Determinants of survival in captive-bred Griffon Vultures *Gyps fulvus* after their release to the wild

Ron Efrat1 | Ohad Hatzofe2 | Ygal Miller2 | Oded Berger-Tal1

1Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Israel
2Science Division, Israel Nature and Parks Authority, Jerusalem, Israel

Correspondence
Ron Efrat, Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion 8499000, Israel.
Email: ronef@post.bgu.ac.il

Funding information
Israel Academy of Sciences and Humanities, Grant/Award Number: Adams fellowship; Keren Hayesod; Segre Foundation; Ben-Gurion University

Abstract
Conservation translocations are a wide-spread tool commonly used to prevent the extinction of species locally and globally. However, conservation translocations are complicated operations which often fail, especially when they involve the release of captive-bred animals. In order to survive, translocated animals need to adapt to a new environment; the success of this adaptation depends, to a large extent, on the characteristics of the release environment and on early life experiences that can affect the animals’ proficiencies. We tested the effects of different early life experiences and differences in the release environment on the survival of captive-bred translocated Griffon Vultures (*Gyps fulvus*) in Israel, where they are critically endangered. We used a mark-resight approach to calculate survival using a large dataset containing 9 years of observations of individually-marked vultures. We found that the Griffon Vultures’ survival was positively affected by their age at release and the time they spent in the wild. We also found that survival was affected by rearing method, release site and release season. Our results emphasize the critical importance of the release protocol to the success of a conservation translocation project. Furthermore, our results show how events occurring during the entire pre-release period can have important repercussions many years later when the captive animal is released into the wild, but also that experience gained post-release plays a major role in the animals’ survival.

KEYWORDS
Captive breeding, conservation translocation, reintroduction, vultures

1 | INTRODUCTION

Conservation translocations are an increasingly popular conservation strategy that aims to improve the status of focal species or restore natural ecosystem functions and processes (Butchart, Stattersfield, & Collar, 2006; Ewen, Armstrong, Parker, & Seddon, 2012; IUCN, 2013; Seddon, Griffiths, Soorae, & Armstrong, 2014). The complex nature of such endeavors makes the translocation process difficult and success rates are relatively low (Berger-Tal, Blumstein, & Swaisgood, 2019; Fischer & Lindenmayer, 2000; Germano et al., 2014); yet the application of scientific approaches is leading to improved results (Seddon & Armstrong, 2016). For a conservation translocation project to succeed, its managers need to consider many different factors such as the biological and ecological...
properties of the translocated species and the release site environment (IUCN, 2013). However, the unique characteristics of each translocation project require a continuous learning process that is based on the ongoing evaluation of the translocation project, making monitoring of the released animals an imperative part of the process (IUCN, 2013; Sutherland et al., 2010; Williams, 2011a, 2011b). Monitoring can measure the success of conservation translocations by assessing the survival rates of translocated animals, and in some cases reveal what affects the animals’ survival and fitness (Seddon, Armstrong, & Maloney, 2007; Sutherland et al., 2010).

Animals that are translocated to a new area, and especially those that are captive-bred and released to the wild, face novel threats and challenges (Bell, 2016; Berger-Tal, Nathan, Meron, & Saltz, 2014). The ability to face these challenges is expected to be strongly affected by the early life experiences of the translocated animal and can probably improve with gained experience, as found for wild-bred animals (Chapman, Morrell, & Krause, 2010; Feenders, Klaus, & Bateson, 2011; Rotics et al., 2016; Sergio et al., 2014; Slagsvold & Wiebe, 2007). Captive-bred animals experience early-life conditions that may be substantially different than the environment into which they will eventually be released (Jule, Leaver, & Lea, 2008; Whiteside, Sage, & Madden, 2016). Furthermore, the captive environment can negatively affect the success of translocations by imposing behavioral and physiological deficiencies, disease and genetic effects of inbreeding and drift (Ebenhard, 1995; Liukkonen-Anttila, Saaartoala, & Hissa, 2000; Mathews, Orros, McLaren, Gelling, & Foster, 2005; Snyder et al., 1996). However, despite its importance to the welfare of animals and the success of translocations, the mechanisms behind captive-breeding’s effects on animals are not yet well understood (Mason, 2010).

Vultures are a group of species that requires intensive conservation efforts, with 17 of the 22 species of vultures currently decreasing (Buechley & Şekercioğlu, 2016; Safford et al., 2019). This decline is also apparent in Israel, with three of five vulture species that used to breed in the country locally extinct, and both species that still breed there critically endangered (Mayrose et al., 2017). The Israeli Griffon Vultures’ (Gyps fulvus) population decreased by 50% in ~18 years, and the number of breeding colonies decreased by over 80% in ~53 years, due to poisoning, electrocutions, habitat loss and low reproduction success rates (Choresh, Burg, Trop, Izhaki, & Malkinson, 2019; Mayrose et al., 2017). To overcome this trend, which started in the 1950s, a conservation translocation project of captive-bred Griffon Vultures has been operating since 1989, with over 150 Griffon Vultures released to the wild between 1993 and 2018. During this period, the project’s managers attempted different captive breeding and release protocols, which all ended in the successful release of vultures to the wild. However, the effects of theses protocols on individual survival post release were never tested. We aimed to inform management decisions regarding the best possible captive-breeding and release protocols for this project so that it can increase its positive effect on the Griffon Vulture populations in Israel and elsewhere.

For this purpose, we used a mark-resight approach to study the survival of captive-bred translocated Griffon Vultures in Israel, and the factors that affect it. We used a long-term observations database of released captive-bred vultures, all marked by individually unique color rings and wing tags, readable from a distance. Using this dataset, we calculated the annual survival of released captive-bred vultures and tested the effect of different factors on their survival: release location and age, season of release, rearing method used in captivity and the time the birds spent in the wild. While the results of this analysis are aimed to be directly implemented to improve the success of the Israeli Griffon Vultures’ translocation project, they can also be used for similar projects. In addition, these results can provide more general conclusions about the importance of early life experience for survival in novel environments.

2 METHODS

2.1 Captive-breeding and release protocol

All captive-bred Griffon Vultures were artificially incubated at the Jerusalem Zoo. Taking the eggs from vulture pairs to be artificially incubated ensured that the parents do not harm them and usually resulted in a replacement clutch. Of the 60 vultures released to the wild during the study period, 47 are offspring of captive Griffon Vultures’ pairs which were kept in different facilities in Israel. These pairs are of non-releasable birds due to physical condition caused by trauma or life history. Another 11 vultures were brought to the captive breeding facilities as eggs and two others as chicks from nests in the wild at Gamla Nature Reserve (32.9 N, 35.73 E) as part of a management measure. During the first 4 months of their lives, chicks were rear in either by vulture pairs (which can be their biological parents or other vultures) or by hand rearing. At the age of ca. 120 days, the chicks were moved to a large aviary at the Hai-bar Carmel breeding facility (32.75 N, 35.01 E) with other vultures that are intended for release. All vultures in this study were released in either the Hai Bar Carmel Nature Reserve, on
Mt. Carmel or at Gamla Nature Reserve, in the Golan Heights, 70 km east of Hai-bar Carmel. Vultures that were released at the Golan Heights were moved to a large aviary at their release location a few months prior to their release.

2.2 | Database

All captive-bred Griffon Vultures were released with an individually unique color ring and since 2007 also with unique wing tags, which can be easily read from a distance using binoculars or a telescope. Besides the initial tagging and ringing, vultures were often trapped during routine monitoring of the wild population; in these cases, their rings and tags were examined and replaced if needed. Rangers from the Israel Nature and Parks Authority (INPA) were instructed to look for these markings whenever they observe a vulture. These observations, alongside observations from the general public and from death records, were recorded by the INPA. Over 5,000 observations were recorded between 1996 and 2018, 3,502 of which were recorded since 2010. Due to this drastic rise in the number of observations since 2010, we only analyzed data of the 60 birds released between 2010 and 2018.

2.3 | Statistical analyses

To estimate the survival of the released Griffon Vultures, we used a mark-resight statistical approach. All analyses were made using the MARK program, according to the Burnham statistical method for joint live encounter and dead recovery data (Burnham, 1993; White & Burnham, 1999). For each analysis we used monthly observation as the time interval between observations, meaning that if there were multiple observations during the same month, only one was considered in the model. To calculate annual survival (S), each month's observation was weighted as 1/12 of the total survival. To achieve better survival estimates, the Burnham statistical method calculates the probability that an animal was alive and observed, given that it is in the sampling area (p), the probability that an animal was found dead and reported (r) and the probability that an animal is in the sampling area, given that it is alive (F, fidelity), all of which were calculated monthly. The studied vultures were assumed to stay in Israel throughout their lives, based on data from 13 GPS-tagged individuals since 2007 (Own data, unpublished) and on the finding that among the 3,502 observations, only 15 were made more than 70 km from the release sites. Therefore, we set fidelity (F) to equal one, implying that all birds were always in the sampling area.

To assess the effects of different pre- and post-release factors on the vultures' survival, we compared groups according to different characteristics. At first, we attempted to analyze the effects of all characterizations in one analysis, but models with more than two groups failed to converge due to the small sample size. Accordingly, we used three separate analyses: (a) release location: the Golan Heights (n = 16 vultures) or the Carmel Mountain (n = 44); (b) rearing method: by adult vultures (n = 19) or by hand rearing (n = 41); (c) release season: winter (December–February, n = 12), Spring (March–May, n = 17), Summer (June–August, n = 10) or Fall (September–November, n = 21). Two covariates were used in each analysis: the age of the bird during release (in months) and the time the bird spent in the wild at the occasion of each observation (time in the wild), the latter was categorized to “first year” and “after first year” in the wild. To better understand the effect of release age on survival, a fourth analysis was done in which the interaction between release age and time in the wild was the only explanatory variable for survival.

Analyses were done in three stages. First, we used a forward model selection using the corrected Akaike Information Criterion (AICc) to select the best covariates explaining p and r, while keeping S with no covariates (Burnham & Anderson, 2002). Second, we compared between models containing one of the groups' covariates (release site, rearing method or release season) and all possible combination with the other covariates (release age and time in the wild), keeping the covariates of p and r as the best model found in the first stage. These models were also compared to a model with no covariates for S and a model with only time in the wild as a covariate for S. Finally, we used model averaging based on the weights given to each model (Anderson, 2008; Cooch & White, 2009) using the RMark package for R (Laake & Rexstad, 2009).

3 | RESULTS

The best models explaining the probability that a vulture was alive and observed (p) and the probability it was found and reported as dead (r) for the effects of release location, rearing method, release season and age at release and time in the wild are presented in Table 1. The models used in the model selection process are presented in Supporting Information. The probability that an animal was alive and observed (p) was similar among all groups, except for birds released in spring, for which the probability was lower (Table 1). The probability that an
animal was found dead and reported (r) was much lower after the first year in the wild for all groups (Table 1).

For the release site analysis, two models’ AIC weight represented more than 50% of the relative likelihood (AIC weights = 0.36, 0.26). Both models included group, release age and time in the wild as explanatory variables for survival, while the model with the higher AIC weight (ΔAIC between the first and second model = 0.63) also included an interaction between time in the wild and age at release (Data S1). Model averaging estimates for survival were 0.219 ± 0.091 and 0.693 ± 0.07 (mean ± SE) for birds released at the Golan Heights and the Carmel Mountain, respectively, during their first year in the wild, and 0.313 ± 0.13 and 0.779 ± 0.0441 for birds released in these two locations later in their life (Figure 1a).

For the rearing method analysis, two models’ AIC weight represented 50% of the relative likelihood (0.27, 0.23). Both models included group, release age and time in the wild as explanatory variables for survival, while the model with the lower AIC weight (ΔAIC between the first and second model = 0.35) also included an interaction between group and age at release and an interaction between time in the wild and age at release (Data S1). Model averaging estimates for survival were 0.494 ± 0.0778 and 0.71 ± 0.0934 for birds reared by human caretakers or by vultures, respectively, during their first year in the wild and 0.672 ± 0.0613 and 0.837 ± 0.0571 for birds reared by these two methods later in life (Figure 1b).

For the release season analysis, two models’ AIC weight represented 50% of the relative likelihood (0.27, 0.23). Both models included group, release age and time in the wild as explanatory variables for survival, while the model with the higher AIC weight (ΔAIC between the first and second model = 0.35) also included an interaction between group and age at release and an interaction between time in the wild and age at release (Data S1). Model averaging estimates for survival were 0.479 ± 0.046 and 0.71 ± 0.055 for birds released in the winter during their first year in the wild and 0.19 ± 0.076 and 0.12 ± 0.054 for birds released during the spring during their first year in the wild (Figure 1b).

---

**Table 1** Best models’ explanatory variables and estimates for p and r

| Explanatory variables | Group        | Estimate ± SE |
|-----------------------|--------------|---------------|
| Release site          |              |               |
| p Release site × release age | Golan | 0.74 ± 0.045  |
|                       | Carmel      | 0.73 ± 0.012  |
| r Experience + release age | 1stY  | 0.85 ± 0.083  |
|                       | Post 1stY   | 0.13 ± 0.069  |
| Rearing method        |              |               |
| p Rearing method × release age | Vultures | 0.74 ± 0.021  |
|                       | Hand        | 0.7 ± 0.016   |
| r Experience + release age | 1stY  | 0.85 ± 0.082  |
|                       | Post 1stY   | 0.13 ± 0.069  |
| Age at release and time in the wild |          |               |
| p Release age | All | 0.73 ± 0.012  |
| r Experience + release age | 1stY  | 0.85 ± 0.082  |
|                       | Post 1stY   | 0.13 ± 0.068  |
| Release season        |              |               |
| p Release season × release age + release season × experience | Winter 1stY | 0.8 ± 0.046  |
|                       |            | Winter post 1stY | 0.71 ± 0.055 |
|                       |            | Spring 1stY    | 0.19 ± 0.076  |
|                       |            | Spring post 1stY | 0.12 ± 0.054 |
|                       |            | Summer 1stY    | 0.75 ± 0.044  |
|                       |            | Summer post 1stY | 0.82 ± 0.023 |
|                       |            | Fall 1stY      | 0.75 ± 0.034  |
|                       |            | Fall post 1stY | 0.66 ± 0.025  |
| r Experience + release age | 1stY  | 0.87 ± 0.078  |
|                       | Post 1stY   | 0.13 ± 0.07   |

Note: p, probability that an animal was alive and observed, given that it is in the sampling area; r, probability that an animal was found dead and reported, 1stY, first year in the wild. The complete models are presented in Data S1.
\[ \pm 0.136, \ 0.563 \pm 0.114, \ 0.696 \pm 0.127, \text{ and } 0.601 \pm 0.86 \]
for birds released during winter, spring, summer or fall, respectively, during their first year in the wild and \(0.645 \pm 0.138, \ 0.725 \pm 0.0959, \ 0.822 \pm 0.0769, \text{ and } 0.754 \pm 0.0594 \) for birds released in these four seasons later in life (Figure 1c).

Finally, release age positively affected the survival of vultures after their first year in the wild but did not change the survival rate of vultures during their first year in the wild (Figure 2).

**FIGURE 1** Survival estimates of translocated captive-bred Griffon Vultures divided into different groups by: (a) release location (Carmel Mountain and the Golan Heights); (b) rearing method during the first 4 months of their lives (hand rearing or reared by adult vultures); (c) release season. Error bars denote standard error

**FIGURE 2** The effect of release age on the survival of translocated captive-bred Griffon Vultures, during their first year in the wild and later (experienced). The grey background denotes 95% CI

### 4 DISCUSSION

In this study we found strong effects of several factors on the post release survival of captive-bred Griffon Vultures in Israel. Survival was affected by release location, rearing method, release season, release age and the time passed after their release to the wild. These factors affect the vultures’ survival by shaping their experiences, usually during their early life stages or shortly after their release. Understanding the effects of an individual’s experiences on its survival can assist in conservation translocations’ decision-making, such as when and how to monitor the released animals and whether and how to assist their adaptation to the new environment (Bosè & Sarrazin, 2007; Oro, Margalida, Carrete, Heredia, & Donázar, 2008). Importantly, our results emphasize the ability of translocations’ managers to make simple yet crucial modifications to their program that can significantly increase the success rate of their translocation project.

A key result of our study is the positive effect release age has on the survival of vultures after their first year in the wild, while not affecting vultures’ survival during their first year after release. The increased survival with age most likely means that vultures acquire important skills during their time in captivity, either due to the properties of their captive environment during this critical period, or because of the effects of maturation regardless of their surroundings (captive or wild). Regardless of their origin, these skills or behavioral changes were found to be important for the vultures’ survival. For example, adult Griffon Vultures move less than juveniles
which potentially exposes them to less risks, show improved physiological skills such as flight, and possibly better social skills such as interactions with conspecifics and non-conspecifics (Harel, Horvitz, & Nathan, 2016; Moreno-Opo, Trujillano, & Margalida, 2016; Mundy, Butchart, Ledger, & Piper, 1992). However, it seems that the challenges of adjusting to the post-release novel environment (Berger-Tal & Saltz, 2014) eliminate the positive effects of age, and they are therefore manifested only after the vultures gain experience in the wild. Alternatively, the observed difference in survival rate between the first year in the wild and later in life might be caused by the removal of less skilled vultures from the population during the first year; a process that can mask the effects of release age on the vultures’ survival during this critical period.

The biggest differences in survival were found between release sites (ca. 40%), despite the two release locations being only 70 km apart. Differences in survival and/or dispersal rates among release sites were previously found for translocated Griffon Vultures (Le Gouar et al., 2008). The very low number of observations of the studied birds outside each of the two release sites suggests that in our study dispersal was insignificant, thus we interpret the difference between release sites as a difference in survival. Le Gouar et al. (2008) suggested that differences among colonies can be explained by spatial heterogeneity of threats to vultures at different locations. This hypothesis probably explains the differences found in our study: while the Carmel Mountain colony has been stable over the last few years, the Golan Heights colony is declining, at least partially due to poisoning which during the period of this study occurred only at the Golan Heights (Choresh et al., 2019 and Authors unpublished data).

Vultures also survived better when reared by adult vultures (parental rearing) compared to when reared by human caretakers (hand rearing). Parental reared birds had 18% and 13% higher survival rate than hand reared birds during the first year in the wild and later in life, respectively. Although lower survival rates are expected for hand reared animals compared with parental reared animals, evidence suggest that under some circumstances hand rearing might even have benefits over parental rearing (Seddon et al., 2007). For example, in a long effort to release captive-bred Sandhill Cranes (Grus canadensis) to the wild, hand rearing was first unsuccessful, but dramatically improved following modifications of the rearing protocol, eventually outperforming parental rearing (Ellis et al., 2000; Ellis, Lewis, Gee, & Smith, 1992). These results suggest that the effects of different rearing methods are complex and should be examined carefully (Seddon et al., 2007). Interestingly, the differences in the rearing methods of the vultures were only during the first ca. 120 days of their lives (afterwards all vultures were moved to a shared aviary), during these days they were fed the same food and at similar feeding intervals. Thus, to better understand the lower survival of hand reared vultures, future studies should thoroughly examine the differences during this short (and probably critical) period, possibly focusing on interactions between the chicks and their parents or the facilities in which they are kept. More generally, this relates to previous studies showing that minor changes in experiences during the captive period can have crucial effects on the behavior and survival of animals post-release (Whiteside et al., 2016; Whiteside, Sage, & Madden, 2015). Pre-release experiences that can aid the development of important post-release skills for the vultures include interactions with other conspecifics, development of flight muscles and encountering different weather conditions. Future studies that will characterize skills that improve pre- and post-release behaviors can help better design the captivity period to assist pre-release animals gain experiences that will develop required skills to increase post-release survival.

Release season also affected survival, with 22% and 18% higher survival rates for vultures released in summer compared with vultures released in winter, for first year in the wild and later in life, respectively. Griffon Vultures usually only migrate during their first couple of years (Mundy et al., 1992). However, the observations used in this study suggest that none of the released captive-reared vultures migrated, possibly because the “urge” to migrate was suppressed by releasing the vultures after their migration usually occurs. Additionally, food is supplied at feeding stations throughout the year, and thus cannot be used to explain the seasonal survival difference. Ruling out differences related to migration and food availability, seasons’ climatic characteristics might be the cause for survival differences. Israel’s Mediterranean climate is characterized by cold and rainy winters (especially in northern Israel, where the vultures are released), hot and dry summers and mild temperatures with occasional rainfall during spring and fall. These conditions affect the temporal distribution of vertical hot air currents (thermals) whose occurrence and strength are dependent on hot weather conditions with no rain and no strong winds. By using thermals, large birds such as vultures can avoid flapping flight and instead soar and glide, minimizing their flight related energy expenditure 3–12 times (Duriez et al., 2014; Norberg, 1996; Videler, 2006). Additionally, the ability to properly use thermals and expend minimum energy during flight is acquired with age (Harel et al., 2016; Harel, Horvitz, & Nathan, 2016). Thus, vultures released in winter are probably
confronted with elevated costs of thermoregulation and flight (Duriez et al., 2014), added to the already high energetic costs required to learn their new environment and required proficiencies (Berger-Tal et al., 2014; Harel, Horvitz, & Nathan, 2016).

We note that the monitoring on which our analyses are based had some limitations. Importantly, better monitoring should include the monitoring of tag loss and the fitness of the translocated animals to increase the accuracy and relevance of the results. Additionally, a larger sample size (a rare attribute of translocations) would allow the use of one model that includes all factors, thus increasing the strength of the model and the accuracy of the results. Nevertheless, the results of this study demonstrate how managers of conservation translocations can learn about the success of their project and what affects it through monitoring, and adapt their captive rearing methods and release protocols accordingly (McCarthy, Armstrong, & Runge, 2012). We presented major differences in survival rates, which mostly depended on captive breeding and release protocols that can be further examined and changed. It is important to note however, that sometimes such changes are unfeasible, either due to financial or ethical considerations. Most important, in our study, even the group with the worst survival rate, which was found for vultures released at the Golan Heights, still increased the total population size of this locally Critically Endangered species. Even more so, although hand reared vultures survive less, 50% of them survive the difficult first year in the wild, and this method allows an increase in the annual yield of the captive breeding program because it enables an extra brood for many pairs. We encourage conservationists to monitor translocated animals in the best possible way they can and analyze their monitoring data on a regular basis. The more monitoring and analyses done on such datasets, the better we can understand and conserve biodiversity.

ACKNOWLEDGMENTS

The conservation translocation project for Griffon Vultures in Israel is led by the Israel Nature and Parks Authority (INPA) and financed by the Porsim Kanaf partnership with support and cooperation from Keren Hayesod, Segre’ Foundation, The I. Meier Segals Garden for Zoological Research at the Tel-Aviv University, The Zoological Center Tel-Aviv—Ramat-Gan, Ramat Hanadiv Gardens, Arkia and El-Al. Chicks’ rearing is done in partnership with the Jerusalem Biblical Zoo. Most of the work done to prepare the vultures for translocation is done by the Hai-bar Carmel Nature Reserve team, led by A. Baron and S. Simchi. We would like to thank all the people who reported observations of tagged Griffon Vultures, and especially the INPA rangers. We also thank G. White and I. Schekler who assisted with the MARK analysis, D. Saltz, O. Spiegel, and N. Anglister for comments on early drafts of this manuscript and two anonymous reviewers for their helpful comments. R.E. was supported by the Israeli Academy of Science’s Adams Fellowship and the Ben-Gurion University’s Negev Fellowship.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Ron Efrat, Ohad Hatzofe, Ygal Miller and Oded Berger-Tal conceived the ideas and designed methodology; Ohad Hatzofe and Ygal Miller collected the data and Ron Efrat organized and analyzed the data; Ron Efrat led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data used for this study belongs to the Israel Nature and Parks Authority. Access to the data will be granted upon request.

ETHICS STATEMENT

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

ORCID

Ron Efrat https://orcid.org/0000-0002-6129-0596

REFERENCES

Anderson, D. R. (2008). In D. R. Anderson (Ed.), Model based inference in the life sciences: A primer on evidence. New York: Springer.

Bell, B. D. (2016). Behavior-based management: Conservation translocations. In O. Berger-Tal & D. Saltz (Eds.), Conservation behavior (pp. 212–246). Cambridge: Cambridge University Press.

Berger-Tal, O., Blumstein, D. T., & Swaisgood, R. R. (2019). Conservation translocations: A review of common difficulties and promising directions. Animal Conservation, 23(2), 121–131.

Berger-Tal, O., Nathan, J., Meron, E., & Saltz, D. (2014). The exploration-exploitation dilemma: A multidisciplinary framework. PLoS ONE, 9, e95693.

Berger-Tal, O., & Saltz, D. (2014). Using the movement patterns of reintroduced animals to improve reintroduction success. Current Zoology, 60, 515–526.

Bosé, M., & Sarrazin, F. (2007). Competitive behaviour and feeding rate in a reintroduced population of Griffon Vultures Gyps fulvus. Ibis, 149, 490–501.

Buechley, E. R., & Şekercioğlu, C. H. (2016). The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. Biological Conservation, 198, 220–228.
Burnham, K. P. (1993). A theory for combined analysis of ring recovery and recapture data. In J. D. Leberton & P. M. North (Eds.), Marked individuals in the study of bird population (pp. 199–213). Basel: Birkhäuser-Verlag.

Burnham, K. P., & Anderson, D. R. (2002). In K. P. Burnham & D. R. Anderson (Eds.), Model selection and inference: A practical information theoretic approach (2nd ed.). New York: Springer-Verlag.

Butchart, S. H. M., Stattersfield, A. J., & Collar, N. J. (2006). How many bird extinctions have we prevented? Oryx, 40, 266. Available from http://www.journals.cambridge.org/abstract_S0030650506000950-278.

Choresh, Y., Burg, D., Trop, T., Izhaki, I., & Malkinson, D. (2019). Fear and exploration in food supply during early life influences boldness in fish. Behavioral Ecology, 21, 501–506.

Chopin, B. B., Morrell, L. J., & Krause, J. (2010). Unpredictability. Cooch, E., & White, G. C. (2009). In E. G. Cooch & G. C. White (Eds.), Program MARK A gentle introduction (18th ed.) Available from paper2://publication/uuid/60AD4742-AFB2-43CE-82E5-08D19E9EDC916.

Burnham, K. P. (1993). A theory for combined analysis of ring recovery and recapture data. In J. D. Leberton & P. M. North (Eds.), Marked individuals in the study of bird population (pp. 199–213). Basel: Birkhäuser-Verlag.

Burnham, K. P., & Anderson, D. R. (2002). In K. P. Burnham & D. R. Anderson (Eds.), Model selection and inference: A practical information theoretic approach (2nd ed.). New York: Springer-Verlag.

Butchart, S. H. M., Stattersfield, A. J., & Collar, N. J. (2006). How many bird extinctions have we prevented? Oryx, 40, 266. Available from http://www.journals.cambridge.org/abstract_S0030650506000950-278.

Choresh, Y., Burg, D., Trop, T., Izhaki, I., & Malkinson, D. (2019). Long-term griffon vulture population dynamics at Gamla nature reserve. Journal of Wildlife Management, 83, 135–144.

Cooch, E., & White, G. (2009). In E. G. Cooch & G. C. White (Eds.), Program MARK A gentle introduction (18th ed.) Available from paper2://publication/uuid/60AD4742-AFB2-43CE-82E5-08D19E9EDC916.

Duriez, O., Kato, A., Tromp, C., Dell’Omo, G., Vyssotski, A. L., Sarrazin, F., & Ropert-Coudert, Y. (2014). How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. PLoS ONE, 9, e84887 Public Library of Science. Available from http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3893159&tool=pmcentrez&rendertype=abstract.

Ebenhard, T. (1995). Conservation breeding as a tool for saving animal species from extinction. Trends in Ecology & Evolution, 10, 438–443.

Ellis, D. H., Gee, G. F., Hereford, S. G., Olsen, G. H., Chisolm, T. D., Nicolich, J. M., ... Hatfield, J. S. (2000). Post-release survival of hand-reared and parent-reared Mississippi Sandhill cranes. The Condor, 102, 104–112.

Ellis, D. H., Lewis, J. C., Gee, G. F., & Smith, D. G. (1992). Population recovery of the whooping crane with emphasis on reintroduction efforts: Past and future. North American Crane Workshop Proceedings, 6, 142–150.

Ewen, J. G., Armstrong, D. P., Parker, K. A., & Seddon, P. J. (Eds.). (2012). Reintroduction biology: Integrating science and management. West Sussex, UK: Wiley-Blackwell.

Feenders, G., Klaus, K., & Batson, M. (2011). Fear and exploration in european starlings (Sturnus vulgaris): A comparison of hand-reared and wild-caught birds. PLoS ONE, 6, e19074.

Fischer, J., & Lindenmayer, D. B. (2000). An assessment of the published results of animal relocations. Biological Conservation, 96, 1–11.

Geronimo, J. M., Field, K. J., Griffiths, R. A., Clulow, S., Foster, J., Harding, G., & Swaigood, R. R. (2014). Moving towards greater success in translocations: Recent advances from the herpetofauna. Animal Conservation, 17, 1–3.

Harel, R., Duriez, O., Spiegel, O., Fluur, J., Horvitz, N., Getz, W. M., ... Nathan, R. (2016). Decision-making by a soaring bird: Time, energy and risk considerations at different spatio-temporal scales. Philosophical Transactions of the Royal Society B: Biological Sciences, 371, 20150397 Available from http://rstb.royalsocietypublishing.org/lookup doi/10.1098/rstb.2015.0397

Harel, R., Horvitz, N., & Nathan, R. (2016). Adult vultures out-perform juveniles in challenging thermal soaring conditions. Scientific Reports, 6, 27865 Nature Publishing Group. Available from http://www.nature.com/articles/srep27865

IUCN (2013). Reintroduction and invasive species specialist groups’ task force on moving plants and animals for conservation purposes guidelines for reintroductions and other conservation translocations. Available from https://portals.iucn.org/library/efiles/documents/2013-009.pdf.

Jule, K. R., Leaver, L. A., & Lea, S. E. G. (2008). The effects of captive experience on reintroduction survival in carnivores: A review and analysis. Biological Conservation, 141, 355–363.

Laake, J., & Rexstad, E. (2009). RMark - an alternative approach to building linear models in MARK. Page Appendix C In E. G. Cooch & G. C. White (Eds.), Program MARK: A gentle introduction Available from http://www.phidot.org/software/mark/docs/book/pdf/app_3.pdf.

Le Gouar, P., Robert, A., Henriquet, S., Choisy, J.-P., Lecuyer, P., Tessier, C., & Sarrazin, F. (2008). Roles of survival and dispersal in reintroduction success of griffon vulture (Gyps fulvus). Ecological Applications, 18, 859–872.

Liukkonen-Attila, T., Saartola, R., & Hissa, R. (2000). Impact of hand-rearing on morphology and physiology of the capercaillie (Tetrao urogallus). Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology, 125, 211–231.

Mason, G. J. (2010). Species differences in responses to captivity: Stress, welfare and the comparative method. Trends in Ecology and Evolution, 25, 713–721 Elsevier Ltd. Available from https://doi.org/10.1016/j.tree.2010.08.011

Mathews, F., Ormos, M., McLaren, G., Gelling, M., & Foster, R. (2005). Keeping fit on the ark: Assessing the suitability of captive-bred animals for release. Biological Conservation, 121, 569–577.

Mayrose, A., Labinger, Z., Steinitz, O., Hatzofe, O., Haviv, E., Perlman, Y., … Leader, N. (2017). In A. Mayrose, G. Vin, Z. Labinger, & O. Steinitz (Eds.), The red book of birds in Israel, Israel: INPA & SPNI Available from https://aves.redlist.parks.org.il

McCarthy, M. A., Armstrong, D. P., & Runge, M. C. (2012). Adaptive management of reintroduction. In J. G. Ewen, D. P. Armstrong, K. A. Parker, & P. J. Seddon (Eds.), Reintroduction biology: Integrating science and management (pp. 256–289). Oxford: Wiley-Blackwell.

Moreno-Opo, R., Trujillano, A., & Margalida, A. (2016). Behavioral coexistence and feeding efficiency drive niche partitioning in European avian scavengers. Behavioral Ecology, 27, 1041–1052.

Mundy, P., Butchart, D., Ledger, J., & Piper, S. (1992). The vultures of Africa. San Diego, CA: Academic Press.

Norberg, U. M. (1996). Energetics of flight. In C. Carey (Ed.), Avian energetics and nutritional ecology (pp. 199–249). Boston, MA: Springer Available from https://doi.org/10.1007/978-1-4613-0425-8_7%5Cnhttp://link.springer.com/chapter/10.1007/978-1-4613-0425-8_7%5Cnhttp://link.springer.com/content/pdf/10.1007/978-1-4613-0425-8_7.pdf.

Oro, D., Margalida, A., Carrette, M., Heredia, R., & Donázar, J. A. (2008). Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. PLoS ONE, 3, e4084.

Rotics, S., Kaatz, M., Resheff, Y. S., Turjeman, S. F., Zurell, D., Sapir, N., … Nathan, R. (2016). The challenges of the first migration: Movement and behaviour of juvenile vs. adult white
storks with insights regarding juvenile mortality. *Journal of Animal Ecology, 85, 938–947* Available from http://doi.wiley.com/10.1111/1365-2656.12525

Safford, R., Andevski, J., Botha, A., Bowden, Christopher G.R., Crockford, N, ... Williams, Nick P. (2019). Vulture conservation: The case for urgent action. *Bird Conservation International, 29, 1–9.*

Seddon, P. J., & Armstrong, D. P. (2016). Reintroduction and other conservation translocations: History and future developments. In D. S. Jachowski, J. J. Millsapugh, P. L. Angermeyer, & R. Slotow (Eds.), *Reintroduction of fish and wildlife populations* (pp. 7–27). Oakland, CA: University of California Press.

Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology, 21, 303–312.*

Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science, 345, 406–412* Available from http://www.sciencemag.org/cgi/doi/10.1126/science.1251818

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

Slagsvold, T., & Wiebe, K. L. (2007). Learning the ecological niche. *Proceedings of the Royal Society B: Biological Sciences, 274, 19–23.*

Snyder, N. F. R., Derrickson, S. R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D., Miller, B. (1996). Limitations of captive breeding in endangered species recovery. *Conservation Biology, 10(2), 338–348.*

Sutherland, W. J., Armstrong, D., Butchart, S. H. M., Earnhardt, J. M., Ewen, J., Jamieson, I., ... Tatayah, V. (2010). Standards for documenting and monitoring bird reintroduction projects. *Conservation Letters, 3, 229–235.*

Videler, J. J. (2006). Bird flight modes. In J. J. Videler (Ed.), *Avian flight* (pp. 118–155). Oxford: Oxford University Press.

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

Whiteside, M. A., Sage, R., & Madden, J. R. (2015). Diet complexity in early life affects survival in released pheasants by altering foraging efficiency, food choice, handling skills and gut morphology. *Journal of Animal Ecology, 84, 1480–1489.*

Whiteside, M. A., Sage, R., & Madden, J. R. (2016). Multiple behavioural, morphological and cognitive developmental changes arise from a single alteration to early life spatial environment, resulting in fitness consequences for released pheasants. *Royal Society Open Science, 3, 160008* Available from http://rsos.royalsocietypublishing.org/lookup/doi/10.1098/rsos.160008

Williams, B. K. (2011a). Adaptive management of natural resources-framework and issues. *Journal of Environmental Management, 92, 1346–1353* Elsevier Ltd. Available from: https://doi.org/10.1016/j.jenvman.2010.10.041

Williams, B. K. (2011b). Passive and active adaptive management: Approaches and an example. *Journal of Environmental Management, 92, 1371–1378* Elsevier Ltd. Available from https://doi.org/10.1016/j.jenvman.2010.10.039

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

*How to cite this article:* Efrat R, Hatzofe O, Miller Y, Berger-Tal O. Determinants of survival in captive-bred Griffon Vultures *Gyps fulvus* after their release to the wild. *Conservation Science and Practice. 2020;2:e308. https://doi.org/10.1111/csp2.308*