On the road to self-sustainability: reintroduced migratory European northern bald ibises *Geronticus eremita* still need management interventions for population viability

SINAH DRENSKE, VIKTORIIA RADCHUK, CÉDRIC SCHERER, CORINNA ESTERER
INGO KOWARIK, JOHANNES FRITZ and STEPHANIE KRAMER-SCHADT

Abstract The northern bald ibis *Geronticus eremita* disappeared from Europe in the Middle Ages. Since 2003 a migratory population has been reintroduced in Central Europe. We conducted demographic analyses of the survival and reproduction of 384 northern bald ibises over a period of 12 years (2008–2019). These data also formed the basis for a population viability analysis simulating the possible future development of the northern bald ibis population under different scenarios. We analysed life stage-specific survival rates, rearing protocols and colonies, and the influence of stochastic catastrophic events and reinforcement translocations on population growth. Life stage-specific survival probabilities were 0.64–0.78. Forty-five per cent of the mature females reproduced, with a mean fecundity of 2.15 fledglings per nest. The complementary population viability analysis indicated that the Waldrappteam population is close to self-sustainability, with an estimated population growth rate of 0.95 and a 24% extinction probability within 50 years. Of the 326 future scenarios tested, 94% reached the criteria of extinction probabilities < 5% and population growth rates > 1. Stochastic catastrophic events had only a limited effect. Despite comparatively high survival and fecundity rates the population viability analysis indicated that to achieve self-sustainability the Waldrappteam population needs further translocations to support population growth and the implementation of effective measures against major mortality threats: illegal hunting in Italy and electrocution on unsecured power poles. The findings of this study are to be implemented as part of a second European LIFE project.

Introduction

In conservation biology, species restoration is playing an increasingly important role in counteracting ongoing biodiversity decline, assisting in the establishment of once-widespread species and restoring populations in areas where they have become extinct (IUCN/SSC, 2013; Destro et al., 2018; Pettorelli et al., 2018). Reintroduction is a key restoration method defined by the IUCN as 'the intentional movement and release of an organism inside its indigenous range from which it has disappeared' (IUCN/SSC, 2013). Reintroductions often aim to minimize interventions to create viable populations with the least necessary human support (Corlett, 2016).

Reintroduction efforts have been undertaken for a wide and increasing range of species (Bennett et al., 2013; Gray et al., 2017; Soorae, 2018), with varying degrees of success. Failures are most often because of factors such as predation, human–wildlife interactions and habitat mismatch, all of which affect the viability and reproduction of the target species (Wimberger et al., 2009; Bennett et al., 2013). There is no general definition of reintroduction success but calculating the population growth rate, population size and reproduction probability has been suggested as a useful approach to determining reintroduction success (Robert et al., 2015). This should be accompanied by determining the frequency of stochastic events (i.e. random catastrophic events such as adverse weather conditions that occur with a given probability and potentially affect demographic rates, and hence reduce the population size at the reintroduction site; Robert et al., 2015). Moreover, it is crucial not only to assess the long-term viability of reintroduced individuals under given

SINAH DRENSKE† (orcid.org/0000-0002-2247-6507), VIKTORIIA RADCHUK (orcid.org/0000-0003-3072-0095), CÉDRIC SCHERER (orcid.org/0000-0003-0465-2543) and STEPHANIE KRAMER-SCHADT*† (orcid.org/0000-0002-9269-4446) Department of Ecological Dynamics, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

CORINNA ESTERER and JOHANNES FRITZ*‡ (Corresponding author, orcid.org/0000-0003-4691-2892, jfritz@waldrapp.eu) Waldrappteam Conservation & Research, Schulgasse 28, 6162 Mutters, Austria

INGO KOWARIK (orcid.org/0000-0002-8251-7163) Institute of Ecology, Chair of Ecosystem Science/Plant Ecology, Technische Universität Berlin, Berlin, Germany

*Contributed equally
†Also at: Institute of Ecology, Chair of Applied Animal Ecology, Technische Universität Berlin, Berlin, Germany
‡Also at: Department of Cognitive Biology, University of Vienna, Althanstrasse, Vienna, Austria

constraints but also to evaluate and rank the impacts of management interventions retrospectively to help adjust management actions and compare alternative future interventions (Pereira & Navarro, 2015; Robert et al., 2015).

Here we analyse long-term demographic data (2008–2019) of a reintroduced migratory European population of the northern bald ibis *Geronticus eremita*, named the Waldrappteam population. We also assess the long-term probability of persistence of the reintroduced population using an individual-based model in which quantification of the effects of the main management measures and of stochastic events on demographic rates during the study period provides the framework for the model. We assess the impacts of future alternative management measures and stochastic events as functions of an individual-based model. We hypothesize that at the present time the northern bald ibis population can survive without further management and release. We predict that the observed demographic rates will ensure population growth and do not differ between the breeding colonies.

Species and study area

The northern bald ibis was categorized as Critically Endangered on the IUCN Red List from 1994 and recategorized as Endangered in 2018 (BirdLife International, 2018). The species is migratory, mainly insectivorous and can live to an age of up to 30 years in captivity. Northern bald ibises 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, where they usually remain until sexual maturity (Fritz et al., 2019). The last remaining wild population of northern bald ibises has changed to a sedentary lifestyle and inhabits the Moroccan coast (Bowden et al., 2008).

In 2002 European scientists started a research project on the species, which in 2014 changed into a European Union LIFE+ funded translocation and conservation project. By late 2021 this reintroduced Waldrappteam population comprised c. 200 individuals, in two breeding colonies in southern Germany and two in Austria (Fritz, 2021). The common wintering area is the nature reserve WWF Oasi Laguna di Orbetello in Tuscany, Italy (Fig. 1). All four breeding colonies are considered to be one population because they share the same wintering ground (Wirtz et al., 2018).

In Andalusia, Spain, another reintroduction project with northern bald ibises, Proyecto Eremita, is ongoing, (Boehm et al., 2020). This population was also founded with hand-reared birds from various zoo breeding colonies, with the aim of establishing a self-sustaining wild population. In contrast to the migratory Waldrappteam population, these birds have a largely sedentary lifestyle. Since 2008 chicks from this Spanish population have been

FIG. 1 The established breeding grounds and the common wintering ground of the Waldrappteam population of northern bald ibis *Geronticus eremita*. Black lines indicate migration routes.

hatching in the wild and by 2020 this population consisted of c. 115 birds (M. Quevedo, pers. comm., 2020). Remote monitoring indicates that to date there has been no overlap of the activity areas of these two populations (for more information on the study species and the reintroduction projects see Supplementary Material 1).

Methods

We included 384 northern bald ibises from the 2008–2019 generations in the study. They had either hatched in zoo breeding colonies (mainly Zoo Rosegg, Austria; Cumberland Wildpark Gruenau, Austria; and Zoo Zurich, Switzerland) and had been raised by human foster parents for release, or they had hatched in the wild as offspring of released birds and had hence been raised by their biological parents. All foster parent-raised individuals originated from the European Endangered Species Programme. Birds for release were trained to follow a microlight plane that led them to the common wintering ground, where they were integrated into the wild population (Fritz et al., 2017a,b). Since 2011, an increasing number of chicks have been raised in the wild by their biological parents and, at their first migration, they follow their conspecifics to the common wintering ground. At the time of the present analysis some of the foster parent-raised individuals had not yet been assigned to a breeding colony because they had not reached sexual maturity and thus had not returned to a breeding area.

Intensive monitoring has yielded comprehensive life history data for each individual. In 2012, 68% of the birds carried GPS tags, and from 2013 onwards the whole population was monitored remotely (Sperger et al., 2017). Initially, only battery-powered devices were used (either specially manufactured devices for our needs or commercial devices made by Fleetronics, Brussels, Belgium; company no longer exists). From 2016 onwards, solar-powered devices became available (custom-made devices from the University of Konstanz, Konstanz, Germany, and commercial devices from Ornitela, Vilnius, Lithuania).

We assigned the 384 individuals to four demographic stages representing age classes with characteristic life-history events (Fig. 2, Supplementary Fig. 1). Stage 1 represents juveniles from fledging until the end of their first year; after the first autumn migration these birds usually remain at the wintering grounds. Stage 2 represents juveniles in their second year; they usually stay year-round at the wintering grounds. Stage 3 represents subadults in their third year; although not mature, most of these birds perform a partial or even full migration. Stage 4 represents adults older than 3 years; these birds usually migrate and reproduce annually although some individuals could remain at the wintering grounds.

We calculated the survival probabilities per stage, sex, colony and raising type (biological or foster parent) using the Kaplan–Meier estimator (Kaplan & Meier, 1958) with the *survival* package (Therneau, 2015) in *R 4.0.3* (R Core Team, 2020). We estimated the survival probabilities for fledglings that were c. 45 days of age. We omitted adult birds that were added temporarily during the breeding season from the calculations of the survival probabilities. These birds do not migrate with the population but are released

temporarily and added to the population during the breeding season, to improve breeding success. They are therefore not a permanent part of the population. We used a likelihood ratio test to test for significance between different classes in Cox proportional hazard models (Kleinbaum & Klein, 2012). We also calculated hatching and fledging rates.

We calculated fecundity as the reproductive rate per nest (i.e. the mean number of fledglings per nest). At the start-up of newly founded colonies, adult males and females were temporarily released at the breeding site and re-caught after the breeding season to compensate for missing mates and to enable the migrant birds to reproduce. The rate of adults added temporarily was successively reduced, and this supplementation was completely terminated at the end of the data period (see also Supplementary Material 2).

Management of the Waldrappteam population

During the course of the reintroduction project a range of management measures were implemented (Table 1). The efficiency of the human-led migration as the main translocation method was improved substantially. The number of translocated and released juveniles per season was increased from c. 10 per season initially, up to 30 per season (Fritz et al., 2017a,b; Fritz, 2021).

Adding adult birds temporarily at the breeding sites to provide mating partners for arriving migrants has proven to be an efficient method to increase the reproduction rate, particularly in small founder colonies. During the study period 38% of the breeding pairs included adults added temporarily and 39% of the fledglings came from such couples.

During 2008–2013 the mean annual loss rate was 25% (44 lost birds in total). Illegal hunting in Italy caused an annual mean of 40% of these losses (14 hunted birds in total). During the LIFE+ period (2014–2019), a campaign against this environmental crime was implemented based on remote GPS monitoring of the whole population, enabling the identification of accidents and the implementation of effective post-poaching measures in the field and for complaints to be sent to the responsible public prosecutors' offices. One perpetrator was charged and convicted, which as a precedent produced a lasting effect (Fritz, 2015; Fritz et al., 2017a,b). With these measures, the mean loss rate from this crime dropped to 17% of the overall annual losses, corresponding to a reduction of 59% from the pre-LIFE+ rate.

During the whole study period (2008–2019), the mean annual loss rate was 31% (224 lost birds in total). Electrocution of birds roosting on unsecured power poles caused an annual mean of 45% of these losses (45 birds in total). In Germany, most unsecured power poles were retrofitted by 2016 because of a legal regulation. Before these measures were introduced, 41% of all electrocution losses (seven cases during 2008–2015)
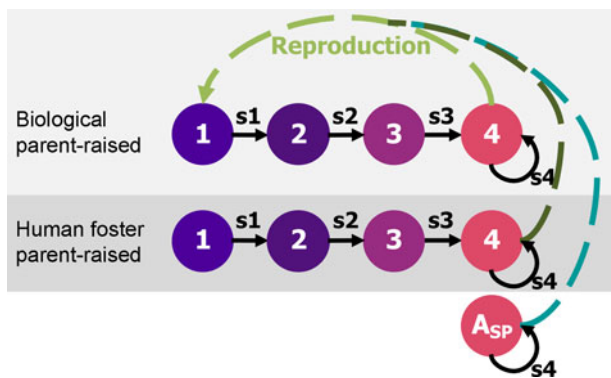
FIG. 2 Life cycle of the northern bald ibis. Life stages are in circles (for definitions, see text); s1–s4 represent the survival probabilities of the respective stages. Light grey section: the part of the population raised by biological parents; dark grey section: the part of the population raised by human foster parents. A_{SP} = adult females added temporarily. Only the female part of the population was considered for the simulations. (Readers of the printed journal are referred to the online article for a colour version of this figure.)

TABLE 1 Quantification of main management measures and stochastic events affecting the Waldrappteam population of the northern bald ibis *Geronticus eremita* during the study period (2008–2019). These data provide the framework for modelling the respective outcomes of different future management interventions and stochastic events.

Management or event type	Specification	Quantification
Translocation & release	Release of zoo offspring by human-led migration	Mean annual release rate 2008–2019: 20.4 juveniles (range 10–30)
Reproduction improvement	Adults added temporarily to improve reproduction	Mean annual per cent of breeding pairs with participation of added adults: 38%; mean annual per cent of fledglings with parent added temporarily: 39%
Mortality reduction	Campaign against illegal hunting during the LIFE+ period (2014–2019)	Losses because of illegal hunting in Italy; 2008–2013: 40%; LIFE+ period: 17%; 59% reduction because of the LIFE+ campaign
Mortality reduction	Retrofitting of unsecure power poles in Germany implemented widely in 2016	Electrocution cases in Germany as proportion of all cases; 2008–2016: 41%; 2017–2019: 4%; 91% reduction because of the retrofitting measures
Stochastic event	Early onset of winter	Frequency: 18%; severity: c. 27% of migrating birds for stages 1 & 4
Stochastic event	Chick predation	Frequency: 9%; severity: c. 21% of the chicks in one breeding colony
Stochastic event	Infections	Frequency: 18%; severity: c. 4% of the population

occurred in Germany, whereas since these measures were introduced (from 2016 onwards) only one further case has been documented in Germany (Fritz et al., 2019). This corresponds to a 91% reduction in the loss rate in Germany because of these retrofitting measures, indicating the possibility of almost complete elimination of this cause of death. Population development during the study period was also impaired occasionally by stochastic events, in particular the early onset of winter, brood failure because of predation, and infections (Table 1).

Population viability analysis

For the population viability analysis and population projections, we focused on the female half of the population (the sex ratio is 1:1). Amongst the fledglings with unknown sex (five individuals in the whole population) we included 50% in the analysis (see also Supplementary Material 2).

We analysed the population trajectories for different scenarios as outlined below. We calculated extinction probability as the proportion of 100 repetitions in which the population went extinct within 50 years (P_{EXT_50}). We calculated the intrinsic growth rate λ as the mean annual finite rate of change of the population size, where $\lambda > 1$ implies population growth and $\lambda < 1$ implies a declining population size. We calculated the effect of input parameters on demographic rates for scenarios where $\lambda > 1$ and $P_{EXT\_50} \leq 5\%$. In addition, we ran generalized linear models (GLMs) and used an ANOVA to rank the contributions of the demographic rates in the different life stages to λ as the response variable using a gamma error structure with inverse link. We also included stochastic events (catastrophic events that could reduce the survival of the population) in the model, with frequency and severity in the given range of stochastic events observed during the study period (Table 1). We calculated how often each combination of scenarios (see below) resulted in $\lambda > 1$ and $P_{EXT\_50} \leq 5\%$.

The model documentation follows the TRACE documentation framework (TRAnsparent and Comprehensive model Evaluation; Grimm et al., 2014; Supplementary Material 3). The model description follows the ODD protocol (Overview Design concepts and Details; Grimm et al., 2006, 2010). An individual-based model was implemented in *NetLogo 6.0.3* (Wilensky, 1999). The corresponding *NetLogo* and *R* scripts are available online (Supplementary Material 4).

For the population viability analysis, we defined three different reproductive rates depending on the included female fledglings and fledglings of unknown sex (Supplementary Material 2). The 'baseline' rate included female fledglings raised by adult wild females (stage 4). The 'status quo' rate also included female fledglings raised by females added temporarily. The 'all chicks' rate also included female fledglings raised by human foster parents. To calculate the reproductive rate, we divided the number of fledglings by all adult females (stage 4) of the population, irrespective of whether they were breeding or not, plus adult females that were added temporarily at the breeding site to compensate for missing mates. Thus, the reproductive rate used in the context of the population viability analysis is an expression of breeding probability, indicating how likely it is that a female will breed.

We also calculated the baseline rate separately for the two breeding colonies in Burghausen and Kuchl, and separately for females raised by biological parents and human foster parents. We implemented generalized linear mixed models (GLMMs) using a Poisson error structure and maximum likelihood to investigate whether any differences in reproduction rate were significant.

We analysed the model for various future scenarios that are based on realistic alternative management measures from which we derived the survival and reproduction values (Table 1). The management scenarios compare situations in which no management took place to scenarios in which baseline demographic rates were improved by management interventions of 10, 25 and 100% (Table 1). We combined three levels of survival rate at each stage and four levels of reproductive rate in a full factorial design. Additionally, we combined the 'status quo' rate and 'all chick' rate with baseline survival probabilities, which resulted in 326 management scenarios (Table 2, Supplementary Material 5). Only for the simulation of the baseline scenario did we draw the demographic rates from the probability distributions defined by the mean and standard deviation of the demographic rates. For all other scenarios we used the calculated mean values of the demographic rates. Of these 326 management scenarios, we chose 14 management scenarios of special interest for closer examination (Table 2), where parameter combinations were within the scope of realistic management interventions that aimed to improve survival and reproduction. If these simulations resulted in $\lambda > 1$ and $P_{EXT\_50} \leq 5\%$, they were chosen for testing the robustness of the population to stochastic events such as periods of inclement weather affecting demographic rates and the supplemental release of foster parent-raised juveniles. This

happened in nine cases (Table 2). For comparison, we also tested the baseline scenario even if $\lambda < 1$ and $P_{EXT\_50} \geq 5\%$, and the 'all chicks scenario without supplements' under stochastic events (Supplementary Material 5).

The number of stochastic event and juvenile supplementation scenarios is given by equation 5.1.2 in Supplementary Material 5. These 11 scenarios were crossed with four levels of stochastic event frequency (5, 10, 15 or 20%), five levels of severity (5, 10, 15, 20 or 25 additional mortalities per stage), two levels of the number of juvenile supplements (15 or 30) and two levels of the timespan for supplementing individuals (4 or 7 years; i.e. number of years in which juveniles are added to the population in addition to natural reproduction; supplemented juveniles remain in the population until their death, injury or disappearance), which resulted in 820 parameter combinations for the stochastic event and juvenile supplementation scenarios.

Results

Of the 384 individuals, 195 could be confirmed as males and 184 as females, resulting in a sex ratio of 1.00:0.94 (male: female). For five juveniles sex was not determined at the time of data analysis. With respect to the raising type, 162 birds were raised in the wild by biological parents (42%), 213 by human foster parents (55%) and nine birds were

TABLE 2 Empirical values for survival per stage and for the three reproductive rates (RRs) of the Waldrappteam population of northern bald ibises as defined in the text (Fig. 4). We used these values and their improvements by 10, 25 or 100% in various combinations for the population simulation of 14 management improvement scenarios, which we designed based on management measures implemented during the study period (Table 1). Improvements of the empirical values are indicated with asterisks (*). The resulting population growth rate (λ) and extinction probability (P_{EXT_50}) are shown in the two right-hand columns. Note that the reproductive rates comprise not just the reproducing females but all adult females in adult stage 4 and take into account only female offspring (i.e. per nest number of offspring); s1–s4 are the survival probabilities of the respective stages.

	Stage 1	Stage 2	Stage 3	Stage 4	RR (females)	$\lambda \pm$ SD	P_{EXT_50} (%)
Empirical values							
$RR_{Baseline}$	0.64 ± SD 0.36	0.74 ± SD 0.35	0.69 ± SD 0.35	0.78 ± SD 0.14	0.53 ± SD 0.17		
$RR_{Status\ quo}$					1.41 ± SD 0.81		
$RR_{All\ chicks}$					3.97 ± SD 2.66		
14 management scenarios of special interest							
Baseline ($RR_{Baseline}$)	0.64	0.74	0.69	0.78	0.53	0.95 ± 0.030	24[1]
+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	1.00*	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 & RR	0.70*	0.81*	0.76*	0.86*	0.58*	1.07 ± 0.005	0
+25% s1−s4 & RR	0.80*	0.92*	0.86*	0.98*	0.66*	1.23 ± 0.004	0
Status quo ($RR_{Status\ quo}$)	0.64	0.74	0.69	0.78	1.41*	1.13 ± 0.006	0
All chicks ($RR_{All\ chicks}$)	0.64	0.74	0.69	0.78	3.97*	1.40 ± 0.012	0

[1]For a simulation across 100 years the extinction probability would be 87%.

supplemented as juveniles (2%). With respect to the breeding colonies, 127 individuals belonged to Burghausen (33%), 89 to Kuchl (23%), 89 to Überlingen (23%) and 22 to Rosegg (6%); 57 juveniles were not yet assigned at the time of data collection. A total of 232 birds died during the data collection period; of these, 123 died during stage 1 (53%), 45 during stage 2 (19%), 33 during stage 3 (14%) and 31 during stage 4 (13%; Supplementary Fig. 1).

At the end of 2019, 152 individuals were alive, including nine that were caught and placed into captivity mainly because of various kinds of severe and permanent injury. We counted these individuals as censored and so they did not affect the survival estimates. Thus, the release colony at the end of the data collection period comprised 143 individuals (69 males and 74 females). With respect to the life stages, 71 individuals belonged to juvenile stage 1 (50%; 37 females, 34 males), 28 to juvenile stage 2 (20%; 11 females, 17 males), 13 to subadult stage 3 (9%; 8 females, 5 males) and 31 to adult stage 4 (22%; 18 females, 13 males). With respect to the breeding colonies, 33 birds belonged to Burghausen (23%), 33 to Kuchl (23%), 51 to Überlingen (36%) and 15 to Rosegg (10%); 11 individuals (8%) were not yet allocated to a colony at the end of the data collection period. With respect to the raising types, 68 birds (48%) were raised by their biological parents, 73 birds (51%) by human foster parents and two birds (1%) were supplemented.

We calculated survival rates for all individuals from the fledging stage onwards. According to the Cox proportional hazard model, survival rates did not differ significantly between stages across the whole population (likelihood ratio test (N = 736) = 3.05, P = 0.4) or between sexes (likelihood ratio test (N = 379) = 0.80, P = 0.4). According to the Kaplan–Meier estimator, mean survival probability was $0.64 \pm SD\ 0.36$ for juvenile stage 1, $0.74 \pm SD\ 0.35$ for juvenile stage 2, $0.69 \pm SD\ 0.35$ for subadult stage 3 and $0.78 \pm SD\ 0.14$

for adult stage 4. The cumulative survival probability until sexual maturity (end of stage 3) was $0.33 \pm SD\ 0.23$. Concerning pre-fledging survival, 72% of the eggs hatched and 83% of the hatched chicks fledged (Table 3).

The survival rates for biological parent- and foster parent-raised individuals differed significantly (likelihood ratio test (N = 375) = 8.26, P = 0.004; Fig. 3), as well as per stage and per raising type (likelihood ratio test (N = 715) = 10.17, P = 0.04). In juvenile stage 1, foster parent-raised individuals showed a higher survival rate ($0.73 \pm SD\ 0.37$) than their biological parent-raised counterparts ($0.52 \pm SD\ 0.30$; Table 2). The survival rates in the two breeding colonies at Burghausen and Kuchl did not differ significantly (likelihood ratio test (N = 216) = 1.56, P = 0.2), nor per stage and per colony, respectively (likelihood ratio test (N = 453) = 5.36, P = 0.3; Table 2).

The number of nests increased over time, with one nest in 2011 and 14 nests in 2019 and a mean of $3.43 \pm SD\ 0.79$ eggs per nest (Table 3). Overall fecundity was $2.15 \pm SD\ 0.70$ fledglings per nest. Fecundity rates amongst foster parent- and biological parent-raised females did not differ significantly (z = 0.68, P = 0.50), nor did the fecundity rates amongst females of the breeding colonies at Burghausen and Kuchl (z = 0.60, P = 0.55).

During the study period, 31 females reached sexual maturity (stage 4). Of these, 45% reproduced by the end of the data collection period. Of these 14 reproducing females, three (21%) reproduced once, five (36%) reproduced twice, five (36%) reproduced three times and one (7%) reproduced six times.

Population viability analysis

Over the data collection period 62 individuals reached adult stage 4, of which 31 were sexually mature females. Analysing

TABLE 3 Breeding statistics of the Waldrappteam population of northern bald ibises during 2011–2019.

| | | Developmental stage | | | | | |
| | | Eggs | | Hatchlings | | Fledglings | |
Year	Number of nests per year	Total	Mean ± SD per nest	Total	Mean ± SD per nest	Total	Mean ± SD per nest
2011	1	3	3.00	3	3.00	3	3.00
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				72[1]		83[2]	

[1]Per cent eggs hatched.
[2]Per cent hatchlings fledged.
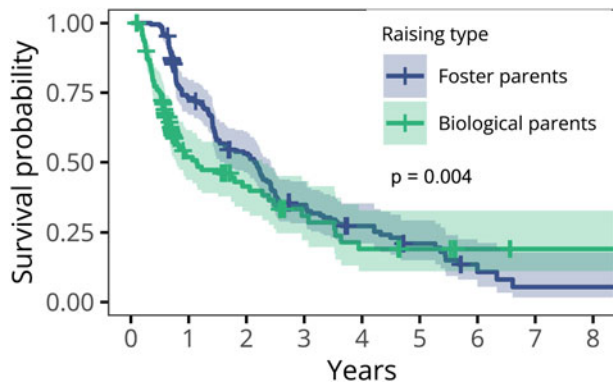
FIG. 3 Survival plot of the raising types of the Waldrappteam population of northern bald ibises; p is the result of the likelihood ratio test. Shading surrounding the lines represents the standard deviation. Because of the young age of this newly founded population, only a small number of individuals reached an age older than 3 years (stage 4) during the study period, which causes a relatively large standard deviation.

these females as potential mothers yielded a baseline reproductive rate of $0.53 \pm SD\ 0.17$ (biological parent- and foster parent-raised females and their female fledglings; Table 2), a status quo reproductive rate of $1.41 \pm SD\ 0.81$ (female fledglings from females added temporarily also included) and an all chick reproductive rate of $3.97 \pm SD\ 2.66$ (human-raised and released female fledglings also included). We used these reproductive rates for the population viability analysis.

Without further implementation of management measures (Table 1), as assumed for the baseline management scenario, the population viability analysis indicated a λ of $0.95 \pm SD\ 0.03$, which is below the 1.00 threshold, with a 24% extinction probability within 50 years (Table 2). The full factorial design resulted in 326 management scenarios (Supplementary Material 5) with λ being 0.95–1.40. λ was > 1 and P_{EXT_50} was $\leq 5\%$ in 308 of the 326 management scenarios (94%); in none of these 308 scenarios did the population go extinct in the 50-year projections. In a first analysis we investigated the frequencies of management scenarios with different demographic rates of the 308 scenarios with positive population development. This enabled us to understand how demographic rates affected population viability (Supplementary Material 5). The 'status quo' and 'all chicks' management scenarios were not considered here (therefore leaving 306 of 308 scenarios) because they were only simulated once with baseline survival values and the respective reproductive rate. In the 306 management scenarios with positive population development, only an increase in adult survival (stage 4) values improved the population viability: a 10 or 25% increase of adult survival increased the viability disproportionately. For example, a 10% increase of adult survival increased viability by 17%, thereby increasing the likelihood of avoiding population extinction (108 of 108 parameter combinations with

adult survival increased by 10% led to positive population growth) compared to the baseline value (90 of 108 parameter combinations (83%) with baseline adult survival led to positive population growth). These results indicate the importance of survival of the adult reproductive stage for population viability. This is supported by the GLMs and the ANOVA ranking the effects of the survival rates (deviance (d) of ANOVA: $d_{stage\ 1} = 0.05$, $d_{stage\ 2} = 0.05$, $d_{stage\ 3} = 0.05$, $d_{stage\ 4} = 0.68$). Here, adult survival (stage 4) had the largest effect (Supplementary Material 6).

All management scenarios in which the reproductive rate was increased by 100% showed positive population development (81 of 81 parameter combinations). Only one management scenario in which the reproductive rate was increased by 25% did not show positive population development: the one in which no survival rate was increased (i.e. baseline values for stages 1–4, +25% reproductive rate management scenario; Table 2). Nevertheless, 88% of the management scenarios with the baseline reproductive rate showed positive population development (71 of 81 parameter combinations). The reproductive rate also had a strong effect on λ ($d_{reproductive\ rate} = 0.58$) in the GLMs.

In the second analysis, 14 management scenarios of special management interest were analysed (Table 2, Fig. 4). For nine of these, λ was > 1 and P_{EXT_50} was $\leq 5\%$. If only the reproductive rate was increased, positive population growth occurred only after an increase of at least 100% (+100% reproductive rate, status quo, all chicks; i.e. a minimum of one female fledgling per female). Increasing only the survival of juveniles (stage 1) did not lead to positive population growth, but increasing adult survival (stage 4) did. An increase in all survival values for stages 1–4 also led to positive population growth; these effects were reinforced by an additional increase in the reproductive rate.

For the stochastic event and juvenile supplementation scenarios, λ was 0.91–1.40. In 714 of 820 scenarios (87%), λ was > 1 and P_{EXT_50} was $\leq 5\%$. Baseline survival values led to positive population growth in 74–79% of the scenarios. Increasing adult survival (stage 4) by 10% led to positive population growth in 89% of the scenarios, whereas a 10% increase in survival in other age categories led to population growth in 100% of the scenarios. Increasing baseline survival by 25% led to positive population growth in 100% of the stochastic event and juvenile supplementation scenarios.

Each combination of stochastic event frequencies and severities occurred 41 times in all 820 stochastic event and juvenile supplementation scenarios. Ninety per cent of the scenarios with a low frequency (5%) and severity (5%) of stochastic events and 80% of the scenarios with a high frequency (20%) and severity (25%) of stochastic events resulted in positive population development. Eighty-eight per cent of the stochastic event and juvenile supplement
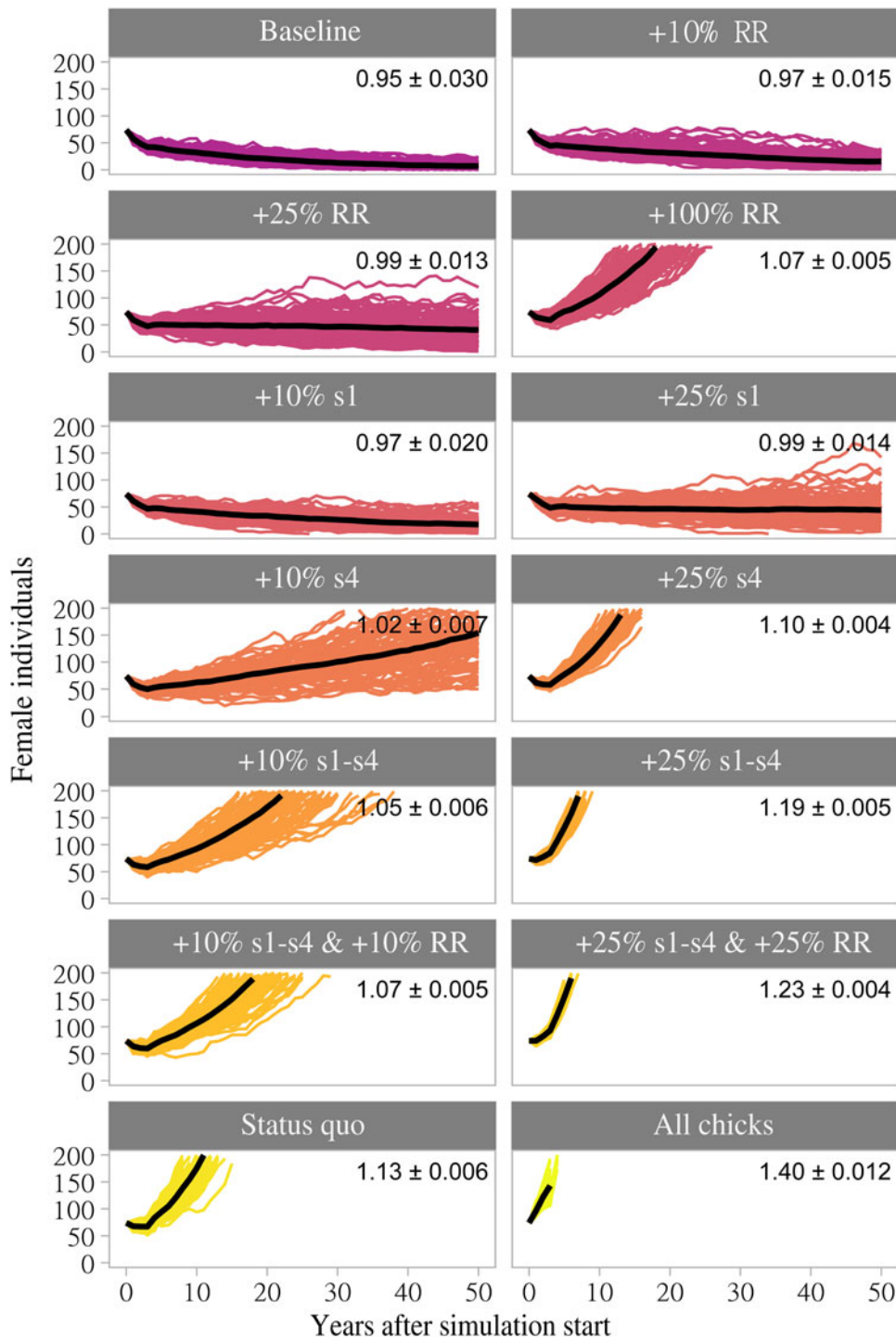
Fig. 4 Numbers of females per year in the 14 management scenarios of special interest for the Waldrappteam population of northern bald ibises (Table 2). Each line corresponds to a run of the respective scenario, and the bold black line is the mean of all 100 runs per scenario. $\lambda \pm$ SD is specified for each scenario. The description of each scenario is indicated in the heading of the graph. s1–s4, stage-specific survival probabilities; RR, reproductive rate. The starting point is 74 females (i.e. the number of females present in 2019).

scenarios with 30 supplemented juveniles per year over 7 years and 86% of the scenarios with 15 supplemented juveniles per year over 4 years resulted in positive population development.

Discussion

The comprehensive 12-year dataset of the reintroduced Waldrappteam northern bald ibis population facilitated a population viability analysis of its future population development under different scenarios. This approach is a powerful tool to evaluate the effectiveness of reintroduction and management scenarios. Such models, based on the best possible evidence, are recommended in the IUCN reintroduction guidelines (IUCN/SSC, 2013) for deciding on future management practices.

The outcome of the population viability analysis baseline scenario, with λ at 0.95 and a 24% extinction probability

within 50 years, supports the rejection of the hypothesis that the reintroduced northern bald ibis population can survive without continuation of the management measures implemented during the study period (Table 1). Nonetheless, the population is close to a transition to sustainability, reflected in the comparatively good survival and fecundity values.

The baseline reproductive rate relates the actual number of fledged female offspring to the entirety of the adult females 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 could be increased significantly through translocation measures up to a rate of 3.97 ('all chicks' reproductive rate). As indicated by the management improvement scenarios, continuing and improving the given translocation measures would have the most significant immediate effect on population development. Furthermore, continuation of measures reducing the causes of primary mortality could further improve survival and population growth.

In agreement with the outcome of the population viability analysis, the sustainable improvement of long-term survival is the primary objective of the reintroduction project, although the intraspecific comparison indicates that the survival values in the Waldrappteam population are already promising for all age classes. Improving the survival rate of adults should be a priority as this has the greatest impact on λ. This 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).

Demographic analysis

The demographic dataset covers a period of 12 years, including the later phase of a feasibility study (2008–2013) in which a small number of birds were released and the following 6-year period of the reintroduction project funded by LIFE+ (2014–2019). The survival probability in our study ranged from 0.64 for juveniles (stage 1) to 0.78 for adults (stage 4). A similar adult survival rate of 81% has been observed for a small relict migratory northern bald ibis population that was discovered in Syria in 2002 (Serra et al., 2014). For the Moroccan population, an annual survival rate estimate of 77% has been reported across all age classes (Bowden et al., 2008), which is within the range of the rates calculated for the Waldrappteam population. However, the Moroccan birds are not marked; their survival rate can only be estimated indirectly based on the annual counts of the pre-breeding population and the number of fledglings (Bowden et al., 2008).

The cumulative survival probability until sexual maturity (stages 1–3) was 0.33. In the relict Syrian population the count of departing fledglings and arriving new breeders at the breeding site in Syria indicates a 14% survival rate until sexual maturity for this declining population (Boehm et al., 2020), which is less than half that of the Waldrappteam population. Satellite tracking of the Syrian juveniles revealed they did not arrive at the common wintering site in Ethiopia because they lost the company of experienced conspecifics and died on the Arabian Peninsula (Serra et al., 2014). This low survival rate of juveniles was a major cause of the extinction of this population in 2015 despite international conservation and translocation efforts (Bowden et al., 2011).

In our population, the first-year survival rate of foster parent-raised juveniles (0.73) was significantly higher compared to that of their biological parent-raised counterparts (0.52). This is in contrast with the widespread experience that released individuals have comparably low survival rates, particularly in the first period after release, because of translocation- and competition-induced stress, dispersal, disease or predation (Parker et al., 2013). This is true particularly for captive-bred individuals, probably because they lack individual experience (Mathews et al., 2005). Our birds underwent extensive pre-release training, which provided them with essential experience regarding navigation, flight techniques, weather conditions, aerodynamics and predator avoidance (Portugal et al., 2014; Voelkl & Fritz, 2017; Fritz et al., 2019). This is assumed to improve post-release survival (Alonso et al., 2011; Houser et al., 2011; Zhang et al., 2017). In the Spanish northern bald ibis reintroduction project (Proyecto Eremita), the mean first-year survival rate for released juveniles of 31% (data for 2004–2018; Boehm et al., 2020) was substantially lower than that of the Waldrappteam population. We assume that minimal pre-release training and unguided autumn dispersal (Muñoz & Ramírez, 2017) account for the lower survival of the juveniles released in Spain (Fritz et al., 2019).

The survival probability rate of the Waldrappteam population from hatching to fledging was 83%, which is substantially higher than the rate of 47% reported for the Moroccan wild population (Bowden et al., 2003). We assume that this difference mainly reflects the quality of the feeding habitats. For the Waldrappteam population, studies indicate high feeding efficiency and a high abundance of food invertebrates (mainly worms and larvae) in the soil of the preferred feeding habitats of meadows and pastures (Zoufal et al., 2007; Fritz et al., 2017a,b). In contrast, the feeding habitats on the Atlantic coast of Morocco consist of semi-natural steppes with sparse cover of perennial and annual vegetation and low availability of freshwater bodies (Bowden et al., 2008). Accordingly, positioning data indicate a small activity radius of c. 2 km around the nesting sites for the Waldrappteam population during the breeding season (Fritz et al., 2017a,b), whereas the foraging area of the two Moroccan colonies covers a strip of c. 4 km inland along a 50-km coastline. The fledgling survival rate in Morocco was even lower in the 1990s before supplementary freshwater

TABLE 4 Comparative statistics on fecundity (mean ± SD number of fledglings per nest) of the Waldrappteam population of northern bald ibises and the crested ibis *Nipponia nippon*. Two populations are managed zoo colonies, which are self-sustaining and free-flying from the start of the breeding season onwards but dependent on human care during winter.

Species	Population, country (period)	Population type	Mean ± SD number of fledglings	Source
Northern bald ibis	Waldrappteam, Europe (2008–2019)	Release, migratory	2.15 ± 0.70	This study
Northern bald ibis	Rosegg, Austria (2005–2016)[1]	Managed zoo colony	2.24 ± 0.32	Boehm et al. (2020)
Northern bald ibis	Proyecto Eremita, Spain (2008–2018)	Release, sedentary	0.97 ± 0.49	Boehm et al. (2020)
Northern bald ibis	Birecik, Turkey (2006–2018)	Semi-wild, managed	1.53 ± 0.20	Boehm et al. (2020)
Northern bald ibis	Palmyra, Syria (2002–2012)	Wild, migratory	1.38 ± 1.13	Boehm et al. (2020)
Northern bald ibis	Konrad-Lorenz research station[2], Austria (2001–2016)	Managed zoo colony	1.25 ± 0.54	Boehm et al. (2020)
Northern bald ibis	Morocco total (2006–2018)	Wild, sedentary	1.23 ± 0.31	Boehm et al. (2020)
Crested ibis	Qinling Mountains, China (2007–2014)	Release, sedentary	1.67 ± 0.17	Wang et al. (2017)

[1]Data from 2012 and 2013 were excluded because of brood control.
[2]Core facility of the University of Vienna.

was provided near the breeding grounds from 1998 onwards (Smith et al., 2008).

In the Waldrappteam population 61% of the mature females reproduced. Most of the non-reproducing females remain at the wintering site. In comparison, 63% of the full-grown (mature) birds in the Moroccan population reproduced (Bowden et al., 2008). These rates are not directly comparable because the Moroccan data are based on counts of unmarked birds. Nonetheless, the data indicate that in this sedentary population in Morocco (with all birds on site) a similar proportion of adults do not reproduce.

The mean annual fecundity of the Waldrappteam population was 2.15 fledged chicks per nest. Fecundity values of northern bald ibis populations vary considerably, with 1.23 fledged chicks per nest in the wild sedentary Moroccan population, 0.97 fledged chicks per nest in the Spanish Proyecto Eremita release population (Table 4; Boehm et al., 2020) and 2.24 fledged chicks per nest in the managed, temporarily wild-living population at Zoo Rosegg in Austria. The fecundity in the Waldrappteam population is therefore near the upper end of this range. This is consistent with the high survival probability from hatching to fledging of the Waldrappteam population (83%) and indicates a high quality of breeding habitats.

Conclusion

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

Based on the modelling outcomes, a major focus for the future management of this population should be further improvement of survival rates, with a particular focus on adult survival. This will be achieved mainly by implementing measures reducing the major mortality causes, namely illegal hunting in Italy and electrocution on unsecured power poles at the breeding sites (Fritz et al., 2019). In addition, the proportion of reproducing females should be increased by establishing a breeding site south of the Alps that can be reached by the migrating birds in spring without crossing the Alpine chain.

The population viability analysis could be improved by including data on the movement of the northern bald ibises. This would help build a spatially explicit population simulation model accounting for differences in the migration routes to and from the colonies. Moreover, a thorough assessment of the factors influencing the viability of the northern bald ibises in the colonies would be an asset. These factors include the availability of food and nesting sites, and the weather in the breeding areas during the migration and in the wintering area (Schaub et al., 2005).

The comparison of the demographic data with populations exhibiting a sedentary lifestyle did not indicate adverse effects of the migratory lifestyle in the Waldrappteam population. The survival rate of adults is similar to those of sedentary populations and the survival rate of released juveniles is higher in the migratory population (73%) compared to the sedentary population in Spain (31%). The high fecundity rate in the Waldrappteam population (2.15 fledged chicks per nest) presumably reflects the migratory behaviour that enables the adults to exploit rich northern feeding grounds during the reproductive period.

The current International Single Species Action Plan for the northern bald ibis (Bowden, 2015) does not include modelling either as an objective or as a recommendation. Systematic, quantitative approaches such as population viability analyses are essential strategic tools that are being used to an increasing extent in animal conservation

and translocation efforts. It is essential that these tools are also implemented increasingly in further species conservation measures for the northern bald ibis. Regarding the Waldrappteam population, the results of this study will be incorporated into further conservation and reintroduction measures. This population should become self-sustaining as part of a second European LIFE project (2022–2028).

Author contribution Study design and conception: SD, JF, SK-S; data analysis: SD, VR; population viability analysis design: SD, VR; population viability analysis programming: SD; programming support: CS; field data collection: CE; writing lead: SD; contribution to writing: VR, IK, JF, SK-S.

Conflicts of interest None.

Ethical standards This research abided by 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,* 38, 700–712.

BIRDLIFE INTERNATIONAL (2018) *Geronticus eremita*. In *The IUCN Red List of Threatened Species* 2018. dx.doi.org/10.2305/IUCN.UK.20182.RLTS.T22697488A130895601.en.

BOEHM, C., BOWDEN, C., SEDDON, P., HATIPOGLU, T., OUBROU, W., EL BEKKAY, M. et al. (2020) Northern bald ibis: history, current status, and future perspectives. *Oryx,* 55, 934–946.

BOWDEN, C.G.R. (2015) *International Single Species Action Plan for the Conservation of the Northern Bald Ibis (*Geronticus eremita*). Technical Series No. 55.* Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA), Bonn, Germany. unep-aewa.org/sites/default/files/publication/unep_aewa_ts55_rev_issap_nbi.pdf [accessed January 2023].

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. (2011) Attempted supplementation of the relict wild eastern population of northern bald ibis in Syria with Turkish semi-wild juveniles. In *Global Re-introduction Perspectives: 2011. More Case Studies from Around the Globe* (ed. P.S. Soorae), pp. 130–134. IUCN/Species Survival Commission Re-introduction Specialist Group, Gland, Switzerland, and Environment Agency-Abu Dhabi, Abu Dhabi, United Arab Emirates.

BOWDEN, C.G.R., SMITH, K.W., EL BEKKAY, M., 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,* 31, 453–462.

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.

FRITZ, J. (2015) Reintroduction of the northern bald ibis in Europe: illegal hunting in Italy during autumn migration as the main threat. *WAZA News 2/2015,* 31–32.

FRITZ, J. (2021) The European LIFE+ northern bald ibis reintroduction project. *Oryx,* 55, 809–810.

FRITZ, J., KRAMER, R., HOFFMANN, W., TROBE, D. & UNSOELD, M. (2017a) Back into the wild: establishing a migratory northern bald ibis *Geronticus eremita* population in Europe. *International Zoo Yearbook,* 51, 107–123.

FRITZ, J., UNSOELD, M. & VOELKL, B. (2019) Back into European wildlife: the reintroduction of the northern bald ibis (*Geronticus eremita*). In *Scientific Foundations of Zoos and Aquariums: Their Role in Conservation and Research* (eds A. Kaufman, M. Bashaw & T. Maple), pp. 339–366. Cambridge University Press, Cambridge, UK.

FRITZ, J., WIRTZ, S. & UNSOELD, M. (2017b) Aspekte der Nahrungsökologie und Genetik des Waldrapps: Reply zu Bauer et al. (2016) Vogelneozoen in Deutschland – Revision der nationalen Statuseinstufungen. *Vogelwarte,* 55, 141–145.

GRAY, T.N.E., CROUTHERS, R., RAMESH, K., VATTAKAVEN, J., BORAH, J., PASHA, M.K.S. et al. (2017) A framework for assessing readiness for tiger *Panthera tigris* reintroduction: a case study from eastern Cambodia. *Biodiversity and Conservation,* 26, 2383–2399.

GRIMM, V., AUGUSIAK, J., FOCKS, A., FRANK, B.M., GABSI, F., JOHNSTON, A.S.A. et al. (2014) Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling,* 280, 129–139.

GRIMM, V., BERGER, U., BASTIANSEN, F., ELIASSEN, S., GINOT, V., GISKE, J. et al. (2006) A standard protocol for describing individual-based and agent-based models. *Ecological Modelling,* 198, 115–126.

GRIMM, V., BERGER, U., DEANGELIS, D.L., POLHILL, J.G., GISKE, J. & RAILSBACK, S.F. (2010) The ODD protocol: a review and first update. *Ecological Modelling,* 221, 2760–2768.

HOUSER, A.M., GUSSET, M., BRAGG, C.J., BOAST, L.K. & SOMERS, M.J. (2011) Pre-release hunting training and post-release monitoring are key components in the rehabilitation of orphaned large felids. *African Journal of Wildlife Research,* 41, 11–20.

IUCN/SSC (2013) *Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0.* IUCN Species Survival Commission, Gland, Switzerland. portals.iucn.org/library/efiles/documents/2013-009.pdf [accessed January 2023].

KAPLAN, E.L. & MEIER, P. (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association,* 53, 457–481.

KLEINBAUM, D.G. & KLEIN, M. (2012) *Survival Analysis: A Self-Learning Text,* 3rd edition. Springer, New York, USA.

LAMPILA, S., ORELL, M., BELDA, E. & KOIVULA, K. (2006) Importance of adult survival, local recruitment and immigration in a declining boreal forest passerine, the willow tit *Parus montanus. Oecologia,* 148, 405–413.

LEBRETON, J.D. & CLOBERT, J. (1991) Bird population dynamics, management, and conservation: the role of mathematical modelling. In *Bird Population Studies* (eds C.M. Perrins, J.D. Lebreton & G.J.M. Hirons), pp. 105–125. Oxford University Press, Oxford, UK.

MATHEWS, F., ORROS, M., MCLAREN, G., GELLING, M. & FOSTER, R. (2005) Keeping fit on the ark: assessing the suitability of captive-bred animals for release. *Biological Conservation*, 121, 569–577.

MUÑOZ, A.-R. & RAMÍREZ, J. (2017) Reintroduced northern bald ibises from Spain reach Morocco. *Oryx*, 51, 204–205.

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

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

PEREIRA, H.M. & NAVARRO, L.M. (eds) (2015) Rewilding European landscapes. In *Rewilding European Landscapes*, 1st edition. Springer, Cham, Switzerland.

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

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

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

R CORE TEAM (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

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

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

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

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

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

SOORAE, P.S. (2018) *Global Reintroduction Perspectives — 2018; Case Studies from Around the Globe*. IUCN/SSC Re-introduction Specialist Group, Gland, Switzerland, and Environment Agency-Abu Dhabi, Abu Dhabi, United Arab Emirates.

SPERGER, C., HELLER, A., VOELKL, B. & FRITZ, J. (2017) Flight strategies of migrating northern bald ibises – analysis of GPS data during human-led migration flights. *AGIT – Journal für Angewandte Geoinformatik*, 3, 62–72.

THERNEAU, T.M. (2015) *A Package for Survival Analysis in R*. cran.r-project.org/web/packages/survival/vignettes/survival.pdf [accessed 17 May 2022].

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

WANG, M., YE, X. P., LI, Y. F., HUO, Z. P., LI, X., & YU, X. P. (2017) On the sustainability of a reintroduced crested ibis population in Qinling Mountains, Shaanxi, Central China. *Restoration Ecology*, 25, 261–268.

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

WIMBERGER, K., DOWNS, C.T. & PERRIN, M.R. (2009) Two unsuccessful reintroduction attempts of rock hyraxes (*Procavia capensis*) into a reserve in the KwaZulu-Natal Province, South Africa. *African Journal of Wildlife Research*, 39, 192–201.

WIRTZ, S., BOEHM, C., FRITZ, J., KOTRSCHAL, K., VEITH, M. & HOCHKIRCH, A. (2018) Optimizing the genetic management of reintroduction projects: genetic population structure of the captive northern bald ibis population. *Conservation Genetics*, 19, 853–864.

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

ZOUFAL, K., FRITZ, J., BICHLER, M., KIRBAUER, M., MARKUT, T., MERAN, I. et al. (2007) Feeding ecology of the northern bald ibis in different habitat types: an experimental field study with handraised individuals. In *Report of the 2nd IAGNBI Meeting* (eds C. Boehm, C.G.R. Bowden, M. Jordan, & C. King), pp. 77–84. RSPB, Sandy, UK.