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RESEARCH ARTICLE

Reinforcement of an endangered goose population: the effect of age and interspecific fostering on survival of released birds

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The release of captive-bred or translocated individuals is a strategy used worldwide to support threatened animal populations. By capture–recapture analysis, we examined the survival of released individuals when reinforcing a critically endangered Lesser White-fronted Goose population. Our analysis includes data from 646 birds, released 1984–2017, including two different age classes, divided in two distinct periods when different techniques were used. Fledglings were released with foster parents of Barnacle Geese in the first period and by a soft release without support of foster parenting in the second period. Yearlings were released by soft release in both periods. We find that use of foster parents enhances survival rates, but these differences were detectable only in the first year of life. Fledglings supported by foster parents showed significantly higher survival compared to yearlings released by soft release, but this difference was not clear when soft release was applied to both groups. Resighting data suggest that most losses occurred during the acclimation period following the release. Foster parenting may enhance survival rates due to social learning enabling the transfer of crucial behaviors (e.g. feeding, anti-predator, and migration) to released individuals. However, these conservation benefits need to be balanced against costs and potential inherent risks related to foster parenting, including the imprinting of undesired behaviors in released individuals, such as hybridization. Based on our results, we advise conservationists to carefully consider foster parenting as one method to improve survival probability, especially if capacity to produce individuals to be released is a limiting factor.

Key words: Acclimatation, bird, capture–recapture, mortality, social learning, soft release

Implications for Practice

- Conservationist practitioners, choosing between releasing techniques, for social learning species, should apply foster parenting, rather than soft release to increase survival.
- Our data indicate that the highest mortality is found during the period immediately following the release. This suggests that supportive measures, such as predator control, may also play an important role for the survival of released individuals.
- Release techniques not only influence survival but also entail costs and potential risks of unwanted side effects. Therefore, when selecting a technique, conservationists must consider financial constraints, animal welfare aspects, and what behavioral traits are to be preserved.
- High resighting probability is crucial to enable capture–recapture analysis of released individuals and can be achieved by citizen science reporting or professional observers.

Introduction

The escalating loss of global biodiversity necessitates more informed decisions and practices for conservation and restoration of populations (Ewen et al. 2012). Translocations, which are defined as the deliberate movement of biota, encompass a range of techniques and have become a common practice in conservation worldwide (Seddon 2010). The success of releases of individuals to aid conservation work relies on a variety of factors, including knowledge about released species' ecology and behavior, support of local communities, funding, coordinated activities among stakeholders, and release technique (Taylor et al. 2017; Berger-Tal et al. 2020).

Translocations of wild specimens are often preferable, as such individuals typically need limited acclimation and few supportive measures but can be limited by the size and conservation

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needs of the source population. Consequently, release of captive-bred individuals, by means of introductions, reintroduction, or reinforcement of populations, enables a wider use within conservation as breeding programs may deliver individuals to be released, regardless of the development of wild source populations (Seddon et al. 2007). Integration of released individuals into their new environment can be conducted via a "hard release," without further support, or a "soft release," including measures to aid the individual during transition from one habitat to another (Resende et al. 2021). Supportive interventions during soft release may, for example, include applying a transition period in a release pen or similar shelter, providing extra feeding possibilities, and implementing anti-predation measures (Sasmal et al. 2015). Further, additional support from human guarding or fostering individuals (conspecifics or other species) can assist the individual during the acclimation period (Mini et al. 2013). In addition to release technique per se, also age and condition of the released individuals can have significant impact on success rate (Parish & Sotherton 2007; King et al. 2013).

For migratory species, the ability of released individuals to complete the annual cycle, and ability to return to the release site (homing) adds challenges for conservation. For flock-living species, migration strategies can be transferred by social learning (Fagan et al. 2012; Mueller et al. 2013). For example, young geese and cranes can learn migration routes and other behavioral traits from their parents (Fritz et al. 2000; Németh & Moore 2007, 2014). Hence, survival of released individuals, naïve to migration, can be increased when supported by wild adult conspecifics (Mini et al. 2013), and social learning may be important for the success of releases (Ellis et al. 2003; Mueller et al. 2013). Artificial guidance, e.g. by using airplanes, of released geese and cranes, has also been used with varying success (Lishman et al. 1997; Sladen et al. 2002; Ellis et al. 2003).

Despite a widespread use of releasing individuals within conservation, scientific evaluations dissecting demographic impact of different techniques are still relatively scarce (Armstrong & Reynolds 2012; Seddon et al. 2014; Robert et al. 2015). Such knowledge is essential to increase the success rate of implementation (Servanty et al. 2014; Berger-Tal et al. 2020). Studies of demographic variables, such as age at release, survival rates, recruitment rate, and reproduction of released individuals, in relation to different translocation techniques would preferably be done with an experimental approach (Dayananda et al. 2021), but such studies are rare (Ranke et al. 2017).

The Lesser White-fronted Goose (*Anser erythropus*) was once a widespread species in Arctic and sub-Arctic regions in Fennoscandia and Northern Eurasia. Across the entire breeding range, fragmentation of the previous distribution began in the early 1900s, with the following geographical separation between birds breeding in Fennoscandia and Russia. Birds breeding in Fennoscandia were migrating along a corridor via Eastern Europe to wintering grounds in Western Asia and the eastern Mediterranean region (Madsen 1991). Even if limited genetic exchange between Lesser White-fronted Geese breeding in Western Russia and Fennoscandia remains (primarily males; Ruokonen et al. 2010), the population in Russia is defined as the Western Main Population and is distinguished from birds breeding in Fennoscandia (Jones et al. 2008). The Fennoscandian population suffered a dramatic decline during the first half of 1900-century and only 60–90 breeding pairs remained in the 1980s. The remnant population in Sweden, which consisted of only 20 pairs in 1980 (Norderhaug & Norderhaug 1984), has been in focus of dedicated conservation efforts and monitoring since the mid-1970s (Andersson 2019). Conservation efforts in Sweden have been geographically focused on one focal population, which has recently been estimated to be 25–35 breeding pairs (year 2022; Larsson et al. 2023). Besides the Swedish population, breeding birds are found in an area in Northern Norway (about 100 individuals in 2020; Marolla et al. 2023). Differences in migration routes (Kruckenberg et al. 2023) and limited genetic exchange (Díez-del-Molino et al. 2020) suggest these two populations should be treated as two separate conservation units. The Swedish National Action Plan formulates a long-term conservation target of 200 breeding pairs in Sweden (Naturvårdsverket 2011).

During a first period (here after period 1) of reinforcements of the wild recipient population (1981–1999), Barnacle Geese (*Branta leucopsis*) were used as foster parents to fledglings of captive-bred Lesser White-fronted Geese (von Essen 1991; Andersson & Holmqvist 2010). In parallel, a smaller number of yearlings (i.e. birds born the previous year) were released in groups without the support of adoptive parents. The use of foster parents had two objectives: (1) reinforce the recipient population demographically to avoid extinction and (2) change migration traditions of Lesser White-fronted Geese breeding in Sweden (von Essen 1991; Andersson 2019). Changing natal migration habits of a population is an unorthodox conservation initiative. But during this time, chances to successfully decrease mortality along the route by other conservation interventions were regarded as extremely low (Andersson 2019).

A second phase (here after period 2) of reinforcement started in 2010, when a soft release technique without using foster parents was applied, but still in the same area as in the earlier period (Naturvårdsverket 2011). In period 2, birds were released in groups of mixed ages (fledglings and yearlings). The alteration of release methods and use of different age classes allow an evaluation of the different techniques used over time.

In this study we use data collected during a period of 33 (1984–2017) years to estimate the effect of different release techniques on survival of released Lesser White-fronted Geese in Sweden. Originally, these survival analyses were carried out to investigate the role of reinforcements in sustaining population viability of the recipient population (Schekkerman & Koffijberg 2020), but they proved to give valuable insights on the effect of different release techniques used. Based on earlier findings for similar species (Ellis et al. 2003; Mueller et al. 2013), we hypothesize that the use of foster parents should positively affect the survival of released Lesser White-fronted Geese, compared to release technique not including foster parenting used from 2010 onwards. Further, we hypothesize that survival of yearlings to be lower compared to fledglings supported by foster parents, but differences being less pronounced during period 2, when soft release was used for both age classes.

Methods

Recipient Population and Release Technique

An ex situ breeding program was initiated in 1977 with the objective to reinforce numbers and avoid extinction of the remnant Lesser White-fronted Goose population breeding in Sweden (von Essen 1991; Andersson & Holmqvist 2010).

The founders of the captive breeding stock of this program included wild-caught birds from Swedish Lapland (Tegelström & von Essen 1996) as well as birds from different captive populations (Ruokonen et al. 2007). In period 1 (1981–1999), 213 (80%) of 266 Lesser White-fronted Geese were released as fledglings with Barnacle Goose foster parents, and 53 (20%) were released without foster parents (detailed data in Table 1). Mean number of released individuals in 1 year was 18.3 birds (range 0–37). Starting 1983, all birds were ringed with individual combinations of color rings for identification in the field.

The foster parents originated from a semi-wild Barnacle Goose population, which facilitated surveys of breeding phenology in the field and logistics. These birds were known to winter at specific sites in the Netherlands (Andersson 2019). In the 1980s, elevated hunting mortality in combination with drastic changes in land use along the traditional migration routes were believed to be detrimental to the survival chances of the Fennoscandian Lesser White-fronted Goose population (Madsen 1991). Beside the objective to decrease mortality by changing migration trajectory to safer winter sites, the use of foster parents also aimed to improve homing performance at the release site (von Essen 1991; Andersson 2019). Resightings of color-ringed released Lesser White-fronted Geese showed that they followed the migration route presented by foster parents (von Essen 1991). Today, the great majority of the Swedish Lesser White-fronted Goose population migrates to well-protected wintering sites in the Netherlands and Germany (Kruckenberg et al. 2023).

Barnacle Goose parents incubated and hatched eggs from captive Lesser White-fronted Geese (four to six eggs per female). Entire foster families were transported by car and helicopter to the Lesser White-fronted Goose breeding area in Swedish Lapland in late June (with some annual variation, see Table S1) and released in small lakes. At arrival, whole foster families were kept in 2×2 m release pens for 2–6 hours until birds relaxed and then released. Releases in period 1, ceased in year 1999 due to concerns about introgression of Greater White-fronted Goose (*Anser albifrons*) genes in captive populations, including the breeding program, of Lesser White-fronted Goose (Ruokonen et al. 2007). Subsequently, the breeding program was dismantled, and all captive birds were euthanized (Naturvårdsverket 2011; Andersson 2019). However, later studies found no indications of introgression in the wild breeding recipient population (Díez-del-Molino et al. 2020).

After a 10-year moratorium, the reinforcement program was resumed in 2010. By then, 10–15 pairs, including descendants of the first program, were known to breed regularly in the previously known area (Naturvårdsverket 2011). The total recipient population size was estimated to be 100–120 individuals in 2012 (Koffijberg & van Winden 2013). Releases in period 2, still ongoing, are built on a complete new captive breeding population with wild-caught founders originating from the Western Main population in Russia (Jones et al. 2008; Díez-del-Molino et al. 2020). From 2010 to 2017, 380 (79% fledglings, 21% yearlings, Table 1) Lesser White-fronted Geese were released in groups using a soft release technique (Resende et al. 2021), including a transition period up to 24 hours in temporary release pens (round pens, diameter 8 m) close to known breeding territories of wild Lesser White-fronted Geese. The release pen included a net roof and surrounding electric fence to avoid predation risk and, in addition, staff guarding the pen until release.

In addition to the foster parent method, during period 1, a smaller number of birds, predominantly 1-year-old birds (yearlings), were released without the support of foster parents but in groups. Birds released as yearlings have spent a year in the breeding station, associated with the captive stock of Lesser White-fronted Geese (including their parents). In period 2, groups of mixed-age classes (fledglings and yearlings) were released together in groups. The same release sites and release period have been used during both release periods (see Table S1). Every year, during both periods, efforts to study the released birds in the field were made. But conditions in the mountains, size of release area, mobility of flocks, and behavior of Lesser White-fronted Geese have made observations challenging. Duration and observer effort have varied between years, but typically three to seven persons spent a total of 2 weeks in the release area after release until the first week of August. During an acclimation period after release, individuals may face elevated risks, and duration can vary between species, season, and individuals (Moseby et al. 2011; Armstrong et al. 2017). For the purpose of this study, we regard the acclimation period to end when the birds start autumn migration, typically 4–7 weeks after release.

Table 1. Numbers of released and individually marked Lesser White-fronted Geese in Sweden in the two release periods 1981–1999 and 2010–2018.

Period	*Fledglings, with foster parents*	*Fledglings, in groups, without foster parents*	*Yearlings, in groups, without foster parents*	*Sex ratio*
1984–1999	213	8	45	52% males, 48% females
2010–2018	—	372	95	52% males, 48% females when sex could be determined. Thirty-six percentage of total number unsexed
Total	213	380	140	

Resighting Data

The data used in the present study includes resightings of all released and individually marked birds in period 1 (1984–1999), and period 2 (2010–2017). During period 1, a system where individual combinations of three to four different plastic colored leg rings was used. In period 2, colored plastic leg rings with engraved symbols (letter or number) were used to increase the possible number of unique combinations. The majority of resightings are reported by volunteers in wintering areas in the Netherlands, but also in staging and molting sites in Germany and Sweden. Beside opportunistic observations by birdwatchers, also dedicated efforts by volunteers at the most important winter, stop-over and molting sites as well in the breeding area add to large numbers of resightings. All resightings outside the breeding area were submitted to the online portal "www.geese.org" (website and database hosted by Wageningen Environmental Research, Dutch Centre for Avian Migration & Demography and Sovon Dutch Centre for Field Ornithology, in close collaboration with the World Conservation Union Goose Specialist Group). However, as observers putting in reports to the online portal can access historical and coming coordinates of observations of that specific individual bird, reports from breeding areas are stored exclusively in the project database. Observations were downloaded from the portal and merged with resighting data from the breeding area. All records are continuously checked and validated by staff in the project. If reported information deviates from what is expected, reporters are contacted to gain complementary information. If supportive information (description and photo) cannot be provided, the resighting is excluded from the data to ensure the accuracy and completeness of the database.

Capture–Recapture Analysis

Annual apparent survival probabilities were estimated from the 6572 live resightings by using the Cormack–Jolly–Seber (CJS) modeling options (Lebreton et al. 1992) in program MARK (White & Burnham 1999).

Prior to analyses, the boundary between years was set to first of May (here after "goose year"). For Lesser White-fronted Geese, spring migration ends in late April or the beginning of May, and behavior passes into the pre-breeding period, where birds use lowland sites near breeding areas to wait (and possibly refuel, to gain condition; Kruckenberg et al. 2023) out the onset of breeding from the second half of May onwards. Moreover, this temporal delineation gives a balanced distribution of resightings during a goose year. Observation probability is high during the end and beginning of the goose year due to gathering flocks in few pre-breeding sites, favorable conditions for reading color rings, and high annual observer effort during this period.

Analyses of survival during the two release periods were made independently, as data were separated by a gap of 10 years without release of birds. Releases started in 1981, but until 1983, the system for color ringing was not fully developed. For period 1, the analyses include data between 1984 and 1999 and birds were released either as fledglings with foster parents or birds released in groups (Table 1). Although birds released in period 1 continued to be reported until 2013, survival estimation was extended no further than 2003, to avoid bias due to aging or selective mortality (only individuals with high intrinsic survival probability remaining) affecting the small sample of surviving birds.

In period 2, our analysis include data between 2012 and 2017, as data were restricted in sample size in 2010 and 2011 with only 5 and 10 birds released, respectively. These 15 birds were included in the dataset from 2012 onwards to increase sample size and accuracy of the estimates for older age classes and treated as if they were marked in 2012 as yearlings (birds released as fledglings in 2011) or adults (released 2010).

In a recent study describing apparent survival, we considered potential effects of sex, age at release (fledgling or yearling), year after release (first, second, and later years), and year (Schekkerman & Koffijberg 2020). But for the purpose of the present study, we used a simpler structure to obtain model-averaged estimates. Hence, in a starting model for each period, effects of sex (male/female/unknown), age at release (fledgling/yearling), bird age, and time (year) on both survival (φ) and resighting probability (p) were considered, with all first-order interactions between these. This model was then simplified by dropping one by one first interactions and then main effects, and by considering a linear time effect instead of independent estimates for each year. Model evaluation was based on the Quasi Akaike Information Criterium (QAICc; Anderson & Burnham 2002), and we first identified the most parsimonious parameterization for the resighting probability p followed by optimizing the model structure for survival φ. Finally, we checked whether the top model found could be improved by a slightly different parameterization for p. We applied an overdispersion parameter estimated by the median $c\hat{}$ method for the model containing the maximum number of terms for which the parameters were estimable ($c\hat{} = 1.9$ for period 1, $c\hat{} = 2.3$ for period 2).

We applied model averaging (Anderson & Burnham 2004) to calculate parameter estimates for presentation and comparison between release methods. Models used in averaging were selected from the 20 top performing models, collectively supported by a QAIC weight of greater than 0.90 in each period. From this set, we omitted models containing effects of sex and time on apparent survival before averaging, as our primary interest lay in estimates of mean survival for different age classes and age at release, and in comparing mean survival rates between periods 1 and 2.

Only eight yearlings (15% of all yearlings) were released supported by foster parents, yielding too few resightings to estimate and compare survival with other groups. These eight birds were therefore omitted from the analysis, rendering the effect of release age completely confounded with release technique (all fledglings with foster parents, all yearlings in groups without during period 1).

Effects of age at release on second-year and adult survival can therefore only be evaluated (independently of the release method) for period 2, when all fledglings and yearlings were released together in groups. Further, in period 2, all geese were released in groups without Barnacle Goose foster parents;

therefore, the effect of release method can only be based on data from fledglings.

Results

Resighting Probability of Ringed Birds

For period 1, 194 out of 266 released birds were observed after release, and our analysis included 3493 resightings. For period 2, 209 individuals out of 380 were observed alive after release and 3079 resightings were reported (Table 1).

Overall mean resighting probability (p) was 0.74 ± 0.02 (SE) and 0.77 ± 0.06 for periods 1 and 2, respectively. In period 1, p increased over time from 0.42 in 1984 to 0.89 in 2002. No clear effect of sex could be found for p (females circa 0.12 higher than males) nor between age groups (first year circa 0.03 higher than older birds). In parallel to period 1, p increased over time in period 2, from 0.41 in 2013 to 0.92 in 2019, without any effect of age and sex.

Apparent Survival Probability

In both period 1 and period 2, the top-ranked models for apparent survival (φ) included bird age (survival differences between first year, second year, and adult and an interaction between bird age and age at release [fledgling or yearling]). Both these effects were strongly supported (period 1: ΔQAIC of top-ranking model without age = 6.35, of top-ranking model without interaction = 2.58; Table S2; period 2: ΔQAIC of top-ranking model without age = 10.3, of top-ranking model without interaction = 7.12; Table S3). In period 1, there was some additional support for a linear increase in φ over time (ranging between 0.07 and 0.15 depending on age of the birds, ΔQAIC = 1.27), but this was not found in period 2.

First-year φ of fledglings was lower in period 2 when the soft release method without foster parents was used, compared to period 1, when they were released with foster parents ($\varphi = 0.38$ (95% CI 0.29–0.49) vs. 0.69 (95% CI 0.60–0.76; Fig. 1). Estimates of φ were lower for all age classes during period 2, when the soft release method for both fledglings and yearlings was implemented, albeit with overlapping confidence intervals (Fig. 1). Independent of release method and age class at release, φ were higher in second year, compared to first year, and thereafter stable or lower (Fig. 1). In both periods, the lowest φ was found for birds released as yearlings ($\varphi = 0.29$ (95% CI 0.16–0.47) and $\varphi = 0.22$ (95% CI 0.10–0.42) for period 1 and period 2 respectively, Fig. 1), during their first year after release (i.e. 2 years of age). Notably, φ for yearlings were lower (non-overlapping 95% CI) than the second-year survival of birds released as fledglings ($\varphi = 0.84$, 95% CI 0.73–0.93) and $\varphi = 0.70$, 95% CI 0.46–0.80) for period 1 and period 2, respectively. However, the effect of age class at release was less pronounced when birds were released in joint groups without support of foster parents (period 2).

Most released individuals were last observed when released or just after the release event (July; Fig. 2). A large proportion was also observed for the last time in August in the release area, that is, before the onset of autumn migration. In period 2, for the 245 birds not being reported later than the first year after release,

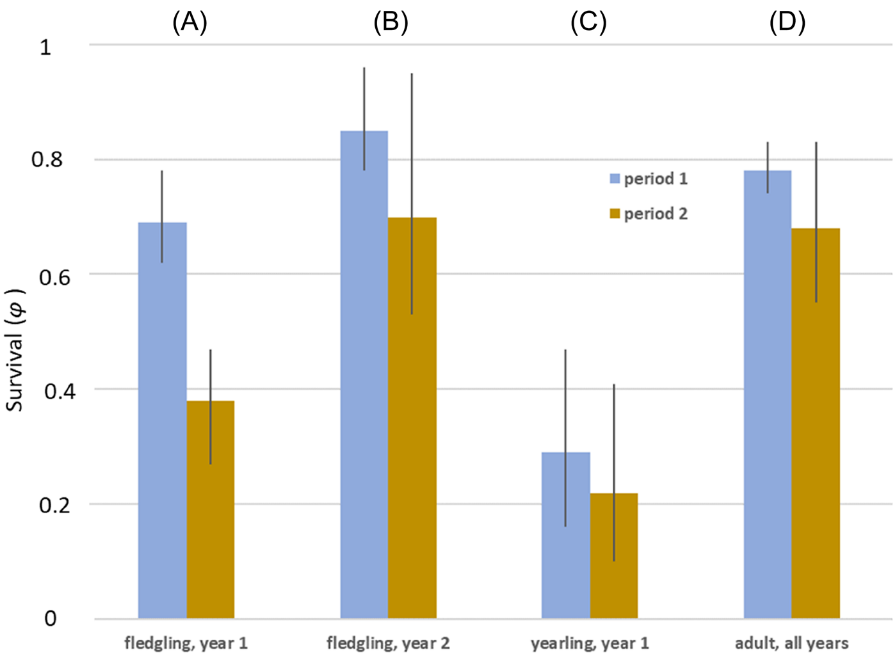

Figure 1. Model-averaged estimates of apparent survival (φ, bars), with 95% CI (whiskers), for Lesser White-fronted Geese released in Sweden during period 1 (1984–1999, light blue) and period 2 (2012–2017, yellow). (A) Survival of fledglings, during the first year after release when supported by foster parents in period 1 compared to period 2, when soft release without foster parenting was used. (B) Survival for birds being released as fledglings with respective method, during the second year after release. (C) Survival for birds released as yearlings without support of foster parenting in both periods. (D) Survival for all birds being older than 3 years (released as fledglings with 2 years after release and yearlings after their first year after release).

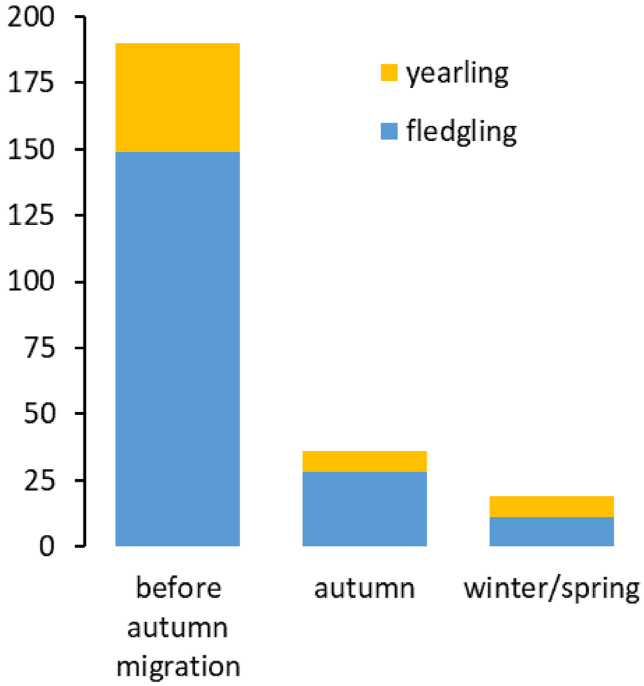

Figure 2. Number of released Lesser White-fronted reported for last time before onset of autumn migration, during autumn migration, or winter, respectively. Graph only represent individuals that were not reported later than the first year following release and category "before autumn migration" mainly consists of birds lost at the release site, first weeks after release. Both fledglings (blue) and yearlings (orange) were released in mid-July. Data from 2010 to 2017, that is, period 2, when no foster parents were used.

78% were reported last time before autumn migration started, 15% during autumn migration, and 8% during winter/spring migration.

Discussion

Lesser White-fronted Geese released as fledglings showed higher survival rates when released with Barnacle Goose foster parents compared to a soft release method without foster parenting. This suggests support for our first hypothesis that use of foster parents enhances survival of released Lesser White-fronted Geese, which is also in accordance with earlier findings for other social bird species (King et al. 2013; Berger-Tal et al. 2020). Interestingly, this difference in survival between the two release techniques did not persist at later life stages. Survival of birds released as yearlings was lower compared to fledglings, independent of the release technique used for the fledglings, which supports our hypothesis that the age of released birds also affect survival.

The higher survival rates of released Lesser White-fronted Geese supported by foster parents may be explained by social learning. Social learning is particularly beneficial for social organisms, allowing the transfer of crucial knowledge between generations and improving migration performance (Alerstam et al. 2003; Fagan et al. 2012). King et al. (2013) report that mortality during the post-release period of translocated young Whooping Cranes (*Grus americana*) was significantly reduced when guided by Sandhill Crane (*Antigone canadensis*) foster parents. Similarly, released Aleutian Canada Geese (*Branta hutchinsii leucopareia*) had higher survival when being supported by wild conspecifics (Rusch et al. 1998). In a natural situation, young geese learn feeding habits (Black et al. 2014) and vigilance to predators (Mini et al. 2013; Scheiber et al. 2013) from their parents early in life.

Losses of individuals due to predation can be decisive for the outcome of translocations of both mammals (Moseby et al. 2011) and birds (Parish & Sotherton 2007). Beside the predation of newly released individuals, being naïve to their new habitat, they face various challenges and dangers, such as limited food availability, especially when combined with unfavorable weather (Black et al. 1997), or physiological constraints to adapt to their new habitat (Champagnon et al. 2016). The outcome of release programs is often determined by the accumulated losses during the acclimation period following the release (Moseby et al. 2011; Armstrong et al. 2017). The existing data for our study population is insufficient to distinctly separate the mortality of released Lesser White-fronted Geese during the acclimation phase from losses after the onset of migration in the first year in the wild. But, in most years, we find a high proportion of released individuals (78%) never being reported outside the release area. As the resighting probability of birds leaving the release area is high, non-reporting suggests early losses, that is, during acclimation rather than during migration or wintering. Field observations in the release area suggest that predation by both mammalian predators (e.g. Red Fox [*Vulpes vulpes*] and American Mink [*Neovison vison*]) and avian predators (White-tailed Eagle [*Haliaeetus albicilla*]) may be important causes of mortality during the acclimation period in the actual release area.

Interestingly, birds released as yearlings showed lower survival rates in the first year after release than second year survival for birds released as fledglings, although with overlapping confidence intervals in period 2. Our analysis cannot differentiate if the lower survival is due to the lack of foster parents (in period 1) or the birds' age and internal state (e.g. molting). Release of fledglings is done a few days prior to the bird becoming fully fledged since flight training is expected to enhance the homing performance of young Lesser White-fronted Geese (Andersson 2019). Yearlings are released on the same day as fledglings, but being in full molt of primary and secondary wing feathers gives a longer period of elevated predation risk as a cost of being flightless (Stahl & Loonen 1998). Consequently, a later release date could have resulted in higher survival of yearlings as they recover the ability to fly in 4–5 weeks.

Using Barnacle Geese as foster parents had the desired additive value to modify migration traditions of the Lesser White-fronted Geese breeding in Sweden, and this change has been reported as an important factor to lower mortality during the non-breeding season and allow early recovery of the recipient population (Naturvårdsverket 2011). Naïve-to-migration individuals of storks (Chernetsov et al. 2004) and cranes (Mueller et al. 2013) have shown a rough inherent ability to navigate and return to the release site. But such innate abilities may not provide full preparation to released individuals; instead, we argue that the positive effects of using foster parents cannot be explained by increased survival during migration and wintering alone. During the early 1980s, the Swedish breeding program was building up capacity in the captive stock and producing limited numbers of birds to be released (Tegelström & von Essen 1996). During period 1, the positive effect of foster parenting on the survival of released birds during acclimation period may have been key to avoid the extinction of the recipient population.

The use of foster parents across species boundaries, as exemplified by Barnacle Geese in Sweden, may give rise to unforeseen and additional conservation challenges. In the context of this study, the altered migration traditions were warranted, but under other circumstances, such changes in behavior may be detrimental for conservation objectives. Feeding preferences and site choice are typically species-specific for geese, and deviations from the species' norm may affect both condition and fitness (Fox et al. 2005). Lesser White-fronted Goose is known to show clear preferences in diet and habitat use (Wang et al. 2013, 2014). Even if no comparative studies in habitat preferences between Lesser White-fronted Geese and Barnacle Goose have been done, learning site choice and feeding habits from another species may imprint released individuals to less optimal habitats. But even if altered habitat preferences may have existed for the released Lesser White-fronted Geese in our study, later studies suggest that the recipient population use their own network of stop-over and wintering sites and feeding habits, independent of the foster parents' preferences (Koffijberg et al. 2005; Ouweneel et al. 2008; Liljebäck et al. 2021; Kruckenberg et al. 2023).

Social imprinting can also affect future partner choice. Six captive-bred male Lesser White-fronted Geese (1.7% of all released individuals) released in period 1 became erroneously imprinted on the foster parent species (Liljebäck et al. 2021). These males later paired with female Barnacle Geese and produced hybrid offspring (Kampe-Persson & Lerner 2007). This issue emerged as a significant challenge for the conservation efforts, contributing to the decision to stop using foster parents in period 2 (Andersson 2019). However, later genetic analysis showed that these hybrids never influenced the gene pool of the Lesser White-fronted Goose population (Díez-del-Molino et al. 2020). In fact, the hybrids, behaviourally, became part of Barnacle Goose population with very little spatial overlap with the Lesser White-fronted Goose population (Liljebäck et al. 2021). Using conspecific foster parents may mitigate many of the potential risks associated with foster parenting described above. However, for a migratory species as the Lesser White-fronted Goose, such an approach would require a large free-flying and domesticated breeding stock with known migratory habits. In this particular case, the number of birds available for creating such a stock is limited, and economical and logistic challenges make implementation difficult under present conditions. Further, translocations of eggs from captive birds to wild breeding pairs could theoretically also be an alternative to reinforce a recipient population. But due to shyness and the preferred breeding habitat of Lesser White-fronted Geese, incubating females is notably hard to locate, and wild breeding pairs may be disturbed by such activities.

We acknowledge that our study is not a true experiment as the two different release techniques were not applied simultaneously but rather used during two distinct periods. However, two aspects of our findings suggest that survival of fledglings was influenced more by the release technique than by other factors that were not controlled for. First, survival was higher for fledglings than for yearlings in period 1 when fledglings were supported by foster parents, but this difference was not clear when both age groups were released without foster parenting in period 2. Secondly, in contrast to found differences in first-year survival in fledglings between the periods, the survival of birds released as yearlings as well as all cohorts older than 2 years did not suggest any between period differences. Birds released as yearlings were most sensitive to predation as they could not fly for a long period after release (due to molting). If predation pressure had changed between period 1 and period 2, differences in survival rates would have been most pronounced for bird released as yearlings.

Conservation efforts inevitably involve trade-offs between conservation gain and various costs and challenges. This long-term release program has sustained a critically endangered recipient population, which has been increasing during the last decade and estimated at 25–35 breeding pairs in 2023. Our results show that foster parenting may result in higher survival rates of released birds, but using foster parents is labor-intensive (Ellis et al. 2003; Fritz et al. 2016; Andersson 2019). Relatively less costly release techniques, as hard release compared to foster parenting, with proven lower survival rates, may consequently be preferred for economic reasons (Resende et al. 2021). Further, various techniques encompass ethical considerations, as newly released individuals may experience unprecedented stresses. Foster parenting includes some inherent risks, and we urge any conservation initiative, prospecting different release techniques to carefully consider all aspects of this practice. Based on our results, we advise conservation initiatives working with endangered social birds, especially when the capacity to produce individuals to be released is restricted, to consider foster parenting to enhance the survival of fledglings and to elevate return rates to release sites by improved migration performance.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Descriptive details about translocation techniques used to release Lesser White-fronted Geese in Sweden 1981–2000 and 2010–2018.
Table S2. Model summary table for release period 1.
Table S3. Model summary table for release period 2.

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