Ornithological
Applications

AmericanOrnithology.org

Volume 124, 2022, pp. 1–10
https://doi.org/10.1093/ornithapp/duab065

RESEARCH ARTICLE

Postrelease survival of captive-bred Egyptian Vultures is similar to that of wild-hatched Egyptian Vultures and is not affected by release age or season

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Submission Date: July 2, 2021; Editorial Acceptance Date: December 13, 2021; Published January 28, 2022

ABSTRACT

Reintroducing species to their historic range or reinforcing extant but endangered populations with individuals from elsewhere are popular conservation efforts to maintain long-term viable populations of animals. These efforts, known as conservation translocations, require proper monitoring of the fate of the animals that are released to assess their success. Nevertheless, effective monitoring is often missing in conservation translocations. Here, we assessed the efficiency of different monitoring methods and estimated survival of captive-bred Egyptian Vultures (*Neophron percnopterus*) that were released to the wild during the first 15 years of a reintroduction project in Israel. First, we inspected data obtained from different monitoring methods and compared observations of color rings and wing tags to location data from GPS transmitters. Then, we used GPS data to estimate apparent survival of vultures that were released to the wild at different ages and different seasons. Finally, we compared the apparent survival of captive-bred and wild-hatched Egyptian Vultures. We show that only a relatively small portion of the birds were visually observed through color rings and wing tags, compared to those for which data were obtained from GPS transmitters. Using data obtained via GPS transmitters we were able to show that release age and season did not alter apparent survival. In addition, we found no differences in apparent survival between captive-bred and wild-hatched Egyptian Vultures during their first migration or during their first two years postrelease or postfledging. Our results show the importance of continuous and effective monitoring and confirm the efficacy of captive-breeding and release of Egyptian Vultures as a conservation tool. We recommend the continuation of monitoring using GPS transmitters, alongside increased observation-based monitoring efforts.

Keywords: biologging, captive breeding, conservation behavior, monitoring, reintroduction, vultures

La supervivencia postliberación de individuos de *Neophron percnopterus* criados en cautiverio es similar a la de individuos criados en libertad y no se ve afectada por la edad o la temporada de liberación

RESUMEN

La reintroducción de especies en su área de distribución histórica o el refuerzo de poblaciones existentes pero en peligro con individuos de otros lugares son esfuerzos de conservación habituales para mantener poblaciones de animales viables a largo plazo. Estos esfuerzos, conocidos como translocaciones de conservación, requieren un monitoreo adecuado del destino de los animales que se liberan para evaluar su éxito. Sin embargo, a menudo falta un monitoreo efectivo en las translocaciones de conservación. Aquí, evaluamos la eficiencia de diferentes métodos de monitoreo y la supervivencia estimada del buitre *Neophron percnopterus* considerando individuos criados en cautiverio que fueron liberados a la naturaleza durante los primeros 15 años de un proyecto de reintroducción en Israel. Primero, revisamos los datos obtenidos de diferentes métodos de monitoreo y comparamos las observaciones de anillos de color y marcas en las alas con los datos de ubicación de transmisores GPS. Luego, usamos los datos de GPS para estimar la supervivencia aparente de los buitres que fueron liberados a la naturaleza en diferentes edades y estaciones. Por último, comparamos la supervivencia aparente de los buitres criados en cautiverio y en libertad. Mostramos que solo una porción relativamente pequeña de las aves fue observada visualmente a través de los anillos de color y las marcas en las alas, en comparación con aquellas para las que se obtuvieron datos de transmisores GPS. Utilizando datos obtenidos a través de transmisores GPS pudimos demostrar que la edad y la temporada de liberación no alteraron la supervivencia aparente. Además, no encontramos diferencias en la supervivencia aparente entre los buitres criados en cautiverio y los que nacieron en estado silvestre durante su primera migración o durante los dos primeros años posteriores a la liberación o al emplumamiento. Nuestros resultados muestran la importancia de un seguimiento continuo y efectivo y confirman la eficacia de la cría en cautiverio y de la liberación de individuos de *N. percnopterus* como herramienta de conservación. Recomendamos la continuación del monitoreo utilizando transmisores GPS, junto con mayores esfuerzos de monitoreo basados en la observación.

Palabras clave: bio-registración, buitres, comportamiento animal y conservación, cría en cautiverio, monitoreo, reintroducción

INTRODUCTION

Conservation translocations within a species' historic range reintroduce or reinforce populations of species that are locally extinct or under threat of extinction (Ewen et al. 2012, IUCN 2013, Corlett 2016). This is a biological conservation measure implemented worldwide in an attempt to reverse the decline of many species. Conservation translocations often necessitate the breeding of animals in captivity and the release of captive-bred animals to the wild (Seddon et al. 2014, McGowan et al. 2017). Despite many successful examples (Maunder and Byers 2005), the high resource investment required, and the general complexity of this effort, makes such projects' success hard to assess in some cases, and in many other cases leads to failure (Fischer and Lindenmayer 2000, Germano et al. 2014, Robert et al. 2015, Taylor et al. 2017). To properly evaluate the success and to improve the utility of these projects, long and intensive monitoring is required (Ewen and Armstrong 2007, Sutherland et al. 2010, Seddon et al. 2014).

Monitoring of any conservation project should estimate the level of achievement of the project's objectives and, through that, improve the methods in order to meet the expected goals (Nichols and Williams 2006, Ewen and Armstrong 2007). For example, monitoring reintroduced animals should provide estimates of their survival and reproduction (Nichols and Armstrong 2012). However, such monitoring is often unfeasible due to logistical and financial constraints (Morant et al. 2020b). A recent review of 293 case studies found that carrying out proper monitoring was the difficulty reported by managers conducting conservation translocations in the largest number of case studies (Berger-Tal et al. 2020). Monitoring becomes more difficult and expensive for long-lived species (Sutherland et al. 2010) and is further hampered by lack of funding and long movements of the released animals; both factors were also high on the list of difficulties mentioned by translocation managers (Berger-Tal et al. 2020). For example, Egyptian Vultures (*Neophron percnopterus*) usually attempt to breed for the first time during their sixth or seventh year, and then raise up to 2 chicks annually (Sanz-Aguilar et al. 2017, Orta et al. 2020). This means that proper monitoring of breeding success and long-term population trends of the species requires expensive, long-term efforts.

Vultures are highly threatened, with 17 out of 22 vulture species currently declining (Buechley and Şekercioğlu 2016a, Safford et al. 2019). Vultures are long-lived, large, scavenging birds that often travel long distances, start breeding at relatively old age, and feed in groups (Buechley and Şekercioğlu 2016b). These characteristics expose vultures to many risks, among them poisoning, electrocution, and direct persecution (Safford et al. 2019, Buechley et al. 2021, Oppel et al. 2021a), and make monitoring of these species' survival and productivity difficult (Efrat et al. 2020a). To counteract vulture population declines multiple conservation efforts have been made, including national and international efforts to mitigate the threats, restore habitats, and reintroduce or reinforce birds at their historic breeding range (e.g., Houston and Piper 2006, Botha et al. 2017, Badia-Boher et al. 2019). Reintroduction and reinforcement of vultures have been used since the 1980s, with some encouraging success stories (e.g., Terrasse et al. 2004) and several ongoing projects aiming to conserve multiple vulture species worldwide (Frey 1992, Pain et al. 2008, Efrat et al. 2020b, Oppel et al. 2021b, Kmetova–Biro et al. 2021).

The Egyptian Vulture is a small vulture species that breeds across much of southern Europe, northern and eastern Africa, the Middle East, and central and South Asia (Birdlife International 2021). The northern populations of the Egyptian Vulture are migratory, and vultures tend to remain at the wintering grounds for their first 2–3 years (Meyburg et al. 2004, Phipps et al. 2019, but see Morant et al. 2020a). Following a recent decline throughout most of its range, the Egyptian Vulture is listed as globally Endangered (Birdlife International 2021). A recent comprehensive study of many of its populations found that in accordance to local population trends, the survival of Egyptian Vultures from eastern Europe and the Middle East is lower than that of conspecifics from Western Europe (Buechley et al. 2021). Buechley et al. (2021) also found that mortality occurs more frequently in northern rather than southern latitudes and that it is often human-induced.

Similar to most other populations around the world, the Israeli Egyptian Vulture population suffered dramatic declines in recent decades and is currently considered locally Critically Endangered (Mayrose et al. 2017). To reverse the negative trend of the species in Israel, a captive-breeding and release program of Egyptian Vultures was established in Israel, with the first birds released to the wild in 2006. Monitoring of this reintroduction project has evolved during the years, from observations of color-ringed and wing-tagged birds and the use of VHF telemetry to remote data downloaded from GPS transmitters that are attached to all newly released birds. Here, we compared different monitoring methods used during the first 15 years of the reintroduction project. We did so by comparing observations of color rings and wing tags to tracking data obtained using GPS transmitters. Then, we estimated the apparent survival of vultures released under different release protocols and compared the apparent survival of the released vultures with that of vultures from an adjacent wild population to test whether the project can be considered successful at this stage.

METHODS

Captive-Breeding and Release Protocol

Captive-breeding of Egyptian Vultures in Israel started in 2005 with the first 3 captive-bred vultures released to the wild in 2006. Between 2006 and 2020, 82 vultures were captive-bred and released to the wild (annual mean ± SD = 6.8 ± 4.6, range: 0–17). During these years, 6 pairs of adult Egyptian Vultures, all originating from the wild in Israel, were used for captive-breeding at Hai-Bar Carmel breeding facility (32.75°N, 35.01°E). These are nonreleasable vultures due to physical conditions caused by trauma. Laid eggs were taken from the nest and artificially incubated, ensuring that the parents did not harm the eggs. Also, this usually resulted in the production of a replacement clutch, which increased the number of captive-breeding birds that were released to the wild.

Hatched chicks were either returned to their biological parents (*n* = 7 of the released vultures), moved to a foster pair (*n* = 17), or hand-reared by human caretakers (*n* = 58) (Supplementary Material Table S1). Hand-rearing was done without the chicks seeing the caretaker except during regular physical examinations which occurred once every week. Once the chicks started showing independent behavior (i.e. feeding independently, moving, and flying; 80–120 days posthatching), they were moved to a large aviary alongside all the other Egyptian Vultures that hatched that year and the ones that hatched in the previous year but were not yet released. The vultures remained in the new aviary until their release, which occurred by opening a large window in the aviary that allows the birds to leave.

All but 9 of the vultures were released at Hai-Bar Carmel Nature Reserve which is situated at the Carmel Mountain ridge (Figure 1) where a breeding population of the species thrived until the 1960s (Mayrose et al. 2017). The other 9 were released at Ramat HaNadiv, 23 km south of Hai-Bar Carmel, at the southern tip of Carmel Mountain's ridge where the species bred at least until the 1950s. Vultures were released during their first (*n* = 58) or second (*n* = 24) year of life. Of the vultures released during their first year, only 3 were released before the time of their first migration, whereas for the rest a delayed release approach was taken and consequently they remained in captivity at least until their first winter (i.e. "skipping" their first migration). Additionally, most vultures were released either in winter (November–January, *n* = 49) or spring (March–June, *n* = 28); while the rest were released in July (*n* = 2), August (*n* = 2), and October (*n* = 1) (Supplementary Material Table S1).

Monitoring

All released vultures were ringed with unique color rings and until 2016 most were also fitted with unique wing tags (in total 32 birds, Supplementary Material Table S1). Between 2006 and 2014, 17 vultures were fitted with a conventional VHF telemetry device that is trackable from up to a few kilometers using an antenna and that may additionally detect lack of movement of the tracked animal, suggesting mortality. In 2013, 2 of the 4 released vultures were fitted with Argos-GPS transmitters (manufactured by Microwave Telemetry); and in 2014, 4 of the 13 released vultures were fitted with a GPS-GSM transmitter (E-obs). All Argos-GPS and GPS transmitters were solar-powered and worked for at least 3 years, to the best of our knowledge. Between 2016 and 2020, 43 of the 47 released vultures were fitted with GPS-GSM transmitters (Ornitela),

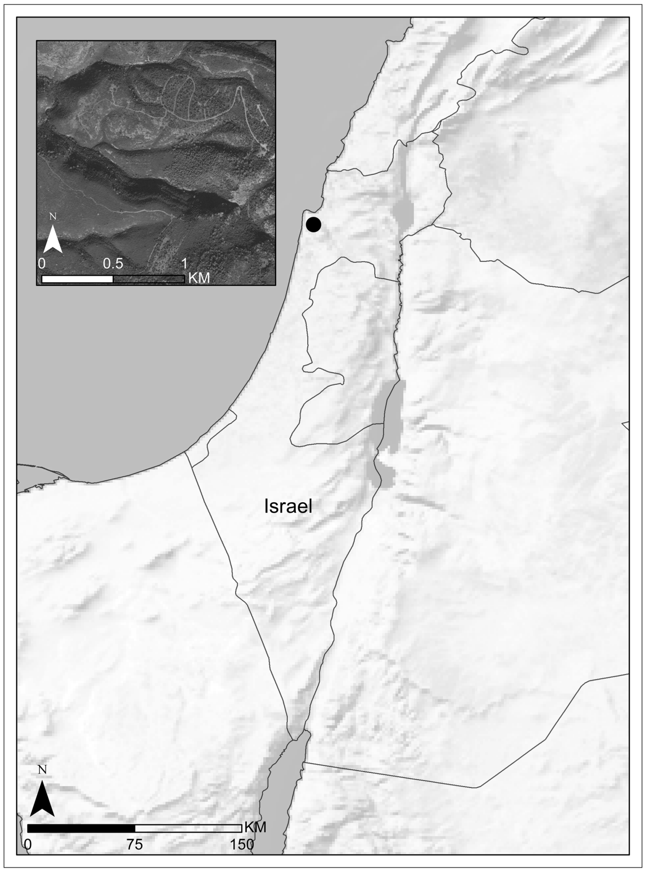

FIGURE 1. A map of the study area (Israel) with the captive-breeding and release facilities at Hai-Bar Carmel marked with a black dot and enlarged in the inserted map at the top left corner.

but the tags of 2 of these vultures fell off before they left the aviary due to human error. We additionally excluded data from 3 of the GPS-tagged vultures that were re-caught soon after their release due to bad physical condition and did not leave the release site for at least a year following their release. All transmitters weighed <2% of the vultures' mass (Bodey et al. 2017) and were fitted in either backpack or leg-loop harness configurations (Anderson et al. 2020) (Supplementary Material Table S1).

Monitoring the released vultures was done using 3 main approaches. Starting immediately after the first release in 2006 and throughout the years, surveys were carried out from a fixed location that oversaw much of the Hai-Bar Carmel area. These surveys were done by volunteers or as part of the routine work of Hai-Bar Carmel staff, using cameras, binoculars, and telescopes on at least a weekly basis, attempting to identify individuals according to their unique markings (wing tag and color ring). The surveys included similar efforts throughout the years. Occasional sightings of wing-tagged or ringed Egyptian Vultures around Hai-Bar Carmel or in other locations were added to the routine surveys database. In addition to the identification of specific individuals, regular nest searching was done at Hai-Bar Carmel at the relevant season. Second, the 17 individuals fitted with VHF telemetry devices were searched for from Hai-Bar Carmel and the surrounding area using omni and directional antennas operated from a vehicle during weekly surveys. When a vulture was located using this method, binoculars were used to ascertain its identity using its unique ring or wing tag. Although Egyptian Vultures do not currently winter in Israel, both survey methods were carried on a weekly basis throughout the year because they targeted both Egyptian and Griffon vultures (*Gyps fulvus*), the second being a resident species. Observations made by locating a vulture equipped with VHF telemetry using antennas were not listed as such in the database, but rather as any other observation of wing tag or ring; thus, we classified all observations as sightings of unique markings. Finally, vultures that were fitted with GPS transmitters were continuously tracked and in case a bird showed signs of mortality (e.g., lack of movement) efforts were made to reach its last known location for further investigation.

Between 2018 and 2020 we fitted GPS-GSM transmitters (Ornitela) to 26 wild Egyptian Vulture chicks in their nests throughout Israel, approximately 2–3 weeks before they fledged: 2 in 2018, 14 in 2019, and 10 in 2020. Transmitters were attached using a leg-loop harness and tracking data were collected in the same way as for the captive vultures.

Observed Vultures and Survival Comparisons

We tested for differences in the proportion of observed vultures between monitoring schemes and among different groups of vultures. For the comparisons based only on GPS data, we defined surviving vultures as those that were still moving (according to their GPS data). We are aware that end of transmission does not necessarily mean that the bird died, but we assume that other cases (e.g., tag failure) are rare and occur randomly and thus do not bias one group's mortality over the other in different comparisons. Yet, because we could not estimate whether a vulture that stopped sending data was dead, we treated our estimates as apparent survival, a common approach used in mark-recapture studies of wild animals (Schaub and Royle 2014).

We first compared data obtained from GPS transmitters to that obtained from observations of leg rings and wing tags by comparing the two datasets for vultures that were equipped with GPS transmitters and color rings. We used a paired-sample test to compare the time between a vulture's release and the time of the last data obtained for this vulture by GPS to that obtained from observations. For vultures that were never observed, a value of 0 was assigned. Because the differences between the two groups were not normally distributed, we used a Wilcoxon Signed Rank test for this comparison. Following this comparison, we used the GPS transmitters' data to compare apparent survival between (1) captive-bred vultures released during their first year and those released during their second year, (2) captive-bred vultures released in winter and those released in spring, and (3) captive-bred and wild-hatched vultures. Other possible comparisons (e.g., rearing method or release site) could not be done due to insufficient sample size.

We focused on the first 2 years of life for wild vultures and the first 2 years in the wild for captive vultures. To this end, we used the Cox proportional-hazard model (Cox 1972) to estimate survival probability curves for each tested group. This model considers survival to be time-dependent, while other covariates are time-independent. It also allows the use of "censored" data (i.e. data from vultures that were not tracked for the entire period). For each variable used in the Cox models, we tested the proportional-hazard assumption (Grambsch and Therneau 1994). Additionally, we tested differences in apparent survival during the vultures' first migration, separately from the entire data, accounting for the period in which mortality is assumed to be the highest in the vultures' life (Rotics et al. 2016, Sergio et al. 2019, Buechley et al. 2021). Differences in apparent survival during first migration were tested by comparing the proportion of surviving individuals out of those that migrated using a generalized linear model (GLM) with a binomial distribution and a logit link function. For this analysis, we did not include the 11 birds for which the first migration occurred in 2021, because it was not yet finished by the time we made the analysis. For both analysis types we used 2 models, 1 including only captive-bred birds and comparing the effects of release age and release season and 1 testing the effect of captive-breeding compared with wild-hatching. Because one GPS-tracked vulture was released in autumn (Supplementary Material Table S1), it was removed from the Cox and GLM models analyses for release age and release season effects but was included in the other models. A preliminary analysis found that adding the year of release as a covariate resulted in a nonsignificant effect and did not improve the models' AIC thus it was not used in the final models. Migration was defined as the time between the first and last day in which a vultures' movement was long (>50 km) and directional towards the expected migratory direction (south during autumn migration).

Data collection continued until the end of August 2021. Comparisons (two-tailed tested with $\alpha = 0.05$) were made using survival and lme4 packages in R version 4.1.0 (R Core Team 2021). Unless otherwise noted, results are reported by their mean ± SD.

RESULTS

Between May 2006 (the release of the first vulture) and August 2021, 51 of the 82 released captive-bred Egyptian Vultures were observed 617 times (12.1 ± 15.7 observations per observed individual). Due to lack of directed efforts to observe Egyptian Vultures in other places, only 21 observations of 9 different vultures were recorded outside Hai-Bar Carmel, throughout Israel. Time elapsed from release to the last observation of vultures ranged between 4 and 3,151 days (624 ± 792). Seventeen of the 32 vultures with wing tags and 10 of the 17 vultures with simple VHF telemetry were never observed. Mortality was confirmed for 17 vultures. Of these, 14 vultures were found following mortality signs estimated from their GPS localizations, 2 were reported by finders abroad that identified their wing tag and/or color ring, and 1 was found by the Hai-Bar Carmel staff.

Time elapsed between release to the wild and last GPS location or last observation for the GPS-tracked captive-bred vultures was 462 ± 489 days (range: 6–2,024) and 342 ± 551 (range: 3–2,254), respectively. Of the 44 GPS-tracked captive-bred vultures, 13 were never observed, while data were obtained from all GPS transmitters. Time elapsed between release and time of the last obtained data was significantly longer for GPS transmitters, compared with observation of color ring and/or wing tag (paired-sample Wilcoxon signed-rank test, $z = -5.22$, $P < 0.001$; Figure 2). Using the GPS data, no effect of release season or release age on apparent survival was found during the first 2 years after release (n = 26, 17, 13, 30, for release during first year, second year, spring, and winter, respectively) or during first migration (n = 12, 9, 8, 13) (Table 1, Figure 3). Wild GPS-tracked vultures were tracked for

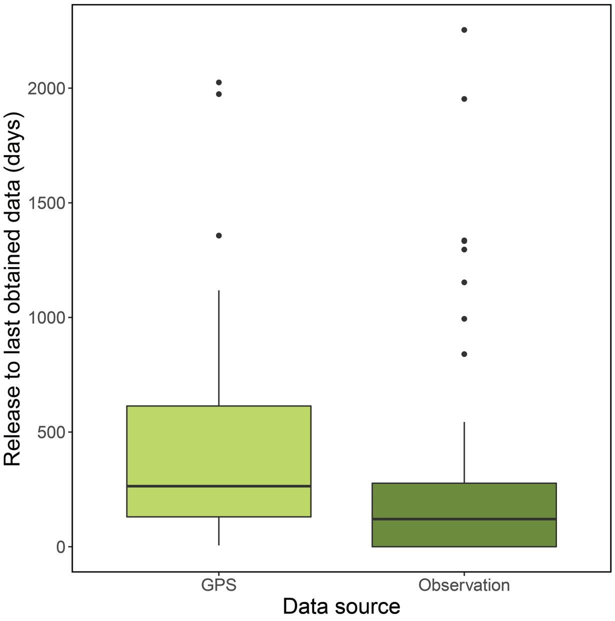

FIGURE 2. Comparison of the time between release and the last observation time for each vulture, obtained from GPS transmitters or from observations of color rings and/or wing tags. $P < 0.001$, calculated using paired Wilcoxon signed rank test.

TABLE 1. Results for models testing the effects of release age, release season, and origin (captive-bred or wild-hatched) on Egyptian Vulture survival during their first two years postrelease or postfledging (Cox proportional hazard models) and during their first migration (generalized linear models). SE = standard error

	Estimate [a]	SE	z	P
Cox proportional-hazard model for release age and season				
Age	1.3	0.42	0.63	0.53
Season	0.9	0.46	−0.24	0.81
Generalized linear model for release age and season				
Intercept	−1.7	1.1	−1.5	0.12
Age—second year	1.7	1.3	1.3	0.2
Season—winter	−1.9	1.3	−1.4	0.15
Cox proportional-hazard model for origin [b]				
Origin	1.4	0.35	0.98	0.33
Generalized linear model for origin				
Intercept	−1.4	0.5	−2.9	0.004
Origin—captive-bred	0.21	0.71	0.3	0.77

[a] Estimate for Cox model is Hazard-Ratio.
[b] Origin = captive-bred or wild-hatched.

454 ± 329 days (range: 30–1,186). No difference in apparent survival was found between captive-bred and wild-hatched vultures during the first 2 years after release for captive-bred birds or first 2 years after tagging for wild-hatched vultures (*n* = 44, 26, respectively) or during their first migration (*n* = 22, 26, respectively) (Table 1, Figure 4). The proportional-hazard assumption was met for all explanatory variables (*P* = 0.077, 0.1, 0.29 for age, season, and captive or wild).

Two breeding attempts of released individuals were recorded during regular surveys of nesting sites at Hai-Bar Carmel. These included a 2019 pair of captive-bred vultures, one that hatched in 2011 and the other in 2014, and a 2020 pair in which one of the vultures was captive-bred that hatched in 2014 and the other was a wild bird, hatched in 2016 (aged according to plumage (Forsman 2016)). Both breeding attempts included building and maintaining a nest and possible, but unconfirmed, incubation. The same pair that attempted to breed at Hai-Bar Carmel in 2019 was observed successfully breeding in 2020 at the Lower Galilee, a few dozen kilometers to the east of Hai-Bar Carmel. The pair fledged a single chick. This marks, to the best of our knowledge, the first chick ever to hatch in the wild to a pair of captive-bred Egyptian Vultures worldwide.

DISCUSSION

We showed that the monitoring scheme had a strong effect on the type and amount of data acquired for a long-lived bird that moves great distances, which bears significant implications for the ability of managers to assess such projects' success and understand the causes of mortality outside the release sites. By using data obtained from GPS transmitters, we found no difference in apparent survival during the first two years postrelease between captive-bred birds released under different release protocols. Furthermore, we did not find any statistical differences in apparent survival between captive-bred and wild-hatched vultures from the same area, demonstrating the success of the captive-breeding project.

No data was ever obtained by observing the rings or wing tags for 38% of all captive-bred vultures, while all GPS transmitters sent data. When considering only birds that had a wing tag, 53% of the wing-tagged vultures were never observed. Because the observers did not record by which method (ring, wing-tag, or telemetry) the vultures were identified, it is hard to separate the effects of each of these methods on monitoring efficiency. Yet, the finding that <50% of the birds equipped with simple telemetry were ever observed suggests that VHF telemetry is not an efficient method for short or long-term monitoring of Egyptian Vultures (Bridge et al. 2011). GPS-tracking proved a more efficient way to monitor captive-bred Egyptian Vultures after their release to the wild compared with observations of color rings and wing tags, with an average 30% longer periods between the time of release and the time of the last obtained data. Moreover, the few observations of released birds at locations other than the release site and the record of released birds breeding far from this site suggest that relying on observations from the release site misses crucial data regarding the success of the project.

Two recently published studies estimated the annual survival of newly released captive-bred Egyptian Vultures as 45.8% for birds released in Italy, Bulgaria, and Israel (including 37 of the vultures used in the current study) and as 56.6% for birds released in their second year of life in Bulgaria (Buechley et al. 2021, Oppel et al. 2021b). The different methods used to calculate survival in these studies did not allow a direct comparison between these studies. However, considering the large uncertainty in the estimations presented in these studies and in the current study, these estimations can be considered very similar to our finding of ~50% apparent survival after the first year in the wild.

Multiple previous studies found reduced survival during migrating birds' first years of life and specifically during their first migration, including for Egyptian Vultures, explained by lack of experience and the challenges of migration (Oppel et al. 2015, 2021b; Rotics et al. 2016, Sergio et al. 2019, Buechley et al. 2021). Captive-breeding is expected to further reduce early life survival by affecting the released animals' behavior (Mathews et al. 2005, Jule et al. 2008, Dickens et al. 2010, Whiteside et al. 2016). Thus, our findings of no difference in apparent survival between captive-bred and wild birds during migration or during their first 2 years postrelease or fledging are surprising and

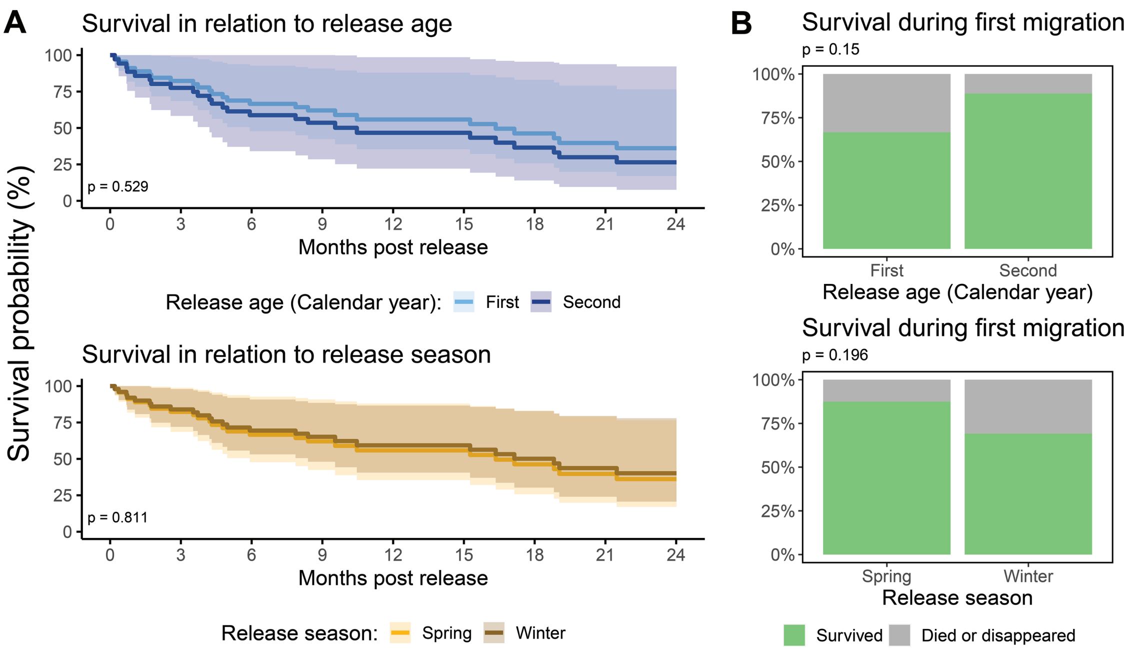

FIGURE 3. Comparison of apparent survival probability between captive-bred birds according to their age of release (top) and their release season (bottom). (A) Results of a Cox proportional-hazard model during the first 2 years after release, denoting the probability of an individual to survive throughout the first 2 years after its release to the wild; (B) apparent survival during first migration (*P* value calculated using generalized linear model).

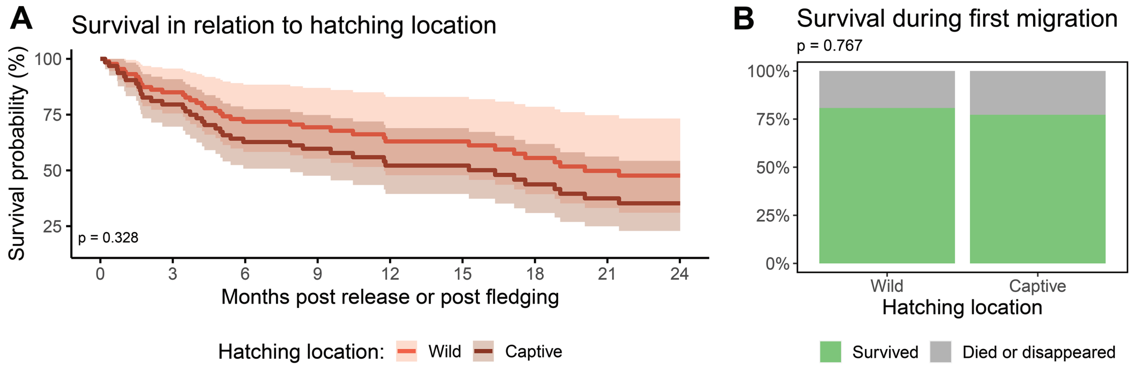

FIGURE 4. Comparison of apparent survival probability between captive-bred and wild-hatched birds. (A) Results of a Cox proportional-hazard model during the first 2 years after release, denoting the probability of an individual to survive throughout the first 2 years after its release to the wild or after it fledged from the nest; (B) apparent survival during first migration (*P* value calculated using generalized linear model).

suggest that either captive-breeding had no adverse consequences for these birds' short-term survival or that other factors compensated for their expected less proficient behavior. Interestingly, our results coincide with those found for a larger sample size of migrating Egyptian Vultures (Buechley et al. 2021) but are different than those found for the Balkan population, where captive-bred Egyptian Vultures' survival was higher than that of wild-hatched Egyptian Vultures (Oppel et al. 2021b). These differences may stem from differences in migration routes and risks along the birds' annual cycle (Phipps et al. 2019, Efrat et al. 2020a, Oppel et al. 2021a).

One possible factor that can explain the captive-bred vultures' higher-than-expected survival is their older age and the fact they have accumulated more experience compared to wild birds during the same period. These age and experience differences result from the delayed release of the captive-bred birds (also known as Headstarting) in which birds were released from captivity at an older age than the age in which Egyptian Vultures fledge in the wild (~240 older on average) and become independent in natural conditions (Alberts 2007, IUCN/SSC 2014). For most of the vultures, delayed release also meant that they had more time to gain experience in the wild before their first migration, because they were released during spring or winter, many months prior to their first migration. Our results, alongside results from previous studies (Buechley et al. 2021, Oppel et al. 2021b), imply that if captive-breeding does have adverse effects on the released vultures, these effects are offset by maturation and/or experience gained during the first few months of life while still in captivity and/or while in the wild prior to their first migration. The lack of difference in apparent survival between vultures released at a different age or in a different season suggests that further research is needed to understand the mechanisms required for gaining the needed experience and the specific time period during which this critical experience is gained.

Importantly, our analyses explored differences in apparent survival during only the first two years after the release of the captive-bred vultures. Testing survival differences after more than two years might provide different results, as was found in previous studies (Le Gouar et al. 2008, Efrat et al. 2020b, Kemp et al. 2020). Differences among groups of captive-bred vultures might not affect their short-term survival because of major difficulties in adjusting to a new environment immediately following their release, which may obscure positive effects of experience gained in captivity or maturity (Dickens et al. 2010, Berger-Tal and Saltz 2014, Berger-Tal et al. 2014). This hypothesis suggests that advantages of one group over the other, for example of vultures released at an older age, are not enough to overcome challenges of the natural environment such as stochastic weather events, food acquisition, or anthropogenic threats before gaining sufficient experience in the wild. But, once such experience is gained, the vultures may overcome these challenges, and then differences among different groups (e.g., age differences) might become apparent to an extent that affects their survival. Alternatively, our results might be affected by the small sample size in some of the comparisons. Specifically, age related differences in captive vultures' apparent survival during the first migration and differences between captive-bred and wild-hatched birds' apparent survival during their first two years in the wild both show nonsignificant trends that agree with previous studies (i.e. higher survival of birds released at an older age and for wild birds; Sarrazin et al. 1994, Efrat et al. 2020b). Finally, when considering which method should be used to obtain data about released animals (e.g., observations of unique markings or GPS data), further considerations should be made besides those presented here. These considerations include, among others, the cost-effectiveness of each method, standardization of monitoring data, and the project's specific monitoring goals (Badia-Boher et al. 2019, Perrig et al. 2019, Morant et al. 2020b).

To conclude, although the current data collected could not yet be used to estimate population viability, it enabled some important insights into the monitoring schemes' efficiency and into the success of the Egyptian Vulture captive-breeding and reintroduction in Israel (Taylor et al. 2017). The higher-than-expected apparent survival of captive-bred vultures alongside the first record of captive-bred Egyptian Vultures successfully breeding in the wild, are encouraging signs of success of this long-term project. Furthermore, our results present another example that using delayed release of captive-bred animals, and specifically of Egyptian Vultures, can be an effective approach for reintroductions (Oppel et al. 2021b). To fully understand the effect of Egyptian Vulture reintroduction on the viability of the population in Israel, we recommend supplementing the current monitoring schemes (color rings and GPS transmitters) with targeted field monitoring that will enable analysis of long-term survival and breeding success both for captive-bred and for wild vultures. The specific methods to be used should be chosen following an examination of the effectiveness and cost of possible monitoring schemes (Badia-Boher et al. 2019, Morant et al. 2020b, Oppel et al. 2021b).

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

ACKNOWLEDGMENTS

Most of the work done to prepare the vultures for translocation is done by the Hai-bar Carmel Nature Reserve team, led by S. Simchi and A. Baron. We would like to thank the people who reported observations of tagged Egyptian Vultures, and especially to Roy Federman, Asaf Dori, Moti Dolev and Sarit Dahan of the INPA who monitored the successful breeding of the captive-bred pair in the wild. Finally, we thank people who helped with field work, especially to Walter Neser, Korin Reznikov and Nili Anglister.

Funding statement: The conservation translocation project for Egyptian Vultures in Israel is led by the Israel Nature and Parks Authority (INPA) and financed by the Porsim Kanaf partnership, The I. Meier Segals Garden for Zoological Research at the Tel-Aviv University, The Zoological Center Tel-Aviv—Ramat-Gan and Ramat Hanadiv Gardens. This work was also supported by grant no. I-1465-413.13/2018 of the German-Israeli Foundation for Scientific Research and Development (GIF). Ron Efrat was supported by the Israeli Academy of Science's Adams Fellowship and the Ben-Gurion University's Negev Fellowship.

Ethics statement: Captive-breeding and trapping of vultures was done under permit 2495/2018 of the Israeli Nature and Parks Authority.

Author contributions: Ron Efrat, Ohad Hatzofe, Ygal Miller and Oded Berger-Tal conceived the ideas. Ron Efrat, Oded Berger-Tal, Thomas Muller and Nir Sapir designed

methodology. Ron Efrat, Ohad Hatzofe and Ygal Miller collected and organized the data and Ron Efrat analyzed the data and led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

Data availability: Data used in this study is available in the Supplementary Material file. For further details please contact the authors.

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