to perch on rocky faces or trees and they have never been tracked on the power poles located in the area. Furthermore, checking the position data it has been seen that during the migration these EVs preferably rested or spent the night on natural or artificial rock walls (quarries) and trees. For example, it doesn't seem that Sara, an individual born in captivity and released in 2015 who still has the GPS device working in 2022, has ever used power poles as diurnal or nocturnal roosts. It appears that we are dealing with an environmental imprinting of the released EVs, previously unknown, which occurs in the phase immediately after the realise and strongly influences the long-term selection of their diurnal and nocturnal roosting habitat. Consequently, there is the need to perform the releases into the wild in a natural setting similar to that of the species nesting, that is, canyons. It's indeed recommended to those who manage release programmes of the EV not to install release aviaries or boxes far from rock walls, especially if there are power lines nearby and even if they are insulated for preventing birds’ electrocution. That's because the vast majority of power lines in Europe and Africa are not insulated to prevent the electrocution of birds.
Estimating the number of non-breeding individuals to assess the viability of the small Egyptian Vulture population breeding on mainland Italy

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The Egyptian Vulture (EV) is amongst the most threatened bids in Italy. After a long-lasting decline occurred in the second half of the 20th century, only 10-13 nesting pairs were estimated to breed in 2019 in two distinct areas, in Sicily and in the southern part of the Italian peninsula. Almost all Italian birds migrate towards sub-Saharan Africa, but in recent times some individuals have been observed in Sicily during winter.

In the framework of the Egyptian Vulture LIFE Project an intense monitoring programme allowed us to collect data on nesting success and the presence of non-breeding individuals on mainland Italy. We used these data to assess the viability of the extremely reduced population living in the southern part of the Italian peninsula (3-4 pairs).
Based on the number of fledged wild juveniles (n = 24) and released captive-bred individuals (n=20) in the period 2017-21, we calculated the number of immatures and sub-adults potentially occurring in southern Italy in 2022, after deducting the mortality. Annual losses of birds were estimated applying the survival probability for juvenile and adult EV calculated by Buechley et al. (2021). Through this theoretical calculation we estimated the presence in Italy of 10 non-breeding individuals, assuming that juveniles aged up 3 years remain in Africa.

We compared our result with the sightings (n = 35) of non-breeding individuals recorded during the breeding season 2022, referred to at least 2-3 distinct immatures and 7 adults/sub-adults.

Our findings suggest that natural recruitment could still maintain this small population in the next future, despite the high level of human-induced mortality of juveniles and adults. However, to avoid the extinction of the EV in southern Italy, urgent measures are needed to reduce the main threats acting in the breeding sites and along the flyway.

<table>
<thead>
<tr>
<th>Expected recruitment of the Egyptian Vulture population on mainland Italy</th>
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<tbody>
<tr>
<td><strong>Juveniles born/released in 2017-2021</strong></td>
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<tr>
<td>Wild born <strong>N 24</strong></td>
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<tr>
<td>Captive-bred juveniles <strong>N 20</strong></td>
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<td><strong>Non-breeding individuals expected in 2022</strong></td>
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<tr>
<td>Estimated <strong>10 individuals</strong> assuming juveniles aged up 3 years remain in Africa</td>
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<td><strong>Non-breeding individuals observed in 2022</strong></td>
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<tr>
<td>Observed <strong>9-10 individuals</strong></td>
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<tr>
<td>2-3 immatures and 7 adults/sub-adults</td>
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Galala raptor count: monitoring spring migration along the Red Sea in Egypt

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Monitoring raptors along migration corridors can be used to assess changes in population size. Along the eastern Mediterranean flyway, several migratory bottlenecks exist where a large number of migratory soaring birds congregate during migration. Using evidence from satellite-tracked Egyptian Vultures (EV) Neophron percnopterus, we established a new observatory at the well-known spring migration bottleneck along the northern Red Sea Coast near Galala, Egypt. The Northern Galala Plateau extends for about 80 km from east to west and reaches an elevation of 750 m above sea level only ~3 km from the coast of the Red Sea. The towering cliffs of the eastern margin of the plateau provide orographic and thermal uplift to migratory soaring birds, thus facilitating very efficient travel during northbound migration.

In March 2022, we explored nine localities around the newly built city of Galala to evaluate for which species long-term migration monitoring would be valuable in this area. We collected data on migrating birds between 1 March and 20 April 2022, with daily observations occurring between 08.00 and 18.00 h local time, except on days when migration intensity was low or logistical difficulties prevented monitoring activities for certain parts of the day. We found that observation locations on top of the Galala plateau offered consistently better observation conditions over a broad range of meteorological conditions than a previous location along the coast. Within 6 weeks we observed >350,000 migratory birds from 28 species. Among these we observed >1,200 EVs, >300,000 Steppe Buzzards, and >10,000 Steppe Eagles and Lesser Spotted Eagles. The intensity of migration and species composition varied over the course of the 6-week observation period. In early March, the migration volume was dominated by Steppe Eagles, followed by the peak of Lesser Spotted Eagle, Short-toed Snake Eagle and EV between 19-24 March. The peak migration period for Black Kites was in late March, and for Steppe Buzzards in early April, even though this species was already the most common species throughout March. Long-term raptor monitoring at three points to the east, north, and west of the city of Galala would require 2–4 observers at each point from late February until late April. Together, these observation points would allow monitoring of globally significant proportions of Lesser Spotted Eagle (25-37%), Steppe Eagle (23-32%), White Stork (10%), Steppe Buzzard (6-11%), EV (3-10%), Short-toed Snake Eagle (3-6%), Black Stork (3-5%) and Black Kite (2-4%) populations from eastern Europe and western and central Asia. Due to the ease of access, proximity to a new university, and support by the local government to develop the site for bird watching, we consider Galala Bird Observatory to have great potential for long-term monitoring of migratory raptor populations and ecotourism to promote the spectacle of bird migration in general.
Peer-reviewed research derived from the abstract:


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Spatial and temporal variability in migration of a soaring raptor across three continents

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Disentangling individual- and population-level variation in migratory movements is necessary for understanding migration at the species level. However, very few studies have analysed these patterns across large portions of species’ distributions. We compiled a large telemetry dataset on the globally endangered Egyptian Vulture (EV) Neophron percnopterus (94 individuals, 188 completed migratory journeys), tracked across ~70% of the species’ global range, to analyse spatial and temporal variability of migratory movements within and among individuals and populations. We found high migratory connectivity at large spatial scales (i.e., different subpopulations showed little overlap in wintering areas), but very diffuse migratory connectivity within subpopulations, with wintering ranges up to 4,000 km apart for birds breeding in the same region and each subpopulation visiting up to 28 countries (44 in total). Additionally, EVs exhibited a high level of variability at the subpopulation level and flexibility at the individual level in basic migration parameters. Subpopulations differed significantly in travel distance and straightness of migratory movements, while differences in migration speed and duration differed as much between seasons and among individuals within subpopulations as between subpopulations. The total distances of the migrations completed by individuals from the Balkans and Caucasus were up to twice as long and less direct than those in Western Europe, and consequently were longer in duration, despite faster migration speeds. These differences appear to be largely attributable to more numerous and wider geographic barriers (water bodies) along the eastern flyway. We also found that adult spring migrations to Western Europe and the Balkans were longer and slower than fall migrations. We encourage further research to assess the underlying mechanisms for these differences and the extent to which environmental change could affect EV movement ecology and population trends.

Peer-reviewed research derived from the abstract:

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The Flyway Action Plan for the Conservation of the Balkan and Central Asian Populations of the Egyptian Vulture *Neophron percnopterus* (EVFAP) was published in 2016 and began implementation the following year, after being endorsed at COP12 by CMS parties as Annex 4 of the Vulture MsAP. Now at the midway point of the 10-year plan, we have reviewed implementation of the Framework for Action.

The review has been carried out using the methodology and scoring as set out by Birdlife International in 2011. This questionnaire (available in English and Russian) was sent to a focal contact for each of the 33 countries in the original EVFAP. Information on any updates to both conservation and legal status were also collated. Countries scored each of the 59 actions for their Implementation (IS; scored 0-4) and Priority (PS; scored 1-4) which combined to produce an Action Priority Index. The National Implementation Score (NIS) was also calculated for each country. Responses were received from 29 countries in total and the NIS ranged from 1.00 to 2.70 with an average of 1.56 for the whole flyway. Countries which were part of the Egyptian Vulture New LIFE project (14 along the flyway) had an average NIS of 1.83, showing the value of large-scale projects such as this in delivering conservation measures.

Following a workshop in November 2022 and the feedback received in the questionnaires some regions were invited to score actions which hadn’t previously been considered such as the impact of energy infrastructure in Central Asia and Caucasus. At this workshop it was also discussed where the priority score for an individual country or region should be significantly different than in the EVFAP when producing the API as threats had previously been assigned at a flyway level.

Excellent progress has been made but there is still much to be done to complete the overall goal of the EVFAP to improve the conservation status of the Egyptian Vulture in the entire FAP range. Notably the highest scoring actions under the API are associated with improved detection, legislation and enforcement surrounding poisoning and the retrofitting and replacement of dangerous energy infrastructure. Working with stakeholders, whether local communities, governments or developers, also further efforts in the remaining five years of the EVFAP. We recommend sharing of best practice and methods continues to be encouraged to ensure the ultimate goal of halting the current population declines.