Raptor reintroductions: Cost-effective alternatives to captive breeding

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Abstract

Reintroductions are becoming a popular tool to prevent extinctions, although their overall success rate is low. Assessing the efficiency and cost-effectiveness of different reintroduction strategies may help identify and promote efficient practices. Captive-breeding is widely used in animal reintroductions, although concerns have been raised about relatively high failure rates and economic costs. Here, we compared the effectiveness of two simultaneously used strategies in the reintroduction of the Bonelli's eagle on the island of Mallorca: The release of captive-bred chicks and wild-reared, translocated non-juveniles. To do so, we estimated the main vital rates for individuals released by both strategies and used these to perform population simulations to assess their overall performances. The use of wild-reared non-juveniles showed a trend with higher numbers of breeding pairs 10 years after the end of releases (14.75 pairs, 95% CI 4–25 vs. 11.21 pairs, 95% CI 2–24) and was the only strategy that prevented extinction in the long term. Following that, based on cost estimations of every strategy and different reintroduction budgets, we assessed the cost-effectiveness of releasing wild-reared non-juveniles compared with two captive-breeding alternatives: Releasing chicks either originally from breeding programmes or extracted from nests in natural populations. Again, releasing wild-reared non-juveniles was the only strategy that prevented long-term extinction in all economic scenarios (i.e. low-budget scenario 21.49 pairs, 95% CI 2–25). The use of chicks sourced from captive-breeding programmes did not guarantee long-term persistence even in high-budget scenarios (14.50 pairs, 95% CI 0–25). Releasing wild-reared non-juveniles boosts early recruitment to the breeding population and early reproduction, which can be key for reintroduction success. However, in some scenarios, post-release effects can be stronger in wild-reared individuals, especially because of high translocation stress and post-release dispersal. Hence, we recommend undertaking careful evaluation of the pros and cons of every strategy and embracing adaptive management to choose best strategies.

Introduction

Animal reintroductions are becoming a widespread tool to combat the current extinction crisis. However, the outcomes of such actions are not always successful, with global failure rates estimated between 33% and 89% (Beck et al., 1994; Wolf et al., 1996; Fischer & Lindenmayer, 2000; Griffiths & Pavajeau, 2008; Brichieri-Colombi & Moehrenschlager, 2016). Economic constraints for conservation are a critical reason to increase the effectiveness of reintroductions (Naidoo et al., 2006). Hence, it is important to identify and promote cost-effective strategies to allocate economic and human resources efficiently. However, although the number of studies reporting the costs of reintroduction attempts is increasing, there is still little evidence from which to extract robust cost-effectiveness conclusions (Fischer & Lindenmayer, 2000; Naidoo et al., 2006; Wakamiya & Roy, 2009; Wilson et al., 2009; Canessa et al., 2014; Morandini & Ferrer, 2017; Ferrer et al., 2018; Pienkowski et al., 2021). In this context, population modelling can be a helpful tool, as it allows for analyses and comparisons between alternative strategies before they are implemented.

Improving knowledge about the factors that affect the success of reintroductions is essential in pinpointing effective strategies and providing evidence-based guidance to managers. As available research shows, potential drivers of reintroduction

outcomes include species-specific behavioural and life-history traits (Wolf *et al.*, 1996; Reed, 1999), the age of released individuals (Le Gouar *et al.*, 2008), habitat quality (White *et al.*, 2012), presence or absence of potential predators (Sheean *et al.*, 2012), numbers of individuals released (Fischer & Lindenmayer, 2000) and the release methods and the origin of the released individuals (i.e. captive-born vs. wild-born) (Hardman & Moro, 2006; Buner & Schaub, 2008; Rummel *et al.*, 2016). A common challenge of reintroductions is that individuals usually show higher chances of mortality during the first months following release (Tavecchia *et al.*, 2009; Armstrong *et al.*, 2017). This phenomenon is known as the 'cost of release' or 'post-release effect' and is usually caused by stresses associated with the translocation process or the adaptation to the area of release (Tavecchia *et al.*, 2009; Dickens *et al.*, 2010; Armstrong *et al.*, 2017).

The use of captive-born individuals from breeding programmes is widespread in reintroductions (Araki *et al.*, 2007). This strategy usually provides large stocks of individuals available for release, which can be key for reintroduction success (Fischer & Lindenmayer, 2000). However, such programmes involve high economic and technical costs associated with animal husbandry (Snyder *et al.*, 1996; Ferrer *et al.*, 2018). Captive-bred individuals also usually show lower survival probabilities than their wild counterparts, possibly because they lack predator avoidance and/or foraging abilities (Buner & Schaub, 2008; Tavecchia *et al.*, 2009). On the other hand, the use of wild-reared individuals is generally associated with higher reintroduction success according to practitioner surveys and reviews (Fischer & Lindenmayer, 2000; Jule *et al.*, 2008; Rummel *et al.*, 2016).

Raptors are among the most threatened taxa worldwide and are common targets of reintroduction projects (McClure *et al.*, 2017). The main reintroduction strategy for raptors is the hacking method, which consists of captive breeding of fledglings in artificial nests – without adult conspecifics and preventing contact with humans – then releasing them as juveniles (Dzialak *et al.*, 2006; Oro *et al.*, 2011). Many hacking schemes rely on captive breeding programmes for stocks of birds to release, which usually substantially raises the costs of reintroductions. A hacking alternative that avoids implementing breeding programmes, and consequently lowers the economic demands associated with the reintroduction, is the use of chicks extracted from wild nests in natural populations (Ferrer *et al.*, 2018). Importantly, the hacking method implies releasing juveniles, which involves no reproduction until birds reach sexual maturity. Instead, early reproduction of released birds can greatly contribute to the success of reintroductions (Morandini *et al.*, 2019). This is usually due to three causes: First, early reproduction implies higher chances of adding new individuals to the population before released birds are removed by mortality in later years; second, these new individuals born in the reintroduction area frequently show higher survival prospects than released conspecifics (Brown *et al.*, 2006) and third, breeding individuals may have reduced probabilities of mortality compared with non-breeders, especially in long-lived territorial species (Morandini *et al.*, 2019). An effective measure to promote

early reproduction is the release of non-juvenile individuals, especially sexually mature ones (Sarrazin & Legendre, 2000; Robert *et al.*, 2002; Evans *et al.*, 2009). However, for strategies relying on captive breeding, this is usually economically demanding, as it means assuming the costs of bird care for years before release (Martínez-Abraín *et al.*, 2011). Instead, the translocation of wild, non-juvenile individuals from natural populations to reintroduction areas could present a cost-effective alternative to boost early reproduction.

Here, using reintroduction simulations, we sought to evaluate the cost-effectiveness of three reintroduction strategies: Hacking based on captive breeding (hereafter 'CaptHack'), hacking based on chicks extracted from wild nests in natural populations ('NestHack') and the translocation of wild, non-juvenile birds from natural populations recovered from rehabilitation centres ('WildTrans'). We compare the contribution with reintroduction success of the two hacking methods and WildTrans, and quantify the costs of all three methods and compare their contribution to long-term population viability under different economic budgets. Our study focuses on the reintroduction of the Bonelli's eagle *Aquila fasciata* in the island of Mallorca, where all three strategies were used simultaneously. Thanks to the detailed monitoring of released birds in the area (2011–2016) and the comprehensive knowledge of the life history of the species in Europe (e.g. Hernández-Matías *et al.*, 2013), we could estimate the key demographic parameters for every reintroduction strategy and develop individual-based population models to simulate reintroductions by all methods. We expect our results to provide important evidence-based insights for practitioners on long-lived species reintroductions.

Materials and methods

Study species and area

The Bonelli's eagle (*A. fasciata*) is a long-lived territorial raptor whose range extends from south-east Asia to the western Mediterranean. It is assessed globally as Least Concern, but as Near Threatened in Europe and Endangered in Spain (Birdlife International, 2015, 2019), where the species underwent severe declines and local extinctions in the last decades. Here, we focus on Mallorca Island, where the species died off around the 1970s due to habitat loss, prey shortages and especially direct persecution. A reintroduction programme was launched in 2011 with the aim of re-establishing a self-sustainable population in the area. A total of 39 individuals were released between 2011 and 2016: 9 chicks via NestHack, 14 chicks via CaptHack and 16 non-juvenile individuals (>1 year old) via WildTrans. All released individuals were tagged with PVC rings and GPS devices. By 2016, five breeding pairs had established in the area, which had successfully raised six chicks.

Model definition and main structure

To assess the effectiveness of CaptHack, NestHack and WildTrans strategies, we designed individual-based models

that simulated the life cycle of the species in a population structured by sex, age and territorial status and limited by density-dependence. We estimated vital rates (i.e. survival, recruitment to the breeding population and productivity) from our own data where possible, but given the small sample size of our reintroduced population, we used estimates from conspecific Iberian populations when specific values were not estimable (Hernández-Matías *et al.*, 2013) (see Methods: Estimation of vital rates). We considered survival and recruitment to the breeding population (hereafter, 'recruitment') to vary with age and release strategy, assuming that hacking birds of both origins and wild birds born in the reintroduction area would share the same estimates. Productivity was assumed to vary with age but not among release strategies. We modelled the different reintroduction scenarios by simulating eagle releases for the first 10 years in overall 50-year simulations with a starting population size of 0 individuals. We accounted for environmental (adult survival and productivity) and demographic stochasticity (all vital rates). Detailed model specifications are provided at Methods: Model settings. Based on these features, we assessed the performance of the evaluated reintroduction strategies using two sets of analyses: First, we assumed the same number of individuals released under hacking and WildTrans strategies to assess their performance in terms of release effort irrespective of their economic cost and second, we assessed the cost-effectiveness of each strategy.

Hacking versus WildTrans effects on reintroduction success

We simulated two different reintroduction scenarios: (1) Releasing only fledglings of hacking origin and (2) releasing only WildTrans individuals. For each of these two scenarios, we simulated the release of 6.5 eagles on average per year (SD = 1), following average numbers of observed releases.

Cost-effectiveness of CaptHack, NestHack and WildTrans

We simulated three different scenarios that consist in the release of (1) CaptHack, (2) NestHack and (3) WildTrans individuals. Each scenario was simulated under three budgets, namely, 15000 €/year (low), 30000 €/year (medium) and 50000 €/year (high). The budgets were chosen after discussion about realistic low-budget, medium-budget and high-budget incomes with managers involved in the

reintroduction. In every scenario, we determined the yearly number of released eagles by dividing the corresponding budget by the individual economic cost of every eagle (Table 1). To calculate such costs, we considered the expenses associated with personnel and bird feeding associated with every released strategy. We did not include costs related to infrastructure acquisition or maintenance and journeys of monitoring or chick removal because these expenses were external to our reintroduction programme. See Data S1: Economic Estimations and Figure S1 for further details. Cost estimates amounted to 11141.6, 5061.6 and 2338.9 €/eagle for CaptHack, NestHack and WildTrans birds, respectively. Taking the resulting numbers as means (SD = 0.5), we simulated different numbers of released eagles for every strategy, budget and simulation year using a normal distribution. The scenarios showing better performance under identical budget caps were considered most cost-effective.

Estimation of vital rates

Survival and recruitment

We developed multievent capture–mark–recapture (CMR) models (Pradel, 2005; Hernández-Matías *et al.*, 2015) to estimate the probabilities of recruitment and survival from 2011 to 2016. The CMR framework allows for accounting of heterogeneity in survival and resighting probabilities between individuals classified in different states, as well as for uncertainty about the states of the individuals. Our analysis considered data on live individuals and mortality events to increase our estimates' precision (Lebreton *et al.*, 1999). Because our sample size was small, increasing model complexity would lead to imprecise or inestimable parameters. Hence, we split our dataset for two different analyses: One for hacking and wild birds born in the reintroduction area (*n* = 29 individuals: 23 hacking and 6 wild-born) and another for WildTrans eagles (*n* = 16 individuals). Model selection was performed using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002). We built capture–recapture histories using quarterly intervals, and the resulting estimates were raised to the power of 4 to obtain annual probabilities. The corresponding variance was estimated using the Delta Method (Powell, 2007). We followed a stepwise model selection procedure, in which we tested different age structures parameter by parameter and used those that minimized AICc in following steps (Burnham & Anderson, 2002). In addition, because of the small sample sizes of our datasets, which can lead to

Table 1 Mean number of yearly released individuals by each reintroduction method and budget scenario

	Budget		
	15000 €/year	30000 €/year	50000 €/year
Reintroduction method			
Wild, non-juvenile Translocation (WildTrans)	6.4	12.83	21.37
Nest-removed hacking (WildHack)	2.96	5.93	9.88
Captive-breeding hacking (CaptHack)	1.35	2.69	4.49

considerable effects of demographic stochasticity, we considered the statistical plausibility of the model (i.e. presence/absence of parameter estimability issues), and the biological realism of model structure and parameter estimates, based on the extensive knowledge available on the demographic features of close-by continental populations (Hernández-Matías et al., 2013). The models were built and run under software E-SURGE (Choquet et al., 2009a), and goodness-of-fit tests were implemented with U-CARE v2.2.2 (Choquet et al., 2009b).

Analysis for hacking and wild eagles born in the reintroduction area

The JMV goodness-of-fit test showed no deviation from assumptions ($X^2 = 0.985$, df = 7, $P = 0.995$). We built a global transition matrix considering GPS tag failure, recruitment and survival probabilities. We first selected the GPS failure and recruitment structures that minimized AICc, and then we tested six survival structures related to the age and territorial status of the eagles (Table 2). Further details are provided in Data S1: Multievent Definition and Selection.

Analysis of wild, non-juvenile, translocated eagles

The JMV goodness-of-fit test showed an adequate fit to the data ($X^2 = 1.87$, df = 8, $P = 0.985$). We defined a simpler model to avoid parameter estimability problems due to the small sample size of this dataset ($n = 16$ individuals). Thus, we did not account for GPS tag failure, but because all individuals of this type had active, working GPS devices throughout the course of the study, we believe that this decision does not violate the tag retention assumption of mark–recapture models. Starting from a general model with four age classes for recruitment and survival, we first selected the recruitment structure that minimized AICc and then tested four different survival structures according to the number of years since release and territorial status of individuals (Table 3). See further details in Data S1: Multievent Definition and Selection.

Table 2 Model selection for the survival parameter in the multievent analysis including hacking and wild birds born in the reintroduction area

Survival structure	No. parameters	Deviance	AICc
A1+A2+(A34*Recruitment status)	13	228.84	256.79
A1+A23+A4	**12**	**235.72**	**261.38**
A1+A2+A34	12	236.96	262.62
Recruitment status	12	237.06	262.72
A1+(A234*Recruitment status)	13	235.28	263.22
A1+A2+A3+A4	13	235.62	263.56

Survival model selection was performed after modelling GPS tag loss and recruitment and selecting the structures that minimized AIC for these parameters. Values 'A1', 'A2', 'A3' and 'A4' stand for the ages 1, 2, 3 and 4 and older in years, respectively. 'Recruitment status' refers to whether or not the individual has joined the breeding population. The selected model is indicated in bold.

Table 3 Model selection for the survival parameter in the multievent analysis for wild non-juvenile translocated eagles

Survival structure	No. parameters	Deviance	AICc
A1+A234	6	86.63	99.88
A1+A2+A34	**7**	**84.78**	**100.47**
A1+A2+A3+A4	8	84.78	102.99
Recruitment status	6	89.34	102.59

Survival model selection was performed after modelling recruitment and selecting the structure that minimized AIC for that parameter. Values 'A1', 'A2', 'A3' and 'A4' stand for number of years since the release of the individual in the reintroduction area: 1, 2, 3 and 4 or more, respectively. 'Recruitment status' refers to whether or not the individual has joined the breeding population. The selected model is indicated in bold.

Adult productivity

Because few data on productivity were available, we estimated productivities for individuals aged 4 and older (hereafter, 'adult productivity') based on reproduction attempts of all territorial pairs, independently of their ages, and considering reproduction events from the same pairs in different years as independent observations. Because productivity is a demographic parameter with a relatively low impact on population viability (Saether & Bakke, 2000), we believe that this did not significantly affect our results.

Use of estimates from conspecific populations

We used estimates from Iberian populations (Hernández-Matías et al., 2013) in cases where the data from the study population were insufficient to obtain reliable estimates. In particular, survival was not estimable for individuals aged four and older of any method, as well as recruitment of all individuals aged three and older, because of the high numbers of surviving individuals at these ages. In these cases (i.e. hacking, WildTrans and wild individuals born in the reintroduction area), we used averaged values from all 12 monitored populations in Hernández-Matías et al. (2013). In addition, because survival was not estimable for 3-year-old WildTrans eagles, we used the estimate obtained from the analysis of hacking and wild individuals born in the reintroduction area. Productivity values of eagles younger than 4 years old were assumed from the population in Catalonia (NE Spain) (Hernández-Matías et al., 2013). Temporal variances to model environmental stochasticity of adult survival and productivity were also calculated as averages of continental populations (Hernández-Matías et al., 2013).

Model settings

Our individual-based model followed a post-breeding census. We simulated fine-scale life-cycle processes stepwise in 1-year steps in this order: (1) Survival and mortality, (2) aging, (3) recruitment to the breeding population, (4) territory acquisition, (5) mating, (6) breeding and (7) release of reintroduced individuals (Figure S2). At the beginning of every year, we

established new adult survival and productivity values following a beta distribution with the temporal variance of each parameter to simulate environmental stochasticity (Morris & Doak, 2002). Senescence was incorporated by reducing survival probabilities to 50% in individuals aged 20 years and older (Chantepie et al., 2016). Territory acquisition and mating are simulated conditional on the availability of both recruited males and females. The model prioritizes the occupation of vacant spots in occupied territories instead of the occupation of new territories. Individuals of higher age were considered more competitive. Therefore, in cases where territory availability is limited, older individuals have priority to enter territories. In the release process, for wild, non-juvenile, translocated eagles, we assigned random ages at release to every individual based on the observed age ratios of released birds in the study reintroduction (i.e. 1/3, 1/6, 1/6 and 1/3 for 2-, 3-, 4-year-olds and adults, respectively). Density dependence was incorporated by considering a ceiling of 25 territories in Mallorca (i.e. 25 breeding pairs), based on species distribution analysis (Viada, C., unpublished data).

Each reintroduction scenario was run for 1000 replicates. Reintroduction success for each strategy was assessed through the expected number of breeding pairs as the mean and the corresponding 95% interpercentile range between 2.5 and 97.5 percentiles (hereafter referred to as the percentile 95% confidence interval, 95% CI) of all the replicates at simulation years 20 and 50. We considered that a scenario prevented long-term extinction when 95% CI did not expand to 0 at year 50. In addition, to strengthen the value of our results, we performed an analysis evaluating parametric uncertainty in main vital rates (see Data S1: Simulations with parametric uncertainty; Figures S3 and S4). All simulations were performed using R(3.6.2) (R Core Team, 2020) and package PopBio (Stubben & Milligan, 2007).

Results

Estimation of vital rates

For hacking and wild eagles born in the reintroduction area, the best-ranked model by AICc showed parameter estimability issues; therefore, we selected the second model in the rank, whose estimates best matched the available demographic knowledge on the species (Table 2) (Hernández-Matías et al., 2013). In this model, yearly probabilities of survival and recruitment to the breeding population for hacking and wild eagles born in the reintroduction area increased with age. For WildTrans birds, because the best model in the AICc rank provided biologically unrealistic survival estimates, we selected the second model in the rank (Table 3). The selected model showed increasing survival probabilities depending on time since release and constant recruitment probabilities. All 3-month and annual demographic estimates are shown in Table 4. Adult productivity was estimated at 1.2 (SD = 0.74) chicks per pair and breeding attempt, which fits the range of known values of conspecific populations (0.63–1.42, Hernández-Matías et al., 2013). Estimates from conspecific continental populations used for modelling are also shown at Table 5.

Population viability analyses

Hacking versus WildTrans effects on reintroduction success

The number of breeding pairs obtained at year 50 for WildTrans was moderately higher (22.24, 95% CI 4–25 breeding pairs) than that for hacking releases (19.90, 95% CI 0–25; Fig. 1). The WildTrans scenario was the only one that prevented long-term extinction.

Cost-effectiveness of CaptHack, NestHack and WildTrans under different economic budgets

The release of WildTrans eagles provides considerably higher numbers of pairs than any hacking strategy under equal economic conditions (Table 6, Fig. 2). Using NestHack individuals showed a better performance than using CaptHack birds. Interestingly, the number of pairs in year 50 using the WildTrans method under the cheapest scenario (i.e. 15000€/year) was remarkably higher than the one for CaptHack under

Table 4 Parameter estimates obtained in the multievent analyses of hacking and wild birds born in the reintroduction area and WildTrans birds

Release method	Parameter	3-month estimate	Annual estimate
Hacking + wild born in reintroduction area	First-year survival	0.854 (0.035)	0.533 (0.087)
	Second-year survival	0.931 (0.033)	0.753 (0.101)
	Third-year survival	0.931 (0.033)	0.753 (0.101)
	First-year recruitment	0.073 (0.027)	0.262 (0.061)
	Second-year recruitment	0.111 (0.060)	0.376 (0.138)
WildTrans	First-year survival	0.829 (0.064)	0.471 (0.145)
	Second-year survival	0.923 (0.074)	0.726 (0.233)
	Third-year survival	0.931 (0.033)[a]	0.753 (0.101)[a]
	First-year recruitment	0.167 (0.068)	0.518 (0.136)
	Second-year recruitment	0.167 (0.068)	0.518 (0.136)

Estimates are presented with standard deviation (SD) inside parentheses. Standard deviation in annual estimates was calculated using the Delta Method.

[a] Third-year survival for WildTrans birds was picked from the analyses of hacking and wild born individuals born in the reintroduction area.

Table 5 Parameter estimates used in the population simulations obtained from sources different from our multievent analyses

Parameter	Estimate + (temp. var.)	Source
Fourth-year survival	0.8436	Hernández-Matías et al. (2013)
Adult survival	0.9042 (0.002)	Hernández-Matías et al. (2013)
>20-year survival	0.500	Assumed (senescence)
Third-year recruitment	0.680	Hernández-Matías et al. (2013)
Fourth-year recruitment	0.934	Hernández-Matías et al. (2013)
Adult recruitment	1	Hernández-Matías et al. (2013)
Second-year productivity	0.286	Hernández-Matías et al. (2013)
Third-year productivity	0.400	Hernández-Matías et al. (2013)
≥Fourth-year productivity	1.2 (0.328)	Own calculation

Estimates are presented with temporal variation (temp. var.) inside parentheses in those parameters where we simulated environmental stochasticity.
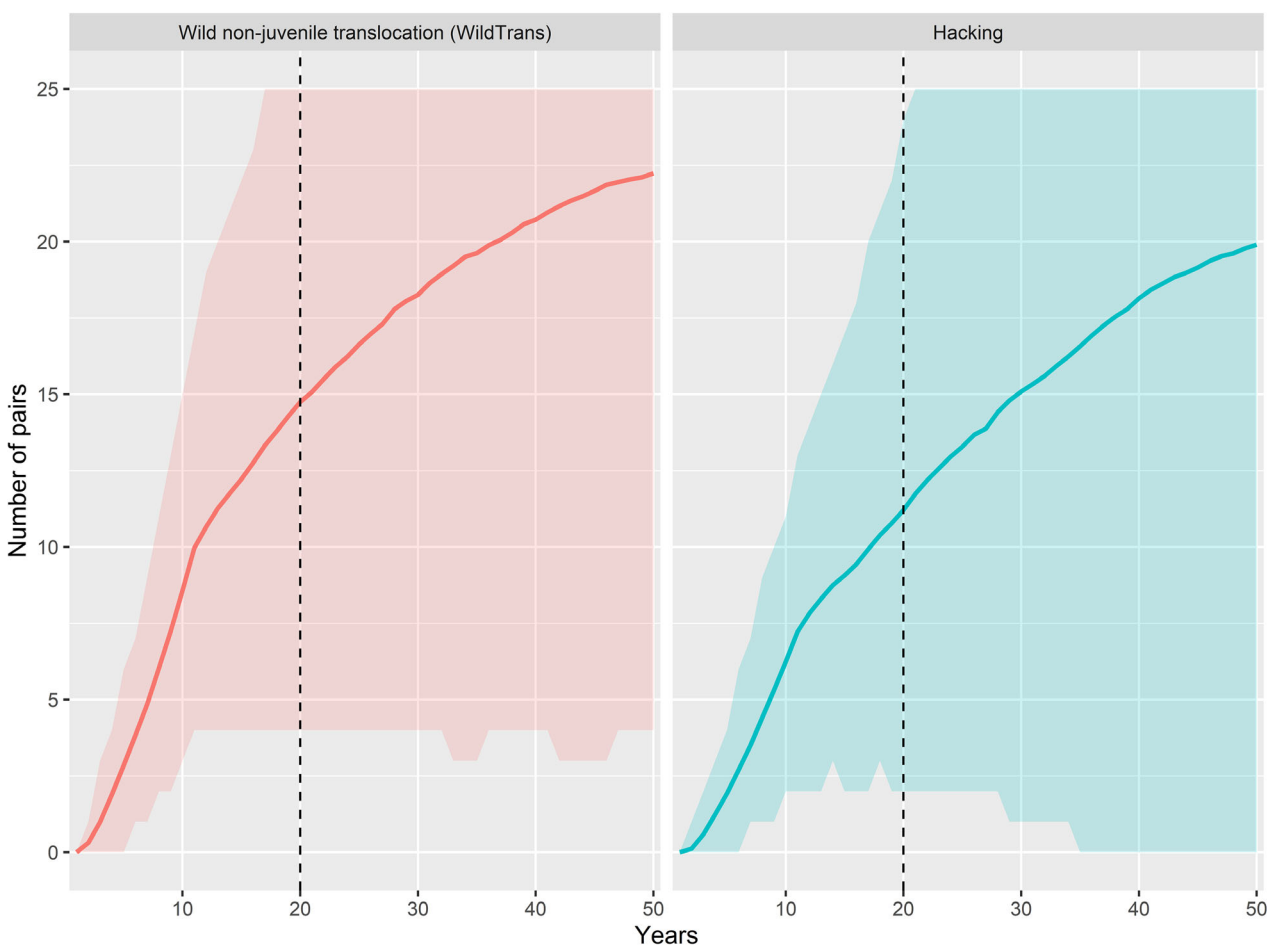

Figure 1 Comparison of the effects of hacking and WildTrans reintroductions on long-term population viability. Simulations are performed for 50 years and 1000 replicates each. Thick lines represent the mean number of breeding pairs per year, and shaded areas indicate 95% confidence intervals.

the most expensive scenario (i.e. 50.000€/year) (21.49 pairs, 95% CI 2–25 and 14.50, 95% CI 0–25, respectively). In fact, 95% CIs for the CaptHack strategy expand to 0 in all scenarios, which shows that the event of an extinction, and therefore reintroduction failure, cannot be discounted in any case.

Discussion

Assessing the cost-effectiveness of different conservation measures is essential to identify optimal strategies in modern conservation practice. Here, we used population analyses to

Table 6 Average numbers of breeding pairs under different budget scenarios and reintroduction methods for years 20 and 50 on reintroduction simulations. 95% CIs are shown in parentheses

	Budget					
	15000 €/year		30000 €/year		50000 €/year	
Reintroduction method						
Simulation year	Year 20	Year 50	Year 20	Year 50	Year 20	Year 50
WildTrans	14.081 (4–25)	21.49 (2–25)	24.23 (17–25)	24.87 (25–25)	24.97 (25–25)	24.98 (25–25)
NestHack	3.70 (0–11)	8.19 (0–25)	9.77 (2–21)	18.29 (0–25)	17.86 (6–25)	23.75 (9–25)
CaptHack	1.18 (0–6)	2.43 (0–21)	3.39 (0–10)	7.58 (0–25)	6.89 (0–16)	14.50 (0–25)
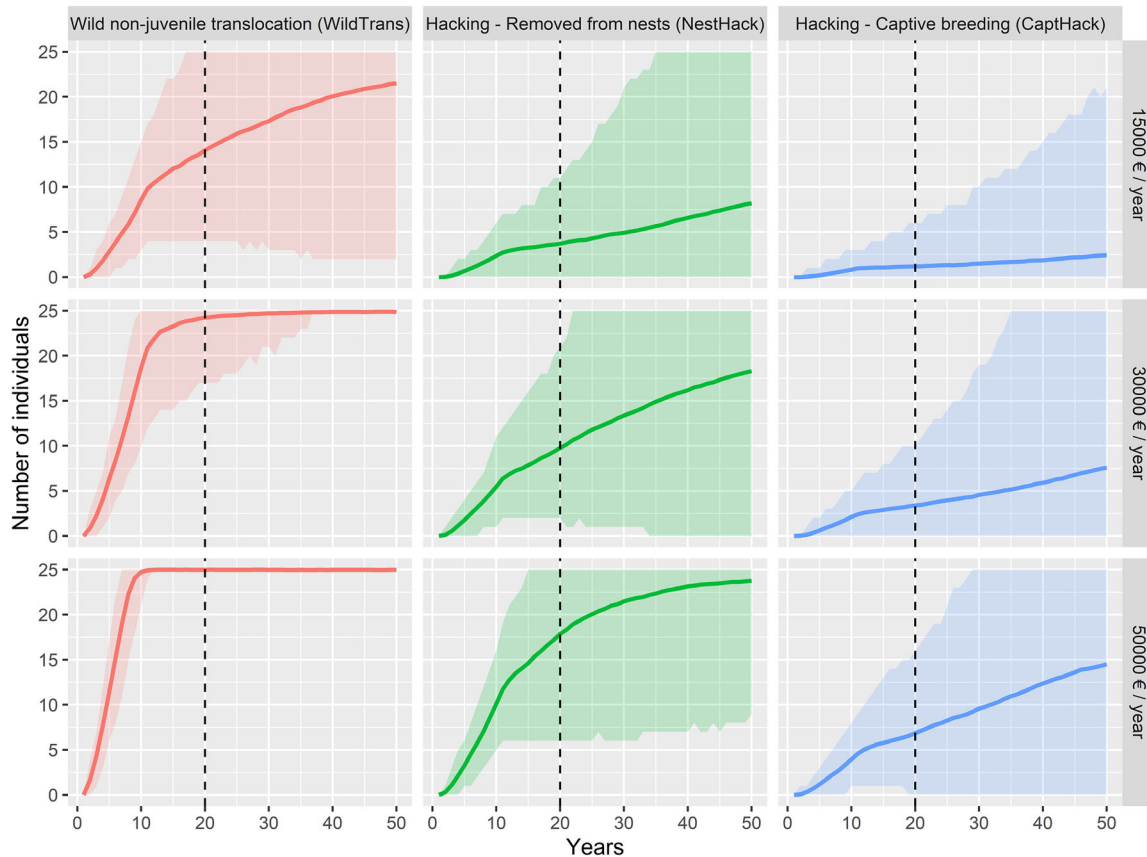
Figure 2 Cost-effectiveness comparison of the effects of WildTrans, NestHack and CaptHack reintroductions on long-term population viability under different budget scenarios. Simulations are performed for 50 years and 1000 replicates each. Thick lines represent the mean number of breeding pairs per year, and shaded areas indicate 95% confidence intervals.

compare the success and cost-effectiveness outcomes of three alternative release strategies used in a reintroduction scheme for the Bonelli's eagle on Mallorca island. Our results strongly support that the translocation of wild, non-juvenile individuals (WildTrans) is the most cost-effective strategy to establish a viable reintroduced population in our case study. Two main reasons may explain this finding. First, releasing birds older than fledglings increases the chances of forming breeding pairs – and successful reproduction – in a shorter period. Second, releasing wild, non-juvenile individuals is

notably cheaper than any hacking strategy, as these methods require the implementation of captive breeding and/or bird care for longer periods. Our findings can be meaningful for other long-lived species reintroduction schemes. In addition, we highlight how including cost-effectiveness criteria in population analyses can improve the allocation of resources and the global results of wildlife reintroductions and reinforcements.

Captive breeding and hacking are widely used techniques in reintroduction programmes, despite their high economic

costs and the scientific concerns about the relatively lower success rates of reintroductions when captive-reared animals are used (Fischer & Lindenmayer, 2000; Mathews *et al.*, 2005; Jule *et al.*, 2008; Rummel *et al.*, 2016). In our results, WildTrans was the only method that prevented long-term population extinction in the smallest and medium-budget scenarios (15.000 and 30.000 €/year), whereas within the highest budget (50.000 €/year), CaptHack was the only method that could not safely avoid extinction. As predicted, recruitment probabilities were considerably higher for WildTrans eagles than for hacking-released conspecifics, to the extent that half of the WildTrans birds joined the pool of potential breeders each year during the first 2 years following release. As such, shortening the time until reproduction of released birds accelerates a shift towards a population largely composed of wild individuals born in the target area, which can contribute greatly to reintroduction success (Evans *et al.*; 2009; Morandini *et al.*, 2019). As shown by Sarrazin and Legendre (2000), this can be achieved by releasing adult captive-bred individuals, but according to our results, translocating wild individuals arises as an effective alternative that avoids the high economic costs of captive breeding until adulthood. Furthermore, in our case, we released eagles of a wide range of ages, and therefore, higher recruitment rates may be expected if adult releases are prioritized. When not considering budget scenarios (i.e. equal numbers of individuals released by each method, Fig. 1), WildTrans was also the only strategy that prevented long-term extinction. Interestingly, survival estimates for WildTrans birds were slightly lower than for those released by hacking, contrary to what could be expected (Buner & Schaub, 2008; Jule *et al.*, 2008). In this study, WildTrans individuals were sourced after injury and treatment in wildlife rehabilitation centres, which could have decreased the survival prospects of some individuals (Kelly *et al.*, 2010; De La Cruz *et al.*, 2013). Nevertheless, even with decreased survival, the WildTrans strategy showed a better performance than hacking in our simulations, which again may highlight the relevance of greater recruitment to the breeding population and early reproduction for reintroduction success (Morandini *et al.*, 2019).

The effectiveness of different release approaches can greatly vary with different reintroduction scenarios. Detailed case- and species-specific evaluations should be performed to choose an adequate strategy, especially because the strength and duration of post-release effects are known to vary according to species, age, sex, habitat quality and even the timing of releases and individual personality (Moehrenschlager & Macdonald, 2003; Carere & Vanoers, 2004; Tocher *et al.*, 2006; Dickens *et al.*, 2010; Le Gouar *et al.*, 2012; Armstrong *et al.*, 2017). Stress can be a main cause of failure in many reintroductions, and its potentially different effects by age and release methods could further explain the survival differences found in our study (Teixeira *et al.*, 2007; Dickens *et al.*, 2010). When wild-reared non-juveniles are relocated (i.e. WildTrans), they are subject to continuous stressors throughout capture, manipulation, transport, captivity and release into a novel environment. As a result,

individuals usually are chronically stressed for weeks, months or even years after release (Dickens *et al.*, 2010; Armstrong *et al.*, 2017). Chronic stress affects cognitive skills and limits the ability of individuals to interact with conspecifics, find environmental cues and learn and remember the location of relevant resources for survival and reproduction, which altogether increase mortality chances (Teixeira *et al.*, 2007). Instead, for captive-reared individuals and birds captured as chicks (i.e. CaptHack, NestHack), the detrimental effects of stress might be milder (Love *et al.*, 2003; Teixeira *et al.*, 2007; Cabezas *et al.*, 2013).

Fast adaptation to novel environments can reduce post-release effects and consequently increase the chances of reintroduction success. This behaviour may be species- or even individual-specific, but it can also depend on the release strategy. Captive rearing (i.e. CaptHack, NestHack) can limit the ability of individuals to fully adapt to wild environments. In particular, for vertebrates that possess a high degree of learned behaviours (i.e. mammals, birds), long-term captivity and the lack of parental care may lead to inability to develop proper predator avoidance or hunting skills, which can lead to increased mortality (Teixeira *et al.*, 2007; Tavecchia *et al.*, 2009). Such effects may be offset with animal training, although this can be a complex option (Griffin *et al.*, 2000). Instead, captive rearing might not have such great impacts in those species with hard-wired behaviour or physiology (Griffiths & Pavajeau, 2008; Cayuela *et al.*, 2019). The age of released individuals can also affect adaptation capacity. In studies involving swift foxes (Moehrenschlager & Macdonald, 2003) and yellow-bellied toads (Cayuela *et al.*, 2019), long-term decreased survival and productivities were detected for released adults in respect to released immatures. Unfortunately, because of our relatively low sample size, we cannot test to which extent these events are affecting our population. Nevertheless, for raptors and many long-lived species survival and productivity are expected to increase with age as a result of experience gains in several skills (i.e. foraging, reproduction, territory acquisition, flight ability, dispersal, etc.) (Sergio *et al.*, 2014). Productivity is usually driven by population density and intraspecific competition, which are expected to be low in reintroduced populations. Hence, negative effects in adult productivity and survival are unlikely to offset the benefits of early reproduction and recruitment provided by non-juvenile releases, as found in this study and Sarrazin and Legendre (2000).

A major concern in raptor translocations when wild-reared individuals are used is post-release dispersal, that is, the permanent movement of released individuals away from the reintroduction area shortly after release. Specifically, most raptor species show strong tenacity to their areas of origin (i.e. 'homing behaviour'), which may prevent them from establishing in release sites. This issue is usually prevented by using the hacking method, because the feeding and care of fledglings in the reintroduction area during the last stages of growth can promote imprinting to the site and deter dispersal (Amar et al., 2008; Martínez-Abraín *et al.*, 2001). Post-release dispersal was not a major issue in our study reintroduction, as all WildTrans individuals were recontacted

after release. In our case, the reintroduction area was an island separated by more than 150 km from the continent (the closest area with an established population). Both natural barriers and long distances between home and release areas are known to promote establishment at reintroduction areas (Van Vuren et al., 1997; Moehrenschlager & Macdonald, 2003). On the other hand, post-release dispersal has also been reported when captive-bred raptors have been released, especially in social species (Mihoub et al., 2014). This behaviour has been described in a wide range of taxa, including mammals (Spinola et al., 2008), birds (Hardman & Moro, 2006), reptiles and amphibians (Germano & Bishop, 2009), fishes (Hervas et al., 2010) and arthropods (Knisley et al., 2005), and might also be affected by the age and sex of released individuals (Moehrenschlager & Macdonald, 2003; Le Gouar et al., 2012). Managers should account for these potential effects in reintroduction planning when age- and sex-specific dispersal patterns in the species to release have been already observed in natural populations (i.e. Nussey et al., 2006; Spinola et al., 2008; Le Gouar et al., 2012).

As quantified here, avoiding the costs of captive breeding can provide important economic savings to reintroduction programmes and economic differences may also increase if we consider further expenses not accounted for in this study. In our specific scenario, we took advantage of wildlife rehabilitation centres to secure wild individuals for WildTrans and active monitoring campaigns to obtain chicks for the NestHack strategy. Even if monitoring and trapping sessions had to be financed to capture such wild individuals, these costs would be very unlikely to exceed the expenses related with the launching and maintenance of breeding programmes (Moran et al., 2005; Ferrer et al., 2018). Therefore, our cost assessments are probably conservative. However, the use of wild-born individuals for both hacking and non-juvenile translocations may present specific challenges that can limit their use. First, healthy source populations for capture or nest-removal may not always be available, especially considering that several target species for reintroduction are endangered throughout their ranges. Detailed evaluation of the impact of extractions to the donor population might be necessary, especially if extractions are intense or continued through time (Ferrer et al., 2014). In contrast, captive breeding programmes may ensure a regular pool of individuals for release and can be of critical importance to ensure the persistence of severely endangered populations. Second, capturing wild individuals or extracting wild chicks from nests may be technically difficult and imply exhaustive monitoring campaigns. In this sense, it is essential to design methods that ensure a large enough number of individuals for release throughout the reintroduction period, as this can be crucial for reintroduction success (Fischer & Lindenmayer, 2000; Rummel et al., 2016). For WildTrans strategies, wildlife recovery centres can be a suitable source of individuals for release, although such a collaboration may require a high level of coordination between centres and reintroduction managers. Third, captive breeding programmes usually have a stronger potential than other alternatives to educate the general public on nature conservation and raise funds (Wiese

et al., 1996). Hence, the choice of a reintroduction strategy should be made after careful evaluation of pros and cons of all alternatives.

Conservation managers often face considerable uncertainties when designing and addressing reintroductions, yet important decisions must be made at many stages (Armstrong & Seddon, 2008). For most threatened species, there are considerable knowledge gaps around their population dynamics, ecological requirements and the effects of captivity and stress on their behaviours (Dickens et al., 2010; Nichols & Armstrong, 2012). Luckily, reintroduction programmes are generally not implemented in a single stage but are rather iterated schemes in which the outcomes of initial decisions can be evaluated to improve management in further steps (Varley & Boyce, 2006; Runge, 2013). In this respect, adaptive management and decision theory have proved to be useful tools to making optimal decisions at the initial and other steps of reintroduction while accounting for the uncertainty present at every step (McCarthy & Possingham, 2007). Such approaches often rely on quantitative methods to guide management (Runge, 2011). In our case, modelling and simulations have provided support for WildTrans as the most desirable strategy to achieve success in the reintroduction of the Bonelli's eagle in Mallorca. However, our small sample size limited the degree of detail of our analyses, as usually happens in imperilled populations. In these cases, intensive, long-time population monitoring is essential to extract detailed insights on population dynamics and trends and support evidence-based decisions (Badia-Boher et al., 2019).

In summary, the translocation of wild-reared, non-juvenile individuals (WildTrans) should be considered as a potentially cost-effective strategy in animal reintroductions. Particularly, the use of non-juveniles can promote recruitment to the breeding population and early reproduction, which can be key for reintroduction success. However, post-release effects of different reintroduction strategies can vary depending on species, age, sex and the particularities of the release area, and therefore practitioners should undertake careful evaluation of the pros and cons of all alternatives. As for raptors, when hacking is chosen, we recommend analysing cost-effective alternatives to implementing captive breeding programmes such as the use of chicks extracted from wild nests from healthy populations. As a final consideration, further research is needed to identify cost-effective strategies from an evidence-based perspective. This fact can contribute to a more efficient use of economic and technical resources and an increase in the global effectiveness of conservation schemes, which is essential to deliver an effective response in light of the current biodiversity crisis.

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Supporting information

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

Data S1. Supplementary file that provides additional information about 1) definition and selection of the multistate analyses ("Multievent Definition and Selection"), 2) the methods used to estimate the economic costs of every release method ("Economic Estimations"), 3) the structure of the individual-based population model ("Population Modelling"), and 4) additional populations simulations that include parametric uncertainty ("Simulations with parametric uncertainty").

Figure S1. Cost calculation representation of all three release methods.

Figure S2. Diagram representing the different steps considered by our individual-based analysis simulating the long-term population dynamics of the reintroduction of the Bonelli's eagle in the island of Mallorca.

Figure S3. Comparison of the effects of hacking and Wild-Trans reintroductions on long-term population viability with parametric uncertainty on adult survival and adult productivity.

Figure S4. Cost-effectiveness comparison of the effects of WildTrans, NestHack and CaptHack reintroductions on long-term population viability under different budget scenarios and accounting for parametric uncertainty in adult survival and adult productivity.