

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*,

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

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

81 **Material & Methods**

82 **Species and study area**

83 The NBI is a threatened species, listed in the IUCN Red List as *critically endangered* from
84 1994 and down listed to *endangered* in 2018. The species is migratory, mainly insectivorous
85 and reaches an age of up to 30 years in captivity. NBI are mainly seasonally monogamous
86 and breed in colonies of up to hundreds of birds (Boehm et al., 2020). Juveniles learn the
87 migration route by following conspecifics to the wintering ground, there they usually remain
88 until they reach sexual maturity (Fritz, Unsoeld, et al., 2019). The last remaining wild
89 population in the world changed to a sedentary lifestyle and lives year round at two breeding
90 sites on the Atlantic coast of Morocco (Bowden et al., 2008).

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

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

95

Figure 1

96 **Data collection & study design**

97 384 NBIs which hatched between 2008 and 2019 are included in the study. Due to insensitive
98 monitoring comprehensive data on genetically determined sex, raising type (either human-
99 raised founder individuals FP, generation F0, or biological parent raised wild individuals BP,
100 generations F1+), breeding colony and potentially date and cause of death or disappearance
101 are available. Reproduction data include egg laying dates, clutch size, and pre-fledging
102 survival probability. In the first years, spatio-temporal data are based exclusively on sight
103 reports. From 2012 on, an increasing proportion of the birds carried GPS tags and from 2014
104 onwards, the whole population could be remotely monitored (Sperger et al., 2017).

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

112 The NBIs of all four breeding colonies are considered as one population, sharing the same
113 wintering ground and separating for breeding, with genetic exchange (Fritz, Kramer, et al.,
114 2017; Fritz, Wirtz, et al., 2017; Wirtz et al., 2018).

115 **Definition of demographic stages and demographic analyses**

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

125

Figure 2

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

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

139 **Population Viability Analysis**

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

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

156 The model documentation follows the TRACE documentation framework (Grimm et al.,
157 2014; SUPPLEMENTARY MATERIAL 3). The model description follows the ODD protocol
158 (Grimm et al., 2006, 2010). An individual-based model (IBM) was implemented in NetLogo
159 6.0.3 (Wilensky, 1999). The corresponding NetLogo and R scripts are provided online
160 (SUPPLEMENTARY MATERIAL 6).

161 **Reproductive Rates**

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

168 Three different reproductive rate (RR) were included into the PVA, depending on the
169 fledglings that were included: $RR_{Baseline}$ includes fledglings raised by adult wild females
170 (stage 4); $RR_{Status\ quo}$ includes in addition female fledglings raised by temporarily added
171 females; $RR_{All\ chicks}$ includes in addition female fledglings raised by human foster-parents.

172 $RR_{Baseline}$ was also calculated separately for the two colonies Burghausen and Kuchl (RR_B and
173 RR_K) and separately for females raised by bird parents (RR_{BP}) and human foster-parents
174 (RR_{FP}). We also implemented GLMMs (generalized linear mixed models) using a Poisson
175 error structure and maximum likelihood fit, to investigate if differences in reproduction are
176 significant.

177 **Scenario development**

178 We analysed the model for two different types of scenarios:

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

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

190 (II) The stochastic event and juvenile supplement scenarios (SJS) assess reproduction
191 improvement by the supplemental release of FP juveniles (F0). For these SJS we crossed
192 S_{Base} and the MScen of special interest where $\lambda > 1$ and $P_{\text{EXT}_{50}} \leq 5\%$ (9 MScen, see
193 results) with 4 levels of stochastic event frequency (5, 10, 15, 20), 5 levels of severity (5, 10,
194 15, 20, 25; additional mortality per stage), 2 levels of the number of supplements (15, 30) and
195 2 levels of the time for supplementing individuals (4 or 7 years).

196

Table 1

197 **Results**

198 **Demography**

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

208 At the end of 2019, 152 individuals were alive including 9 individuals which were delivered
209 to zoos for various reasons. Thus, the release colony at end of the data collection consisted of
210 143 individuals, 69 males and 74 females (sex rate of 1.00:1.07). Concerning the life stage,
211 N=71 individuals belonged to stage 1 (50%; 37f, 34m), N=28 to stage 2 (20%; 11f, 17m),
212 N=13 to stage 3 (9%; 8f, 5m) and N=31 to stage 4 (22%; 18f, 13m). Concerning the colonies,
213 N=33 bird belonged to the colony Burghausen (23%), N=33 to Kuchl (23%), N=51 to
214 Überlingen (36%) and N=15 to Rosegg (10%); 11 individuals (8%) were not yet allocated to
215 a colony. Concerning the raising types, N=68 birds (48%) were BP raised, N=73 FP raised
216 (51%) and N=2 birds (1%) were supplemented.

217 **Survival**

218 Survival was calculated for all individuals from fledging onwards. According to the cox
219 proportional hazard model survival rates between stages across the whole population did not
220 differ significantly (LRT, $N = 736$, 3.05 , $p = 0.4$). Neither did they differ significantly
221 between the sexes (LRT, $N = 379$, 0.8 , $p = 0.4$). According to the Kaplan-Meier estimator,
222 survival probability was for stage 1 $0.64 (\pm 0.36)$ for stage 2 $0.74 (\pm 0.35)$, for stage 3 $0.69 (\pm$
223 $0.35)$ and for stage 4 $0.78 (\pm 0.14)$. The cumulative survival probability until sexual maturity
224 (end of stage 3) was $0.33 (\pm 0.23)$. Concerning pre-fledging survival, 72% of the eggs
225 hatched and 83% of the hatched chicks fledged (TABLE 2).

226 Table 2

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

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

234 Figure 3

235 **Fecundity**

236 The number of nests increased steadily with 1 nest in 2011 and 14 nests in 2019, with a mean
237 of $3.43 (\pm 0.79)$ eggs per nest (TABLE 2). Overall fecundity was 2.15 fledglings per nest (\pm
238 0.70). Fecundity rates of females raised by human-foster parents and females raised by their
239 bird parents (BP) in the wild did not differ significantly ($z = 0.68$, $p = 0.50$), neither fecundity
240 rates among the colonies Burghausen and Kuchl ($z = 0.60$, $p = 0.55$).

241 The annual rate of reproducing adult females (s4) was $0.61 (\pm 0.20)$. From a total of 27
242 potentially reproductive females $N=13$ (48%) never reproduced till end of the data collection
243 period, $N=4$ (15%) reproduced once, $N=4$ (15%) twice, $N=5$ (19%) three times and $N=1$ (4%)
244 6 times.

245 **Population Viability Analysis**

246 **Reproductive Rate**

247 Over the whole period of data collection, a total of 62 individuals reached stage 4. Analysing
248 31 females of these 62 individuals of both sexes in stage 4 as potential mothers resulted in a
249 RR_{Baseline} of $0.53 (\pm 0.17)$; TABLE 1) (wild BP and FP mothers and their female fledglings),
250 $RR_{\text{Status Quo}}$ of $1.41 (\pm 0.81)$ (additionally female fledglings from temporarily added females
251 included) and $RR_{\text{All Chicks}}$ of $3.97 (\pm 2.66)$ (additionally human raised and released female
252 fledglings included). These reproductive rates were used for the PVA.

253 **Management scenarios (MScen)**

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

257 The full factorial design resulted in 326 MScen (SUPPLEMENTARY MATERIAL 4). Across all
258 326 MScen lambda ranged between 0.95 and 1.40. Lambda was >1 and $P_{EXT_{50}} \leq 5\%$ in 308
259 out of 326 MScen (94 %), in all these 308 MScen the population did not go extinct. In a first
260 analysis we investigated the frequencies of MScen with different demographic rates out of
261 306 of 308 MScen with positive population development, to understand how demographic
262 rates affect population viability (FIG. 4). The two MScen “Status quo” and “All chicks” were
263 not considered here, because they were only simulated once with baseline survival values and
264 the respective RR. In the 306 MScen with positive population development only s4 shifted to
265 increasing survival values, as given by the improved MScen. An increase of s4 by 10% or
266 25% increased the viability disproportionately (each 108 times) compared to the baseline
267 value (90 times). These results indicate the importance of survival of the reproductive stage
268 for population viability. This is supported by the GLMs and the ANOVA ranking the effect
269 of the survival rates (deviance d of ANOVA: $d_{s1} = 0.05$, $d_{s2} = 0.05$, $d_{s3} = 0.05$, $d_{s4} = 0.68$).
270 Here, s4 had the largest effect, together with reproductive rates (SUPPLEMENTARY MATERIAL
271 5).

272

Figure 4

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

276 88% of the MScen with RR_{Baseline} showed positive population development (71 times). The
277 reproductive rate had a strong effect on lambda, too ($d_{RR} = 0.58$) in the GLMs.

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

285 **Stochastic event and juvenile supplement scenarios (SJS)**

286 Here we developed 820 scenarios, taking 11 MScens: nine MScen of special interest where
287 lambda >1 and $P_{EXT_50} \leq 5\%$, the S_{Base} scenario and once the "All chicks" scenario without the
288 supplements, as the supplements are already included in the $RR_{\text{All Chicks}}$ (see under
289 SUPPLEMENTARY MATERIAL 2). The number of SJS is given by the equation in
290 SUPPLEMENTARY MATERIAL 4. Lambda was between 0.91 and 1.40. In 714 out of 820 SJS
291 (87 %) lambda was >1 and $P_{EXT_50} \leq 5\%$. Baseline survival values led to positive population
292 growth in 74-79% of the SJS. Increase of survival of adults (stage 4) by 10% led to positive
293 population growth in 89% of the SJS, while 10% survival increase in other age categories led
294 to population growth in 100% of the SJS considered. Increasing baseline survival by 25% led
295 to positive population growth in 100% of the SJS.

296 Each combination of stochastic event frequencies and severities occurred 41 times in all 820
297 SJS. 90% of the SJS with low frequency (5%) and severity (5%) of stochastic events and also
298 80% of the SJS with high frequency (20%) and severity (25%) of stochastic event resulted in
299 positive population development (FIG. 5). 88% of the SJS with 30 supplemented juveniles per

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

302 Figure 5

303 **Discussion**

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

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

313 **Survival**

314 Survival rate of the *Waldrappteam* population is ranging from 64% for juveniles (stage 1) to
315 78% for adults (stage 4). A matching adult survival rate of 81% is published for a small
316 migratory NBI relict population, which was discovered in the Middle East in 2002 (Serra et
317 al., 2014). Since the Moroccan birds are not marked, their survival rate can only be estimated
318 due to the annual counts of the pre-breeding population and the number of fledglings
319 (Bowden et al., 2008). This results in an overall annual survival rate of 77%, what is also in
320 accordance with the calculated rates of the *Waldrappteam* population.

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

323 arriving new breeders at the breeding site in Syria indicates 14% survival rate until sexual
324 maturity (Boehm et al., 2020), what it less than half the rate of the *Waldrappteam* population.
325 Satellite-tracking of the Middle East juveniles revealed, that they did not arrive at the
326 common wintering site in Ethiopia, because they lost the company of experienced
327 conspecifics and died at the Arabic Peninsula (Serra et al., 2014). This low survival rate of
328 juveniles was a major cause for the extinction of this population in 2013, despite international
329 conservation and translocation efforts (Fritz & Riedler, 2010; Bowden et al., 2012; Serra,
330 2015).

331 In our population, first-year survival of foster-parent raised and released juveniles (73%; FP)
332 was significantly higher compared to bird-parent raised juveniles (52%; BP). This contrasts
333 the widespread experience that released individuals have comparably low survival rates,
334 particularly in the first period after release, due to translocation and competition induced
335 stress, dispersal, diseases or predation (Parker et al., 2013), wherein this is true in particular
336 for captive-bred individuals, probably because they lack individual experiences (Mathews et
337 al., 2005). Our birds undergo an extensive pre-release training, which provides them with
338 essential experiences regarding navigation, flight techniques, weather conditions,
339 aerodynamics and predator avoidance (Portugal et al., 2014; Voelkl & Fritz, 2017; Fritz,
340 Unsoeld, et al., 2019). This is assumed to improve post-release viability (Alonso et al., 2011;
341 Houser et al., 2011; Zhang et al., 2017). In a Spanish NBI reintroduction project (*Proyecto*
342 *Eremita*), the mean first-year survival rate for released juveniles was substantially lower with
343 31% (Boehm et al., 2020; data from 2004-2018), compared to the *Waldrappteam* population.
344 We assume that minor pre-release training and unguided autumn dispersal (Muñoz &
345 Ramírez, 2017) account for the strongly deviating survival rate of the juveniles released in
346 Spain (Fritz, Unsoeld, et al., 2019).

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

361 **Fecundity**

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

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

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

378 Table 3

379 **Population Viability Analysis**

380 Due to the outcome of the PVA baseline scenario, with lambda 0.95 and 24% extinction
381 probability within 50 years, the hypothesis that this reintroduced NBI population can survive
382 without further management and release at the end of the data collection period (2019) is to
383 be rejected. This result is not unexpected because the reintroduction project started just in
384 2014 and is still ongoing. Nonetheless, the population is already close to transition into a state
385 of self-growth (with lambda >1.0) what also coincides with the comparatively good survival
386 and fecundity values.

387 The baseline reproductive rate relates the actual number of fledged female offspring to the
388 entirety of adult females (s4) in the population, including the 39% non-reproducing females.
389 It is an expression of the reproductive potential in the population. The given baseline rate of
390 0.53 can be significantly increased by translocations measures, up to a rate of 3.97 (RR_{All}
391 $Chicks$). As indicated by the management improvement scenarios continuing with the given
392 translocation measures has the most significant immediate effect on lambda and extinction
393 probability (TABLE 1). In comparison, an increase in the survival rate has a relatively small

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

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

403 **Conclusion**

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

408 According to the modelling outcome, a major focus of future management of the release
409 population will be on further improvement of the survival rates with particular focus on
410 adults (stage 4). This will mainly be achieved by the implementation of measures against the
411 major mortality causes, illegal hunting in Italy and electrocution on unsecured power poles at
412 the breeding sites (Fritz, 2015; Fritz et al., 2019). Also, the proportion of reproducing females
413 (61%) should be increased by the establishment of a breeding site south of the Alps which
414 can be easily reached in spring without crossing the Alpine chain.

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

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

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

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

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

434 **Author contribution**

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

438 **Acknowledgements**

439 The Waldrapteam is co-financed with a 50% contribution from the LIFE financial
440 instrument of the European Union (LIFE+12-BIO_AT_000143, LIFE Northern Bald Ibis).
441 SD, VR, CD and SKS are associated with the DFG funded research training group
442 „BioMove“ (RTG 2118-1).

443 **Conflicts of interest**

444 None.

445 **Ethical standards**

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

447

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- 590
- 591

592 **Table 1**

593 In the upper part, the table shows the given empirical values for survival per stage and for the
 594 three reproductive rates as defined in the text. These values and their improvements by 10%,
 595 25% or 100% were used in different combinations for the NetLogo simulation of 14
 596 management improvement scenarios, as outlined in the lower part of the table. Improvement
 597 of the empirical values are indicated by bold numbers. The resulting Lambda and extinction
 598 probability (P_{EXT_50}) are shown in the two right columns. Please note that reproductive rate
 599 comprises not only the reproducing females but all adult females in stage 4 and takes into
 600 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							
RR _{Baseline}	0.64 (±0.36)	0.74 (±0.35)	0.69 (±0.35)	0.78 (±0.14)	0.53 (±0.17)		
RR _{Status quo}					1.41 (±0.81)		
RR _{All chicks}					3.97 (±2.66)		
Management improvement scenarios I - 14 scenarios of special interest							
Baseline (RR _{Baseline})	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 (RR _{Status quo})	0.64	0.74	0.69	0.78	Jän.41	1.13 (±0.006)	0%
All chicks (RR _{All chicks})	0.64	0.74	0.69	0.78	Mär.97	1.40 (±0.012)	0%

601
602

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

603

604 **Table 2**

605 Breeding statistics of the *Waldrapteam* 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	

606

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

608

609

610 **Table 3**

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

Species	Population, Country (period)	Population type	Mean fledglings	Source
NBI	<i>Waldrappteam</i> , 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	<i>Proyecto Eremita</i> , 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

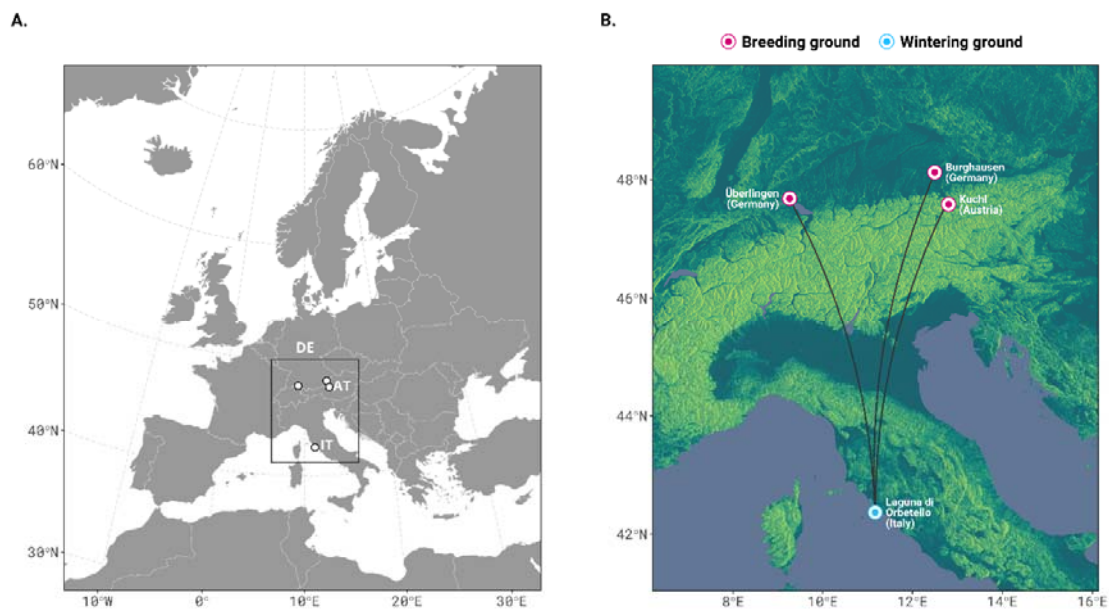
613
614 ¹ Konrad-Lorenz research station, core facility University of Vienna.

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

616

617 **Figure 1**

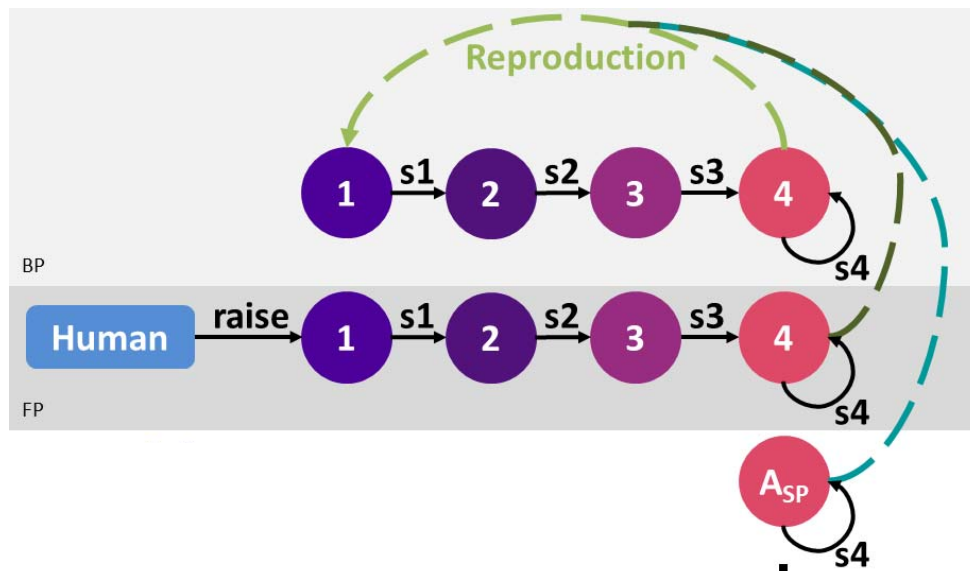
618 Study site of Northern Bald Ibis in Europe. a) Location of the study area in Europe. b) Closer
619 look on two already established breeding sites (pink) in Burghausen (Bavaria, Germany) and
620 Kuchl (State of Salzburg, Austria) and new colonies in Ueberlingen (Baden-Württemberg,
621 Germany; pink)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



624
625

626 **Figure 2**

627 Life cycle graph of the Northern Bald Ibis. Life stages are in circles, for definition see text; s1
628 to s4 are the survival probability of the regarding stages; light grey section: biological parent
629 (BP) raised proportion of the population; dark grey section: human foster parent (FP) raised
630 part of the population; A_{SP}: temporarily added females. Only the female part of the
631 population is considered for the simulations.

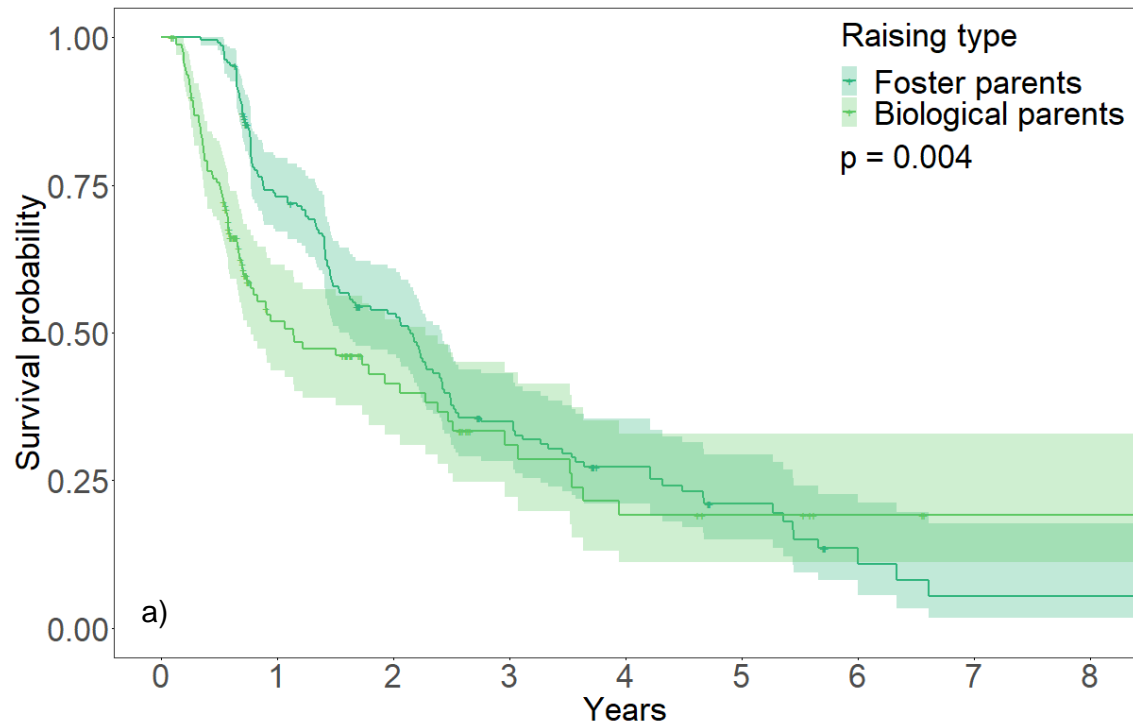


632

633 **Figure 3**

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

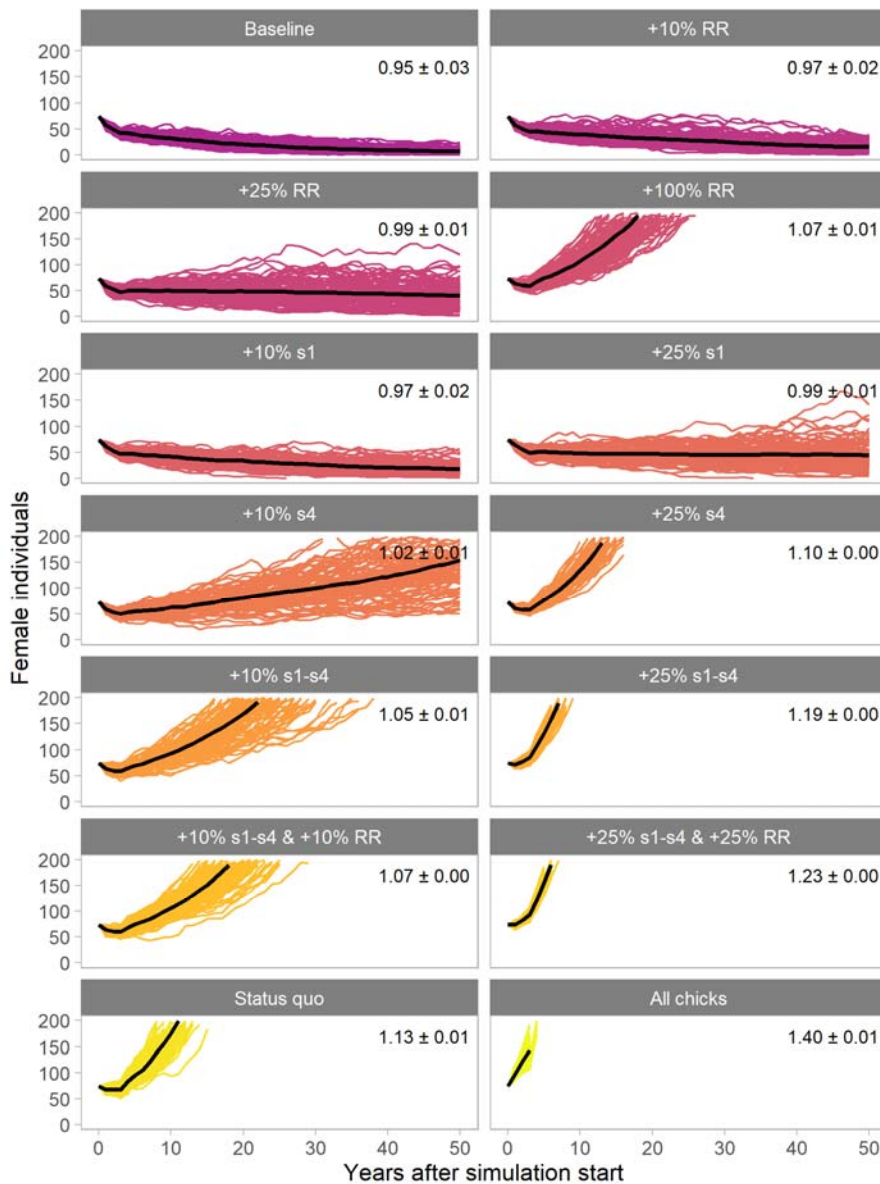
635 represent the standard deviation.



636

637 **Figure 4**

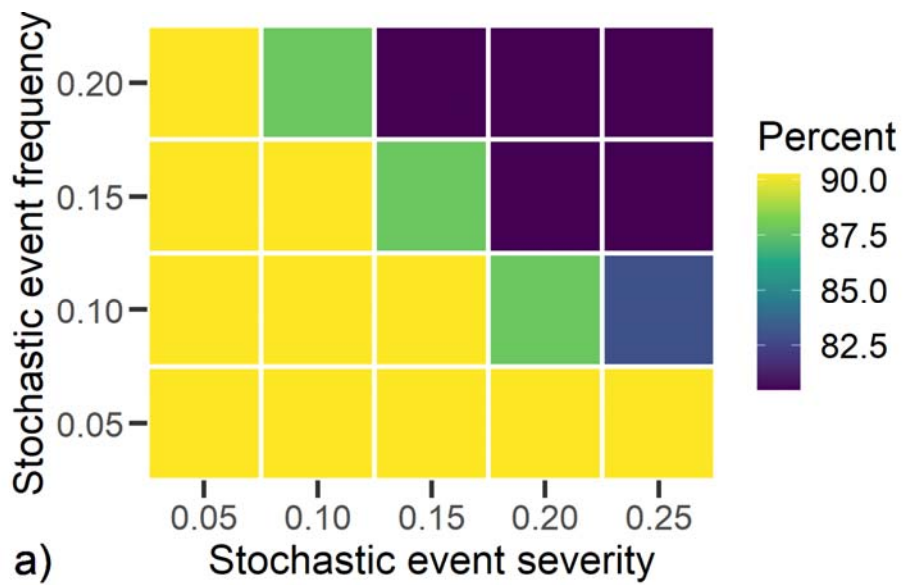
638 Number of females per year in the 14 scenarios of special interest. Each line of a facet
639 corresponds to a run of the respective scenario. The bold black line represents the average of
640 all 100 runs per scenario. Lambda \pm standard deviation are specified for each scenario. The
641 description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



643

644 **Figure 5**

645 Percentage of the respective combination of stochastic event frequency and severity in the
646 714 sub-scenarios where $\lambda > 1$ and extinction probability $P_{EXT_50} \leq 5\%$. In all sub-
647 scenarios, each combination occurred 41 times.



648