1 **Halfway to self-sustainability: Reintroduced migratory European** 2 **Northern Bald Ibises (*Geronticus eremita*) still need management** 3 **interventions for population viability**

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25 **Abstract**

26 Northern Bald Ibis (NBI) have disappeared from Europe already in Middle Age. Since 2003 a
27 migratory population is reintroduced in Central Europe. We conducted demographic analyses
28 of survival and reproduction of 384 NBI over a period of 12 years (2008-2019). These data
29 also formed the basis for a population viability analysis (PVA) simulating the possible future
30 development of the NBI population in different scenarios. We tested life-stage specific
31 survival rates for differences between these stages, raising types and colonies as well as the
32 influence of stochastic events and NBI supplements on the population growth.

33 Stage specific survival rates ranged from 0.64 to 0.78. 61% of the mature females reproduce
34 with a mean fecundity of 2.15 fledglings per nest. The complementary PVA indicated that the
35 release population is close to self-sustainability with a given lambda 0.95 and 24% extinction
36 probability within 50 years. Of the 326 future scenarios tested, 94 % reached the criteria of
37 <5% extinction probability and population growth rates >1. In case of positive population
38 growth, stochastic events had a limited effect. Of 820 sub-scenarios with different stochastic
39 event frequencies and severities 87 % show population growth despite the occurrence of
40 stochastic events.

41 Predictions can be made based on the results of the individual-based model as to whether and
42 under what circumstances the reintroduced NBI population can survive. This study shows
43 that a PVA can support reintroduction success that should work closely together with the
44 project in the field for mutual benefit, to optimize future management decisions.

45

46 **Introduction**

47 In conservation biology, species restoration plays an increasingly important role to counteract
48 the currently ongoing dramatic decline of biodiversity, to assist the colonization of once
49 widespread species and to restore whole populations that have become extinct (IUCN/SSC,
50 2013a; Destro et al., 2018; Pettorelli et al., 2018). Reintroductions are a key restoration
51 method, defined by the IUCN as “the intentional movement and release of an organism inside
52 its indigenous range from which it has disappeared”. Reintroductions commonly aim at
53 minimizing interventions and allow for viable populations with lowest possible human
54 support (Corlett, 2016).

55 Reintroduction efforts have been performed for an increasing range of species (Frey, 1992;
56 Bennett et al., 2013; Fritz, Kramer, et al., 2017; Gray et al., 2017; Soorae, 2018), showing
57 different levels of success. Impairments are mainly due to species interactions like predation,
58 human-wildlife interactions and missing habitat suitability that all affect species’ viability
59 and reproduction (Wimberger et al., 2009; Bennett et al., 2013; Robert et al., 2015). There is
60 no general definition of reintroduction success (Robert et al., 2015), but it is recommended to
61 calculate the population growth rate, population size and reproduction probabilities and the
62 frequency of stochastic events, i. e. events that occur with a given probability and reduce the
63 population size in the reintroduction site (Robert et al., 2015). Besides, it is of paramount
64 importance to not only assess the long-term success of reintroductions under given
65 constraints, but also to evaluate and rank the impact of management interventions taken in a
66 retrospective way to be able to adjust management actions (Pereira & Navarro, 2015; Robert
67 et al., 2015).

68 In this paper, we retrospectively analyse long-term demographic data (2008-2019) of a
69 European migratory release population of the Northern Bald Ibis (*Geronticus eremita*,

hereafter NBI) and assess the long-term success of the reintroduction alongside the impact of management measures in an individual-based model (IBM). In 2002, a European group of scientists, called *Waldrappteam* and headed by J. Fritz, started an NBI research project which in 2014 changed into an EU LIFE+ funded reintroduction project. Their mainly used translocation action is the Human-Led Migration. Chicks from zoo breeding colonies are raised by human foster parents at breeding sites north of the Alps and trained to follow a microlight airplane, which leads them to the wintering site (Fritz, Kramer, et al., 2017; see also SUPPLEMENTARY MATERIAL 1).

We hypothesize that at the given stage the NBI population can survive without further management and release. We predict that observed demographic rates will ensure population growth and do not differ between the colonies.

Material & Methods

Species and study area

The NBI is a threatened species, listed in the IUCN Red List as *critically endangered* from 1994 and down listed to *endangered* in 2018. The species is migratory, mainly insectivorous and reaches an age of up to 30 years in captivity. NBI are mainly seasonally monogamous and breed in colonies of up to hundreds of birds (Boehm et al., 2020). Juveniles learn the migration route by following conspecifics to the wintering ground, there they usually remain until they reach sexual maturity (Fritz, Unsoeld, et al., 2019). The last remaining wild population in the world changed to a sedentary lifestyle and lives year round at two breeding sites on the Atlantic coast of Morocco (Bowden et al., 2008).

The European release population consists of four breeding colonies in southern Germany (Burghausen, Überlingen) and Austria (Kuchl, Rosegg). The common wintering area is

located in Italy, in the Tuscan nature reserve WWF Oasi Laguna di Orbetello (Fig. 1) (Fritz, Unsoeld, et al., 2019).

Figure 1

Data collection & study design

384 NBIs which hatched between 2008 and 2019 are included in the study. Due to insensitive monitoring comprehensive data on genetically determined sex, raising type (either human-raised founder individuals FP, generation F0, or biological parent raised wild individuals BP, generations F1+), breeding colony and potentially date and cause of death or disappearance are available. Reproduction data include egg laying dates, clutch size, and pre-fledging survival probability. In the first years, spatio-temporal data are based exclusively on sight reports. From 2012 on, an increasing proportion of the birds carried GPS tags and from 2014 onwards, the whole population could be remotely monitored (Sperger et al., 2017).

Founder individuals are raised by human foster parents (FP). In autumn of their first year, they followed a microlight air-plane to the wintering ground where they were released (Fritz, Kramer, et al., 2017). Since 2011, chicks are raised in the wild by their biological bird parents (BP). They follow their conspecifics to the common wintering ground along the migration corridor, which was established during release of the founder individuals. At time of the study, some of the released founder individuals were not yet assigned to a breeding colony, as they have not yet migrated back to a breeding area.

The NBIs of all four breeding colonies are considered as one population, sharing the same wintering ground and separating for breeding, with genetic exchange (Fritz, Kramer, et al., 2017; Fritz, Wirtz, et al., 2017; Wirtz et al., 2018).

Definition of demographic stages and demographic analyses

For the determination of demographic stages, the 384 NBI were assigned to four stages representing age classes with characteristic life-history events (FIG. 2; see also SUPPLEMENTARY FIG. 2). Stage 1 are juveniles from fledging until end of their first year of life; after the first autumn migration these birds usually remain at the wintering grounds. Stage 2 are juveniles in their second year of life; they usually stay year-round at the wintering grounds. Stage 3 are subadult birds in their third year of life; although not mature, most of them perform a partial or even full migration. Stage 4 are adults older than 3 years; these birds usually migrate and reproduce annually, even though some individuals may remain at the wintering ground.

Figure 2

For the calculation of survival probabilities per stage, sex, colony and raising type we used the Kaplan-Meier estimator (Kaplan & Meier, 1958) with the 'survival'-package v. 3.2-7 in R v. 4.0.3 (Therneau, 2015; R Core Team, 2020). We estimated survival probabilities for fledglings around 45 days of age. Adult birds that were only temporarily added during the breeding season to improve breeding success were discarded from the calculations of the survival probabilities. We used a likelihood ratio test (LRT) to test for significance between different classes in Cox proportional hazard models (Kleinbaum & Klein, 2012). We also calculated hatching rate and fledging rate.

Fecundity was calculated as the mean number of fledglings per nest. At the start-up of new founded colonies, adult males and females were temporarily added at the breeding site to compensate for missing mates and to enable the birds to reproduce. The rate of temporarily added adults was successively reduced and completely terminated at the end of the data period.

Population Viability Analysis

For the Population Viability Analysis (PVA) we focus our analyses and population projections on the female half of the population (underlying a sex-ratio of 1:1). We tested how different values of demographic rates used for the four stages, as analysed from field data, influence population trajectories and population viability.

We analysed the population trajectories per scenario (see below) and calculated the extinction probability as the number of runs of 100 repetitions per scenario where the population went extinct (0 individuals) within the simulated 50 years (P_{EXT_50}), and the intrinsic growth rate of the population (λ), calculated as the mean of the annual finite rate of change in population size. Then, we analysed the distribution of the input parameters of demographic rates in scenarios where $\lambda > 1$ and $P_{EXT_50} \leq 5\%$. In addition, we ran generalized linear models (GLMs) and conducted an analysis of variance (anova) to rank the contribution of demographic rates in the different stages on λ as response variable, using a gamma error structure with inverse link. Besides, we calculated how often each combination of stochastic event frequency (5-20%) and severity (5-25%) and each combination of numbers of supplements (15 or 30) and time span of intervention (4 or 7 years) occurred in sub-scenarios resulting in $\lambda > 1$ and $P_{EXT_50} \leq 5\%$.

The model documentation follows the TRACE documentation framework (Grimm et al., 2014; SUPPLEMENTARY MATERIAL 3). The model description follows the ODD protocol (Grimm et al., 2006, 2010). An individual-based model (IBM) was implemented in NetLogo 6.0.3 (Wilensky, 1999). The corresponding NetLogo and R scripts are provided online (SUPPLEMENTARY MATERIAL 6).

Reproductive Rates

For the PVA we only considered female fledglings. From fledglings with unknown sex 50% were included. For the analysis we included all adult females in the release population (stage 4), irrespective whether they were breeding or not, plus adult females which were temporarily added at the breeding site to compensate for missing mates. Thus, different to RR_{Nest} this reproductive rate is an expression of breeding probability, it indicates how likely it is that a female will breed.

Three different reproductive rate (RR) were included into the PVA, depending on the fledglings that were included: $RR_{Baseline}$ includes fledglings raised by adult wild females (stage 4); $RR_{Status\ quo}$ includes in addition female fledglings raised by temporarily added females; $RR_{All\ chicks}$ includes in addition female fledglings raised by human foster-parents. $RR_{Baseline}$ was also calculated separately for the two colonies Burghausen and Kuchl (RR_B and RR_K) and separately for females raised by bird parents (RR_{BP}) and human foster-parents (RR_{FP}). We also implemented GLMMs (generalized linear mixed models) using a Poisson error structure and maximum likelihood fit, to investigate if differences in reproduction are significant.

Scenario development

We analysed the model for two different types of scenarios:

(I) The management scenarios (MScen) compare situations where no management took place (baseline scenario S_{Base}), i.e. release of fledglings or temporary release of adults, to scenarios where baseline demographic rates were improved by 10%, 25% and 100%. We combined three levels of survival rates at each stage and four levels of RR in a full factorial design. Additionally, we combined $RR_{Status\ quo}$ and $RR_{All\ chicks}$ with baseline survival probabilities, which resulted in 326 MScen (TABLE 1, SUPPLEMENTARY MATERIAL 4). Only for the

simulation of S_{Base} we draw the demographic rates from the probability distributions defined by mean and standard deviation to test Hypothesis 1 (H1). For all other scenarios we used the calculated mean values of demographic rates. Besides, we chose 14 scenarios of special interest for closer examination (TABLE 1). All parameter combinations were within the scope of realistic management measures to improve survival and reproduction.

(II) The stochastic event and juvenile supplement scenarios (SJS) assess reproduction improvement by the supplemental release of FP juveniles (F0). For these SJS we crossed S_{Base} and the MScen of special interest where $\lambda > 1$ and $P_{EXT_50} \leq 5\%$ (9 MScen, see results) with 4 levels of stochastic event frequency (5, 10, 15, 20), 5 levels of severity (5, 10, 15, 20, 25; additional mortality per stage), 2 levels of the number of supplements (15, 30) and 2 levels of the time for supplementing individuals (4 or 7 years).

Table 1

Results

Demography

From the 384 individuals, 195 were males and 184 females, what gives a sex rate of 1.00:0.94 (m:f). For 5 juveniles, sex was not determined at time of data analysis. Concerning the raising type, N=162 birds were raised in the wild by bird-parents (42%; BP), N=213 individuals by foster-parents (55%; FP) and N=9 supplemented as juveniles (2%). Concerning the breeding colonies, N=127 individuals belonged to Burghausen (33%), N=89 to Kuchl (23%), N=89 to Überlingen (23%), N=22 to Rosegg (6%) and N=57 juveniles were not yet assigned at time of the data collection. 232 birds died during the data collection period; out of that N=123 during stage 1 (53%), N=45 during stage 2 (19%), N=33 during stage 3 (14%) and N=31 during stage 4 (13%; see also SUPPLEMENTARY FIG. 1).

At the end of 2019, 152 individuals were alive including 9 individuals which were delivered to zoos for various reasons. Thus, the release colony at end of the data collection consisted of 143 individuals, 69 males and 74 females (sex rate of 1.00:1.07). Concerning the life stage, N=71 individuals belonged to stage 1 (50%; 37f, 34m), N=28 to stage 2 (20%; 11f, 17m), N=13 to stage 3 (9%; 8f, 5m) and N=31 to stage 4 (22%; 18f, 13m). Concerning the colonies, N=33 bird belonged to the colony Burghausen (23%), N=33 to Kuchl (23%), N=51 to Überlingen (36%) and N=15 to Rosegg (10%); 11 individuals (8%) were not yet allocated to a colony. Concerning the raising types, N=68 birds (48%) were BP raised, N=73 FP raised (51%) and N=2 birds (1%) were supplemented.

Survival

Survival was calculated for all individuals from fledging onwards. According to the cox proportional hazard model survival rates between stages across the whole population did not differ significantly (LRT, $N = 736$, 3.05 , $p = 0.4$). Neither did they differ significantly between the sexes (LRT, $N = 379$, 0.8 , $p = 0.4$). According to the Kaplan-Meier estimator, survival probability was for stage 1 $0.64 (\pm 0.36)$ for stage 2 $0.74 (\pm 0.35)$, for stage 3 $0.69 (\pm 0.35)$ and for stage 4 $0.78 (\pm 0.14)$. The cumulative survival probability until sexual maturity (end of stage 3) was $0.33 (\pm 0.23)$. Concerning pre-fledging survival, 72% of the eggs hatched and 83% of the hatched chicks fledged (TABLE 2).

Table 2

Survival between the two raising types FP and BP differed (LRT, $N = 375$, 8.26 , $p = 0.004$; FIGURE 3), also per stage and per raising type (LRT, $N = 715$, 10.17 , $p = 0.04$). In stage 1 FP raised individuals showed a higher survival rate (FP = 0.73 ± 0.37 , BP = 0.52 ± 0.30), while in stage 4 BP raised adults showed a higher survival rate (FP = 0.72 ± 0.22 , BP = 0.92 ± 0.17 ; TABLE 1). The survival rates in the two colonies Burghausen and Kuchl did not significantly

differ, neither for the whole colonies (LRT, $N = 216$, 1.56 , $p = 0.2$) nor per stage and per colony, respectively (LRT, $N = 453$, 5.36 , $p = 0.3$; TABLE 1).

Figure 3

Fecundity

The number of nests increased steadily with 1 nest in 2011 and 14 nests in 2019, with a mean of $3.43 (\pm 0.79)$ eggs per nest (TABLE 2). Overall fecundity was 2.15 fledglings per nest (± 0.70). Fecundity rates of females raised by human-foster parents and females raised by their bird parents (BP) in the wild did not differ significantly ($z = 0.68$, $p = 0.50$), neither fecundity rates among the colonies Burghausen and Kuchl ($z = 0.60$, $p = 0.55$).

The annual rate of reproducing adult females (s4) was $0.61 (\pm 0.20)$. From a total of 27 potentially reproductive females $N=13$ (48%) never reproduced till end of the data collection period, $N=4$ (15%) reproduced once, $N=4$ (15%) twice, $N=5$ (19%) three times and $N=1$ (4%) 6 times.

Population Viability Analysis

Reproductive Rate

Over the whole period of data collection, a total of 62 individuals reached stage 4. Analysing 31 females of these 62 individuals of both sexes in stage 4 as potential mothers resulted in a $RR_{Baseline}$ of $0.53 (\pm 0.17)$; TABLE 1) (wild BP and FP mothers and their female fledglings), $RR_{Status Quo}$ of $1.41 (\pm 0.81)$ (additionally female fledglings from temporarily added females included) and $RR_{All Chicks}$ of $3.97 (\pm 2.66)$ (additionally human raised and released female fledglings included). These reproductive rates were used for the PVA.

Management scenarios (MScen)

Without further management and translocation measures, as assumed for the baseline scenario, the PVA indicates a lambda of 0.95 (± 0.030), below the 1.0 threshold with 24% extinction probability within 50 years (TABLE 1).

The full factorial design resulted in 326 MScen (SUPPLEMENTARY MATERIAL 4). Across all 326 MScen lambda ranged between 0.95 and 1.40. Lambda was >1 and $P_{EXT_50} \leq 5\%$ in 308 out of 326 MScen (94 %), in all these 308 MScen the population did not go extinct. In a first analysis we investigated the frequencies of MScen with different demographic rates out of 306 of 308 MScen with positive population development, to understand how demographic rates affect population viability (FIG. 4). The two MScen “Status quo” and “All chicks” were not considered here, because they were only simulated once with baseline survival values and the respective RR. In the 306 MScen with positive population development only s4 shifted to increasing survival values, as given by the improved MScen. An increase of s4 by 10% or 25% increased the viability disproportionately (each 108 times) compared to the baseline value (90 times). These results indicate the importance of survival of the reproductive stage for population viability. This is supported by the GLMs and the ANOVA ranking the effect of the survival rates (deviance d of ANOVA: $d_{s1} = 0.05$, $d_{s2} = 0.05$, $d_{s3} = 0.05$, $d_{s4} = 0.68$). Here, s4 had the largest effect, together with reproductive rates (SUPPLEMENTARY MATERIAL 5).

Figure 4

All MScen where RR was increased by 100% showed positive population development (81 times). Only one MScen where RR was increased by 25% was rejected, i. e. the one where no survival rate was increased (i. e. baseline values for s1-s4, RR +25% MScen; TABLE 1). Still,

88% of the MScen with $RR_{Baseline}$ showed positive population development (71 times). The reproductive rate had a strong effect on lambda, too ($d_{RR} = 0.58$) in the GLMs.

In the second analysis 14 MScen of special management interest were analysed (TABLE 1, FIG. 5). For nine out of these, lambda was >1 and $P_{EXT_50} \leq 5\%$. If only RR was increased, positive population growth only occurred from an increase of at least 100% (“+100% RR”, “Status quo”, “All Chicks”), i. e. a minimum of one female fledgling per female. Increasing only the survival of juveniles s_1 did not lead to positive population growth but increasing adult survival s_4 did. An increase in all survival values s_1 - s_4 also led to positive population growth; these effects were reinforced by an additional increase in the reproductive rate.

Stochastic event and juvenile supplement scenarios (SJS)

Here we developed 820 scenarios, taking 11 MScens: nine MScen of special interest where lambda >1 and $P_{EXT_50} \leq 5\%$, the S_{Base} scenario and once the "All chicks" scenario without the supplements, as the supplements are already included in the $RR_{All\ Chicks}$ (see under SUPPLEMENTARY MATERIAL 2). The number of SJS is given by the equation in SUPPLEMENTARY MATERIAL 4. Lambda was between 0.91 and 1.40. In 714 out of 820 SJS (87 %) lambda was >1 and $P_{EXT_50} \leq 5\%$. Baseline survival values led to positive population growth in 74-79% of the SJS. Increase of survival of adults (stage 4) by 10% led to positive population growth in 89% of the SJS, while 10% survival increase in other age categories led to population growth in 100% of the SJS considered. Increasing baseline survival by 25% led to positive population growth in 100% of the SJS.

Each combination of stochastic event frequencies and severities occurred 41 times in all 820 SJS. 90% of the SJS with low frequency (5%) and severity (5%) of stochastic events and also 80% of the SJS with high frequency (20%) and severity (25%) of stochastic event resulted in positive population development (FIG. 5). 88% of the SJS with 30 supplemented juveniles per

year over 7 years and also 86% of the SJS with 15 supplements per year over 4 years resulted in positive population development.

Figure 5

Discussion

This paper presents an analysis of demographic development, survival, and reproduction of a reintroduced Northern Bald Ibis population. It covers a period of 12 years, including the late phase of a research project (2008-2013), where small number of birds were released, and the following six-year period of the LIFE+ funded reintroduction project (2014-2019).

The comprehensive 12-year data set allowed a Population Viability Analysis (PVA) of the future population development under different scenarios. PVA is a powerful mean to evaluate the effectiveness of reintroduction and management scenarios. Such models based on the best possible evidence are recommended in the IUCN reintroduction guidelines to decide on further management (IUCN/SSC, 2013b).

Survival

Survival rate of the *Waldrappteam* population is ranging from 64% for juveniles (stage 1) to 78% for adults (stage 4). A matching adult survival rate of 81% is published for a small migratory NBI relict population, which was discovered in the Middle East in 2002 (Serra et al., 2014). Since the Moroccan birds are not marked, their survival rate can only be estimated due to the annual counts of the pre-breeding population and the number of fledglings (Bowden et al., 2008). This results in an overall annual survival rate of 77%, what is also in accordance with the calculated rates of the *Waldrappteam* population.

The cumulative survival rate of the *Waldrappteam* population until sexual maturity (stage 1 to 3) was 33%. In the Middle East relict population, the count of departing fledglings and

arriving new breeders at the breeding site in Syria indicates 14% survival rate until sexual maturity (Boehm et al., 2020), what is less than half the rate of the *Waldrappteam* population. Satellite-tracking of the Middle East juveniles revealed, that they did not arrive at the common wintering site in Ethiopia, because they lost the company of experienced conspecifics and died at the Arabic Peninsula (Serra et al., 2014). This low survival rate of juveniles was a major cause for the extinction of this population in 2013, despite international conservation and translocation efforts (Fritz & Riedler, 2010; Bowden et al., 2012; Serra, 2015).

In our population, first-year survival of foster-parent raised and released juveniles (73%; FP) was significantly higher compared to bird-parent raised juveniles (52%; BP). This contrasts the widespread experience that released individuals have comparably low survival rates, particularly in the first period after release, due to translocation and competition induced stress, dispersal, diseases or predation (Parker et al., 2013), wherein this is true in particular for captive-bred individuals, probably because they lack individual experiences (Mathews et al., 2005). Our birds undergo an extensive pre-release training, which provides them with essential experiences regarding navigation, flight techniques, weather conditions, aerodynamics and predator avoidance (Portugal et al., 2014; Voelkl & Fritz, 2017; Fritz, Unsoeld, et al., 2019). This is assumed to improve post-release viability (Alonso et al., 2011; Houser et al., 2011; Zhang et al., 2017). In a Spanish NBI reintroduction project (*Proyecto Eremita*), the mean first-year survival rate for released juveniles was substantially lower with 31% (Boehm et al., 2020; data from 2004-2018), compared to the *Waldrappteam* population. We assume that minor pre-release training and unguided autumn dispersal (Muñoz & Ramírez, 2017) account for the strongly deviating survival rate of the juveniles released in Spain (Fritz, Unsoeld, et al., 2019).

The survival rate from hatching to fledging in the *Waldrappteam* population is 83%, what is substantially higher compared to a given value of 47% for the Morocco wild population (Bowden et al., 2003). We assume this difference to be mainly related to the quality of the feeding habitats. For the European birds, studies indicate a high feeding efficiency and a correspondingly high abundance of food animals (mainly worms and larvae) in the soil of meadows and pastures as the preferred feeding habitats (Zoufal et al., 2007; Fritz et al., 2017) while the feeding habitats at the Atlantic coast in Morocco consist of semi-natural steppes with sparse cover of perennial and annual vegetation and low availability of fresh water sources (Bowden et al., 2008). Accordingly, position data indicate a small activity range of about two kilometres radius around the nesting sites for the European birds during the breeding season (Fritz et al., 2016) while the foraging area of the two Moroccan colonies covers a strip of about 4 km inland along 50 km coastline. The fledgling survival rate in Morocco was even lower in the 90's before supplementary fresh water was provided near to the breeding grounds from 1998 on (Smith et al., 2008).

Fecundity

In the *Waldrappteam* population 61% of the mature females (stage 4) actually reproduce. The majority of the non-reproducing females remain at the wintering site. In comparison, 63% of the *full-grown* birds in the Moroccan population reproduce (Bowden et al., 2008). These rates are not directly comparable, because the Moroccan data are based on counts of un-marked birds. But the data indicate that also in this sedentary population with all birds on site a similar proportion of the adults is not reproducing.

In the *Waldrappteam* population, the average annual fecundity was 2.15 fledged chicks per nest. TABLE 3 outlines fecundity values for other NBI populations, based on data published in (Boehm et al., 2020). The values vary considerably, with 1.23 fledged chicks per nest in the

wild sedentary Moroccan population and 0.97 in the Spanish *Proyecto Eremita* population (release sedentary). The highest rate with 2.24 refers to the semi-wild managed population at Zoo Rosegg in Austria. The comparison indicates that fecundity in the *Waldrappteam* population is at the upper end, which is consistent with the high survival rate from hatching to fledging (83%) and indicates a high quality of the breeding habitats. The rate of 1.67 for a Chinese sedentary release population of the Crested ibis (*Nipponia nippon*) lies in the range of the NBI populations.

Table 3

Population Viability Analysis

Due to the outcome of the PVA baseline scenario, with λ 0.95 and 24% extinction probability within 50 years, the hypothesis that this reintroduced NBI population can survive without further management and release at the end of the data collection period (2019) is to be rejected. This result is not unexpected because the reintroduction project started just in 2014 and is still ongoing. Nonetheless, the population is already close to transition into a state of self-growth (with $\lambda > 1.0$) what also coincides with the comparatively good survival and fecundity values.

The baseline reproductive rate relates the actual number of fledged female offspring to the entirety of adult females (s_4) in the population, including the 39% non-reproducing females. It is an expression of the reproductive potential in the population. The given baseline rate of 0.53 can be significantly increased by translocation measures, up to a rate of 3.97 ($RR_{All\ Chicks}$). As indicated by the management improvement scenarios continuing with the given translocation measures has the most significant immediate effect on λ and extinction probability (TABLE 1). In comparison, an increase in the survival rate has a relatively small

effect on lambda, where improvement in the survival rate of adults (s4) has the greatest impact. This is common knowledge and has also been confirmed for other long-lived species (Lebreton & Clobert, 1991; Lampila et al., 2006; Pistorius et al., 2006; Schaub et al., 2009; O'Shea et al., 2011). Sustainable improvement of the survival on long-term should be an objective for the project, even though intraspecific comparison indicates that in the *Waldrappteam* population survival values are already in a good range for all age categories.

The simulation of stochastic event scenarios with different frequency and severity led to only a slight impairment of the population development. The simulations also indicated that increasing survival or fecundity could mitigate the effect of stochastic events.

Conclusion

Despite comparatively good survival and fecundity data the PVA indicated that the *Waldrappteam* population needs further management and translocation. It is important at this stage to plan the kind and duration of further management and translocation measures based on a quantitative, systematic analysis.

According to the modelling outcome, a major focus of future management of the release population will be on further improvement of the survival rates with particular focus on adults (stage 4). This will mainly be achieved by the implementation of measures against the major mortality causes, illegal hunting in Italy and electrocution on unsecured power poles at the breeding sites (Fritz, 2015; Fritz et al., 2019). Also, the proportion of reproducing females (61%) should be increased by the establishment of a breeding site south of the Alps which can be easily reached in spring without crossing the Alpine chain.

An interspecific comparison of the demographic data did not indicate adverse effects of the migratory lifestyle in the *Waldrappteam* population. The survival rate of adults is similar to

sedentary populations and the survival rate of released juveniles is even substantially higher in the migratory population (73%) compared to a sedentary population in Spain (31%).

The high fecundity rate in the *Waldrappteam* population (2.15) is presumably a consequence of the migratory behaviour that allows the adults to exploit rich northern feeding grounds during the reproduction period.

The actual *International Single Species Action Plan* for the NBI (Bowden 2015) does not include modelling, neither as an objective nor as a recommendation. This indicates that systematic, quantitative approaches, such as the PVA, are still not well established and recognizes as a strategic tool for animal conservation. The study presented here show that the PVA could essentially contribute to the improvement of conservation measures for this and other endangered animal species and populations.

The model could be improved by including movement of the NBI in the PVA assessment to build a spatially explicit population simulation model accounting for differences in the migration routes from and to the colonies. In addition, a thorough assessment of the factors significantly influencing the viability of the NBI in the colonies would be an asset, such as the availability of food or nesting sites, the weather in the breeding areas, during the migration and in the winter area (Schaub et al., 2005).

Author contribution

SD, SKS and JF conceived and designed the study, SD and VR analysed data, SD led the writing, CS supported programming, and CE collected field data. SKS, JF, IK and VR substantially contributed to the writing.

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Conflicts of interest

None.

Ethical standards

This research followed the *Oryx* guidelines on ethical standards.

References

- ALONSO, R., OREJAS, P., LOPES, F. & SANZ, C. (2011) Pre-release training of juvenile little owls *Athene noctua* to avoid predation. *Animal Biodiversity and Conservation*, 34, 389–393.
- BENNETT, V.A., DOERR, V.A.J., DOERR, E.D., MANNING, A.D., LINDENMAYER, D.B. & YOON, H.J. (2013) Causes of reintroduction failure of the brown treecreeper: Implications for ecosystem restoration. *Austral Ecology*.
- BOEHM, C., BOWDEN, C.G.R., SEDDON, P.J., HATIPOĞLU, T., OUBROU, W., EL BEKKAY, M., ET AL. (2020) The northern bald ibis *Geronticus eremita*: history, current status and future perspectives. *Oryx*, 1–13.
- BOWDEN, C.G.R., AGHNAJ, A., SMITH, K.W. & RIBI, M. (2003) The status and recent breeding performance of the critically endangered Northern Bald Ibis *Geronticus eremita* population on the Atlantic coast of Morocco. *Ibis*, 145, 419–431.
- BOWDEN, C.G.R., HAMOUD, A., JBOUR, S., FRITZ, J., PESKE, L., RIEDLER, B., ET AL. (2012) Attempted supplementation of the relict wild Eastern population of Northern Bald Ibis in Syria with Turkish semi-wild juveniles. *IUCN Reintroduction Specialists Group Case Studies Part III*, 130–134.
- BOWDEN, C.G.R., SMITH, K.W., BEKKAY, M. EL, OUBROU, W., AGHNAJ, A. & JIMENEZ-ARMESTO, M. (2008) Contribution of research to conservation action for the Northern Bald Ibis *Geronticus eremita* in Morocco. *Bird Conservation International*, 18, 74–90.
- CORLETT, R.T. (2016) Restoration, Reintroduction, and Rewilding in a Changing World. *Trends in Ecology and Evolution*.
- DESTRO, G.F.G., DE MARCO, P. & TERRIBILE, L.C. (2018) Threats for bird population restoration: A systematic review. *Perspectives in Ecology and Conservation*, 16, 68–73.
- FREY, H. (1992) Die Wiedereinbürgerung des Bartgeiers (*Gypaetus barbatus*) in den Alpen. *Egretta*, 35, 85–95.
- FRITZ, J. (2015) Reintroduction of the Northern Bald Ibis in Europe: Illegal Hunting in Italy during Autumn Migration as the Main Threat. *WAZA Magazin*, 31 p.
- FRITZ, J., HOFFMANN, W. & UNSÖLD, M. (2016) Back into European ecosystems: The LIFE + Northern Bald Ibis reintroduction project in Central Europe. In *Report of 4th IAGNBI Meeting Seekirchen* (Ed. C Böhm & C Bowden).
- FRITZ, J., KRAMER, R., HOFFMANN, W., TROBE, D. & UNSÖLD, M. (2017) Back into the wild: establishing a migratory Northern bald ibis *Geronticus eremita* population in Europe. *International Zoo Yearbook*, 51, 107–123.
- FRITZ, J. & RIEDLER, B. (2010) Neue Hoffnung für das Überleben einer hoch bedrohtesten Zugvogelart im Mittleren Osten: Freisetzung von Jungvögeln bei den letzten migrierenden Waldrappen in Syrien. *Vogelwarte*, 48, 417–418.
- FRITZ, J., UNSÖLD, M. & VOELKL, B. (2019) Back into European Wildlife: The Reintroduction of the Northern Bald Ibis (*Geronticus eremita*). In *Scientific Foundations*

- 487 *of Zoos and Aquariums: Their Role in Conservation and Research* (eds A. Kaufman, M.
488 Bashaw & T. Maple), pp. 339–366. Cambridge University Press.
- 489 FRITZ, J., WIRTZ, S. & UNSOELD, M. (2017) Aspekte der Nahrungsökologie und Genetik des
490 Waldrapps □: Reply zu Bauer et al. (2016) Vogelneozoen in Deutschland - Revision
491 der nationalen Statureinstufungen. *Vogelwarte*, 55, 141–145.
- 492 GRAY, T.N.E., CROUTERS, R., RAMESH, K., VATTAKAVEN, J., BORAH, J., PASHA, M.K.S., ET
493 AL. (2017) A framework for assessing readiness for tiger *Panthera tigris* reintroduction:
494 a case study from eastern Cambodia. *Biodiversity and Conservation*, 26, 2383–2399.
- 495 GRIMM, V., AUGUSIAK, J., FOCKS, A., FRANK, B.M., GABSI, F., JOHNSTON, A.S.A., ET AL.
496 (2014) Towards better modelling and decision support: Documenting model
497 development, testing, and analysis using TRACE. *Ecological Modelling*, 280, 129–139.
498 Elsevier B.V.
- 499 GRIMM, V., BERGER, U., BASTIANSEN, F., ELIASSEN, S., GINOT, V., GISKE, J., ET AL. (2006) A
500 standard protocol for describing individual-based and agent-based models. *Ecological*
501 *Modelling*, 198, 115–126.
- 502 GRIMM, V., BERGER, U., DEANGELIS, D.L., POLHILL, J.G., GISKE, J. & RAILSBACK, S.F.
503 (2010) The ODD protocol: A review and first update. *Ecological Modelling*, 221, 2760–
504 2768.
- 505 HOUSER, A.M., GUSSET, M., BRAGG, C.J., BOAST, L.K. & SOMERS, M.J. (2011) Pre-release
506 hunting training and post-release monitoring are key components in the rehabilitation of
507 orphaned large felids. *African Journal of Wildlife Research*, 41, 11–20.
- 508 IUCN/SSC (2013a) Guidelines for Reintroductions and Other Conservation Translocations.
509 IUCN Species Survival Commission, Gland, Switzerland.
- 510 IUCN/SSC (2013b) Guidelines for Reintroductions and Other Conservation Translocations.
511 Version 1.0. Gland, Switzerland.
- 512 KAPLAN, E.L. & MEIER, P. (1958) Nonparametric Estimation from Incomplete Observations.
513 *Journal of the American Statistical Association*, 53, 457–481.
- 514 KLEINBAUM, D.G. & KLEIN, M. (2012) Survival analysis: A Self-Learning Text, 3rd edition.
515 Springer Science+Business Media.
- 516 LAMPILA, S., ORELL, M., BELDA, E. & KOIVULA, K. (2006) Importance of adult survival,
517 local recruitment and immigration in a declining boreal forest passerine, the willow tit
518 *Parus montanus*. *Oecologia*, 148, 405–413.
- 519 LEBRETON, J.D. & CLOBERT, J. (1991) Bird population dynamics, management, and
520 conservation: the role of mathematical modelling. In *Bird population studies* (eds C.M.
521 Perrins, J.D. Lebreton & G.J.M. Hirons), pp. 105–125. Oxford University Press, Oxford.
- 522 MATHEWS, F., ORROS, M., MCLAREN, G., GELLING, M. & FOSTER, R. (2005) Keeping fit on
523 the ark: Assessing the suitability of captive-bred animals for release. *Biological*
524 *Conservation*, 121, 569–577.
- 525 MUÑOZ, A.-R. & RAMÍREZ, J. (2017) Reintroduced northern bald ibises from Spain reach

526 Morocco. *Oryx*, 51, 204–205.

527 O'SHEA, T.J., ELLISON, L.E. & STANLEY, T.R. (2011) Adult survival and population growth
528 rate in Colorado big brown bats (*Eptesicus fuscus*). *Journal of Mammalogy*, 92, 433–
529 443.

530 PARKER, K.A., EWEN, J.G., SEDDON, P.J. & ARMSTRONG, D.P. (2013) Post-release
531 monitoring of bird translocations: Why is it important and how do we do it? *Notornis*,
532 60, 85–92.

533 PEREIRA, H.M. & NAVARRO, L.M. (eds) (2015) Rewilding European Landscapes. In
534 *Rewilding European Landscapes* p. , 1st edition. Springer International Publishing,
535 Cham.

536 PETTORELLI, N., BARLOW, J., STEPHENS, P.A., DURANT, S.M., CONNOR, B., SCHULTE TO
537 BÜHNE, H., ET AL. (2018) Making rewilding fit for policy. *Journal of Applied Ecology*,
538 55, 1114–1125.

539 PISTORIUS, P.A., FOLLESTAD, A. & TAYLOR, F.E. (2006) Declining winter survival and fitness
540 implications associated with latitudinal distribution in Norwegian Greylag Gese Anser
541 anser. *Ibis*, 148, 114–125.

542 PORTUGAL, S.J., HUBEL, T.Y., FRITZ, J., HEESE, S., TROBE, D., VOELKL, B., ET AL. (2014)
543 Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight.
544 *Nature*, 505, 399–402.

545 R CORE TEAM (2020) R: A language and environment for statistical computing. R Foundation
546 for Statistical Computing, Vienna, Austria.

547 ROBERT, A., COLAS, B., GUIGON, I., KERBIRIOU, C., MIHOUB, J.B., SAINT-JALME, M. &
548 SARRAZIN, F. (2015) Defining reintroduction success using IUCN criteria for threatened
549 species: A demographic assessment. *Animal Conservation*, 18, 397–406.

550 SCHAUB, M., KANIA, W. & KÖPPEN, U. (2005) Variation of primary production during winter
551 induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *Journal of*
552 *Animal Ecology*, 74, 656–666.

553 SCHAUB, M., ZINK, R., BEISSMANN, H., SARRAZIN, F. & ARLETTAZ, R. (2009) When to end
554 releases in reintroduction programmes: Demographic rates and population viability
555 analysis of bearded vultures in the Alps. *Journal of Applied Ecology*, 46, 92–100.

556 SERRA, G. (2015) The Northern Bald Ibis is extinct in the Middle East - but we can't blame it
557 on IS. *Ecologist*.

558 SERRA, G., LINDSELL, J.A., PESKE, L., FRITZ, J., BOWDEN, C.G.R., BRUSCHINI, C., ET AL.
559 (2014) Accounting for the low survival of the Critically Endangered northern bald ibis
560 *Geronticus eremita* on a major migratory flyway. *Oryx*, 49, 312–320.

561 SMITH, K.W., AGHNAJ, A., EL BEKKAY, M., OUBROU, W., RIBI, M., ARMESTO, M.J. &
562 BOWDEN, C.G.R. (2008) The provision of supplementary fresh water improves the
563 breeding success of the globally threatened Northern Bald Ibis *Geronticus eremita*. *Ibis*,
564 150, 728–734.

565 SOORAE, P.S. (2018) Global Reintroduction Perspectives -2018; Case studies from around the
566 globe. IUCN/SSC Re-introduction Specialist Group & Environment Agency-ABU
567 DHABI, Gland, Switzerland.

568 SPERGER, C., HELLER, A., VOELKL, B. & FRITZ, J. (2017) Flight Strategies of Migrating
569 Northern Bald Ibises – Analysis of GPS Data During Human-led Migration Flights.
570 *AGIT □ Journal für Angewandte Geoinformatik*, 3, 62–72.

571 THERNEAU, T.M. (2015) A Package for Survival Analysis in R.

572 VOELKL, B. & FRITZ, J. (2017) Relation between travel strategy and social organization of
573 migrating birds with special consideration of formation flight in the northern bald ibis.
574 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160235.

575 WILENSKY, U. (1999) NetLogo. Center for Connected Learning and Computer-Based
576 Modeling, Northwestern University, Evanston, IL.

577 WIMBERGER, K., DOWNS, C.T. & PERRIN, M.R. (2009) Two Unsuccessful Reintroduction
578 Attempts of Rock Hyraxes (*Procavia capensis*) into a Reserve in the KwaZulu-Natal
579 Province, South Africa. *African Journal of Wildlife Research*, 39, 192–201.

580 WIRTZ, S., BOEHM, C., FRITZ, J., KOTRSCHAL, K., VEITH, M. & HOCHKIRCH, A. (2018)
581 Optimizing the genetic management of reintroduction projects: Genetic population
582 structure of the captive Northern Bald Ibis population Sarah Wirtz. *Conservation*
583 *Genetics*, 19, 853–864.

584 ZHANG, M., HUANG, Y., HONG, M., ZHOU, S., HUANG, J., LI, D., ET AL. (2017) Impacts of
585 man-made provisioned food on learned cub behaviours of giant pandas in pre-release
586 reintroduction training. *Folia Zoologica*, 66, 58–66.

587 ZOUFAL, K., FRITZ, J., BICHLER, M., KIRBAUER, M., MARKUT, T., MERAN, I., ET AL. (2007)
588 Feeding ecology of the Northern Bald Ibis in different habitat types: An experimental
589 field study with handraised individuals. In *Report of the 2nd IAGNBI Meeting* p. .

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Table 1

In the upper part, the table shows the given empirical values for survival per stage and for the three reproductive rates as defined in the text. These values and their improvements by 10%, 25% or 100% were used in different combinations for the NetLogo simulation of 14 management improvement scenarios, as outlined in the lower part of the table. Improvement of the empirical values are indicated by bold numbers. The resulting Lambda and extinction probability (P_{EXT_50}) are shown in the two right columns. Please note that reproductive rate comprises not only the reproducing females but all adult females in stage 4 and takes into account only to female offspring. In brackets: Standard deviation.

Results and PVA scenarios/stage	s1	s2	s3	s4	Reproductive rate (females)	Lambda	P _{EXT_50}
Empirical values							
RRBaseline	0.64 (±0.36)	0.74 (±0.35)	0.69 (±0.35)	0.78 (±0.14)	0.53 (±0.17)		
RRstatus quo					1.41 (±0.81)		
RRAll chicks					3.97 (±2.66)		
Management improvement scenarios I - 14 scenarios of special interest							
Baseline (RRBaseline)	0.64	0.74	0.69	0.78	0.53	0.95 (±0.030)	24% *
+10% RR	0.64	0.74	0.69	0.78	0.58	0.97 (±0.015)	3%
+25% RR	0.64	0.74	0.69	0.78	0.66	0.99 (±0.013)	0%
+100% RR	0.64	0.74	0.69	0.78	01.Jun	1.07 (±0.005)	0%
+10% s1	0.70	0.74	0.69	0.78	0.53	0.97 (±0.020)	1%
+25% s1	0.80	0.74	0.69	0.78	0.53	0.99 (±0.014)	1%
+10% s4	0.64	0.74	0.69	0.86	0.53	1.02 (±0.007)	0%
+25% s4	0.64	0.74	0.69	0.98	0.53	1.10 (±0.004)	0%
+10% s1-s4	0.70	0.81	0.76	0.86	0.53	1.05 (±0.006)	0%
+25% s1-s4	0.80	0.92	0.86	0.98	0.53	1.19 (±0.005)	0%
+10% s1-s4 and RR	0.70	0.81	0.76	0.86	0.58	1.07 (±0.005)	0%
+25% s1-s4 and RR	0.80	0.92	0.86	0.98	0.66	1.23 (±0.004)	0%
Status quo (RRstatus quo)	0.64	0.74	0.69	0.78	Jän.41	1.13 (±0.006)	0%
All chicks (RRAll chicks)	0.64	0.74	0.69	0.78	Mär.97	1.40 (±0.012)	0%

* For a simulation across 100 years the extinction probability would be 87%.

Table 2

Breeding statistics of the *Waldrappteam* population: in brackets: Standard deviation.

Year	Number of nests per year	Developmental stage					
		Eggs		Hatchlings		Fledglings	
		Total number	Mean per nest	Total number	Mean per nest	Total number	Mean per nest
2011	1	3	3.00 (NA)	3	3.00 (NA)	3	3.00 (NA)
2012	5	11	2.20 (± 1.30)	9	1.80 (± 1.10)	8	1.60 (± 1.34)
2013	7	23	3.29 (± 0.76)	9	1.29 (± 1.25)	6	0.86 (± 1.21)
2014	8	23	2.88 (± 0.64)	15	1.88 (± 0.64)	13	1.63 (± 0.74)
2015	6	19	3.17 (± 0.75)	19	3.17 (± 0.75)	17	2.83 (± 0.75)
2016	6	30	5.00 (± 2.45)	15	2.50 (± 1.64)	13	2.17 (± 1.47)
2017	9	35	3.89 (± 1.62)	24	2.67 (± 1.41)	18	2.00 (± 1.66)
2018	10	37	3.70 (± 0.48)	32	3.20 (± 0.79)	26	2.60 (± 0.52)
2019	14	53	3.79 (± 1.12)	43	3.07 (± 1.64)	37	2.64 (± 1.50)
Total	66	234	3.43 (± 0.79)	169	2.51 (± 0.70)	141	2.15 (± 0.70)
Survival				0.72 ¹		0.83 ²	

¹ percent of eggs hatched; ² percent of hatchlings fledged.

Table 3

Comparative statistics on fecundity with mean number of fledglings per nest. SD = standard deviation. Bottom line Crested Ibis (*Nipponia nippon*).

Species	Population, Country (period)	Population type	Mean fledglings	Source
NBI	Waldrappteam , Europe (2008-2019)	release migratory	2.15 ($\pm$ 0.70)	Actual analysis
NBI	Rosegg, Austria (2005-2016) ²	semi-wild, managed	2.24 ($\pm$ 0.32)	Böhm et al., 2020
NBI	Proyecto Eremita , Spain (2008-2018)	release sedentary	0.97 ($\pm$ 0.49)	Böhm et al., 2020
NBI	Birecik, Turkey (2006-2018)	semi-wild, managed	1.53 ($\pm$ 0.20)	Böhm et al., 2020
NBI	Palmyra, Syria (2002-2012)	wild migratory	1.38 ($\pm$ 1.13)	Böhm et al., 2020
NBI	KLF ¹ , Austria (2001-2016)	semi-wild, managed	1.25 ($\pm$ 0.54)	Böhm et al., 2020
NBI	Morocco total (2006-2018)	wild sedentary	1.23 ($\pm$ 0.31)	Böhm et al., 2020
Crested Ibis	Qinling Mountains, China (2007-2014)	release sedentary	1.67 ($\pm$ 0.17)	Wang et al., 2017

¹ Konrad-Lorenz research station, core facility University of Vienna.

² Date from 2012 and 2013 were excluded due to brood control.

Figure 1

Study site of Northern Bald Ibis in Europe. a) Location of the study area in Europe. b) Closer look on two already established breeding sites (pink) in Burghausen (Bavaria, Germany) and Kuchl (State of Salzburg, Austria) and new colonies in Ueberlingen (Baden-Württemberg, Germany; pink) and Rosegg (Kärnten, Austria) with released NBI. The common wintering ground is the WWF Oasi Laguna di Orbetello in Tuscany, Italy (blue). Black lines: migration routes.

Figure 2

Life cycle graph of the Northern Bald Ibis. Life stages are in circles, for definition see text; s_1 to s_4 are the survival probability of the regarding stages; light grey section: biological parent (BP) raised proportion of the population; dark grey section: human foster parent (FP) raised part of the population; A_{SP} : temporarily added females. Only the female part of the population is considered for the simulations.

Figure 3

Survival plot of the raising types. The p-values are the results of the LRT. Shades of the lines represent the standard deviation.

Figure 4

Number of females per year in the 14 scenarios of special interest. Each line of a facet corresponds to a run of the respective scenario. The bold black line represents the average of all 100 runs per scenario. Lambda $\pm$ standard deviation are specified for each scenario. The description of each scenario can be found in the heading of the facet. s1-s4 are the survival probabilities, RR is the reproductive rate. The starting point is 74 females.

Figure 5

Percentage of the respective combination of stochastic event frequency and severity in the 714 sub-scenarios where $\lambda > 1$ and extinction probability $P_{EXT_50} \leq 5\%$. In all sub-scenarios, each combination occurred 41 times.