**Evaluating population resilience to anticipated stressors using integrated population modeling: a case study of Peregrine Falcons**

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**ABSTRACT**

Reliable estimates of demographic parameters are fundamental to understanding population dynamics and guiding conservation efforts. Integrated population models (IPMs) provide a powerful framework for jointly analyzing diverse data sources to estimate demographic rates and population trajectories, evaluate resilience to environmental stressors, and project population dynamics info the future. We applied a Bayesian IPM to assess the demographic performance and long-term viability of a Peregrine Falcon population that recently recolonized Hungary after regional extinction in the 1960s. Using 27 years (1997–2023) of count, productivity, and mark–recapture–recovery data, we estimated age-specific survival, productivity, and recruitment rates,

22    and used the fitted IPM to conduct stochastic population viability analysis (PVA)  to explore how

23    plausible demographic perturbations (e.g., arising from predation, habitat alteration, or climatic

24    variability) might influence persistence. Annual adult survival averaged 0.79 (95% CRI: 0.73–

25    0.85), juvenile survival 0.50 (0.35–0.69), and productivity 1.9 fledglings per breeding attempt

26    (1.44–2.53), yielding a mean national, annual population growth rate of $\lambda = 1.21$ (0.81–2.07). The

27    recruitment probability of two-year-old females was estimated at (0.76; 0.39–0.98).

28    Scenario-based PVAs showed that the population growth rate responded more strongly to

29    changes in adult survival than to equivalent changes in juvenile survival and productivity. They

30    also revealed that moderate declines in adult survival (<0.70) or productivity (<1.3 fledglings per

31    pair) had the potential to  push $\lambda$ below unity, underscoring the need to maintain both high

32    survival and productivity. By linking hierarchical modeling with stochastic forecasting, we

33    demonstrate how an IPM can be extended into a PVA framework to evaluate demographic

34    resilience and identify quantitative thresholds associated with population vulnerability. This

35    approach provides a transparent, generalizable workflow for translating long-term monitoring

36    data into predictive tools for assessing population vulnerability.

37    *Keywords:* avian demography, decision thresholds, conservation triggers, integrated population

38    model, Peregrine Falcon, population viability analysis, Eagle Owl

39

40    **LAY SUMMARY**

41    •    Peregrine Falcons disappeared from Hungary in the 1960s but returned in the late 1990s

42         and have since recolonized much of the country.

- We analysed 27 years of monitoring data to understand what drives the growth and long-term stability of this recovering population.

- Annual adult and juvenile survival and breeding success in Hungary were similar to other Peregrine populations, and the national population increased rapidly during recovery at about 21% per year on average.

- We used demographic modelling to stress-test the mountain subpopulation using many plausible combinations of survival and productivity to simulate the potential impact of the expanding Eurasian Eagle Owl.

- Our results show that the population is especially sensitive to changes in adult survival and moderate reductions in survival or breeding success could lead to population decline.

- This study shows how long-term monitoring can help identify early warning signs of population vulnerability and guide conservation decisions.

## INTRODUCTION

Understanding the demographic mechanisms that regulate population growth and persistence is fundamental to ecology, evolution, and conservation biology. Reliable estimates of vital rates such as survival, fecundity, and immigration rates provide the quantitative basis for assessing population status, diagnosing causes of decline, and identifying actions most likely to promote recovery (Caswell 2001; Sæther & Bakke 2000; Stahl & Oli 2006). Demographic analyses further enable the evaluation of population responses to perturbations in key vital rates, allowing conservation biologists to identify life-history components that exert the greatest leverage on population growth rate ($\lambda$) or extinction risk (Caswell et al. 2001; Koons et al. 2016; van de Kerk

65    et al. 2020). Such analyses are essential for evidence-based management because they identify

66    demographic "pressure points" where interventions, such as management actions to reduce adult

67    mortality or increase productivity, can yield the largest population-level benefit (Morris & Doak

68    2002; Schaub & Kery 2022). Yet, robust inference about vital rates is challenging when data

69    come from heterogeneous sources or variable monitoring designs, as is often the case for long-

70    lived, wide-ranging birds of prey.

71        Hierarchical Bayesian integrated population models (IPMs) offer a coherent framework to

72    meet this challenge. IPMs jointly analyze multiple data sources (typically population counts,

73    productivity, and mark–recapture or -recovery data) within a single framework, yielding

74    internally consistent estimates of demographic parameters while accounting for both process and

75    observation error (Besbeas et al. 2002; Kéry & Schaub 2012; Plard et al. 2019; Schaub & Kéry

76    2022). By borrowing strength across data types, IPMs improve precision, allow estimation of

77    latent processes such as immigration or recruitment probabilities, increase the power to find

78    relationships between demographic rates and environmental covariates, and therefore facilitate

79    management decisions (Abadi et al. 2010; Tenan et al. 2021). When coupled with population

80    viability analyses (PVAs; Beissinger & McCullough 2002; Morris & Doak 2002; Chaudhary &

81    Oli 2020), IPMs provide a flexible platform for forecasting and evaluating alternative

82    management or perturbation scenarios (Saunders et al. 2018; Schaub et al. 2024a). Although the

83    use of IPMs for PVA has increased substantially in recent years, many applications still rely on a

84    limited number of predefined scenarios. Here, we extend this approach and apply a full factorial

85    design with several factors, wherein we systematically explore a broad range of plausible

86    demographic perturbations. This allows population vulnerability to be evaluated across a

87    continuous demographic space rather than a small set of scenarios. A generalizable, avian-

88   oriented workflow of this nature would enable the direct translation of long-term monitoring data

89   into conservation-relevant decision thresholds and quantitative benchmarks that define when

90   demographic rates might fall below sustainable levels. Therefore, developing and demonstrating

91   such an IPM–PVA linkage can yield a powerful, transferable analytical approach for avian

92   conservation planning.

93          After suffering catastrophic declines in the mid-20th century due to organochlorine

94   pesticides, particularly DDT and cyclodienes such as dieldrin, many Peregrine populations

95   recovered following pesticide bans, reintroduction efforts, and enhanced legal protection

96   (Ratcliffe 1967, 1993; Cade et al. 1988; Kéry et al. 2025). These declines and subsequent

97   recoveries are among the best-documented examples of human-driven demographic change in

98   wildlife (Newton 1979, 1998; Newton 2017a, 2017b). Studies of productivity and survival reveal

99   the characteristic raptor life history with high adult survival ($\approx 0.75$–$0.85$), lower first-year

100  survival ($\approx 0.30$–$0.40$), and moderate fecundity of two to three fledglings per successful nest

101  (Newton et al. 2016; Prommer et al. 2025; Badia-Boher et al. 2026). Population growth in such

102  species is therefore most sensitive to changes in adult survival, although variation in productivity,

103  recruitment, and juvenile survival can influence dynamics and local persistence (Dobson et al.

104  2024; Koons et al. 2017). While demographic reconstructions have clarified historical population

105  trajectories (Oli et al. 2023; Kéry et al. 2018, 2021), comprehensive IPM-based assessments

106  linking long-term monitoring data to population viability remain limited for Peregrines.

107          The recolonization of Hungary by Peregrine Falcons provides an exceptional opportunity

108  to examine population recovery following regional extinction. Peregrines had disappeared from

109  Hungary by the 1960s but began recolonizing in 1997, aided by legal protection and extensive

110  nest-box installation on cliffs, trees, power pylons, and tall buildings (Prommer et al. 2025). The

population has since re-established across much of its historical range, forming a spatially

structured population occupying both natural and anthropogenic breeding sites. Yet, despite this

apparent success, local variation in breeding success persists and may be influenced by climatic

variation, habitat heterogeneity, and interactions with the expanding Eagle Owl (*Bubo bubo*)

population, a potential predator and competitor that can depress local Peregrine productivity

(Mearns & Newton 1988; Prommer et al. 2025) and may also cause significant predation to

juveniles and adults (Frank Rau, personal communication?). Understanding how these ecological

and demographic factors interact is essential for predicting the long-term viability of this

recovering population.

Here we analyze a 27-year dataset (1997–2023) from the recently recolonized Hungarian

Peregrine population (Prommer et al. 2025) by implementing a Bayesian integrated population

model and population viability analysis within a single inferential framework. The IPM part

combines information from population count data, productivity records, and individual encounter

histories to estimate retrospective population dynamics and demographic parameters.

Specifically, our objectives were to (1) estimate age-specific survival, productivity, and

recruitment while accounting for temporal variation and observation uncertainty; and (2) identify

the demographic rates that most strongly influence population growth. We use the PVA part to

evaluate how increasing competition and predation by the Eagle-Owl (via reduced survival and

productivity) might affect long-term persistence of a Peregrine Falcon population. By linking

empirical data with model-based projections, we demonstrate how an integrated IPM–PVA

workflow can reveal the demographic foundations of recovery and resilience in a recolonizing

Peregrine Falcon population and illustrate a broadly applicable analytical framework for

conservation of raptors facing comparable pressures.

134

**METHODS**

**Study area**

Hungary covers 93,030 km$^2$ and lies in Central Europe, in the Carpathian Basin, surrounded

by the Carpathian Mountains, and is dominated by the Great Plain and low elevation hills and

mountains. The predominant landscapes, covering one-third of the country, consist of mountains

and hills with mostly low cliffs, deciduous forests, forest-steppes, and pastures, each with distinct

natural vegetation types (Hortobágyi and Simon 2000). The remaining two-thirds of the country is

dominated by lowlands, primarily comprising agricultural land and woodlands, with grasslands

comprising smaller proportion of landcover.

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**Demographic data collection**

**Population monitoring data.** The Peregrine Conservation Working Group Program,

managed by MME-BirdLife Hungary (hereafter referred to as MME), has been organizing

surveys since the return of the species in 1997. These national surveys usually involve various

contributing partners and aim to collect data on territory occupancy and productivity. Surveys

target historic, recent, and potential new nest sites. Surveys were conducted during the breeding

season (March to May); each territory was visited 1-3 times annually during the breeding season.

Given the absence of high mountains and large cliff faces, and the relative ease of access to

smaller cliffs, rocks, quarries, and nest boxes on transmission line towers, the detection

probability of a breeding pair during a visit to an occupied territory is thought to be ~1.0. The

observed population increased from two to 122 pairs between 1997 and 2023, and we used the

number of breeding pairs recorded in each year as an index of abundance. The number of

157 fledglings produced at most occupied territory was recorded and used in the productivity

158 analyses.

159 **Ringing, resighting, and recovery data.** We used ringing, resighting, and recovery (i.e.,

160 findings of dead birds that were ringed as chicks) data provided by the Hungarian Center for Bird

161 Ringing. Individuals were ringed as nestlings with standard aluminum rings on their left leg and

162 individually coded color rings on their right. Resightings were almost exclusively limited to

163 breeding adults at nests where trail cameras were installed, or during the ringing of nestlings,

164 when protective adults were photographed. Occasionally, also juveniles and immatures with

165 colour rings were photographed. In a few cases, ringed individuals were found injured or dead

166 (recoveries). In our analyses, we considered both resightings and recoveries within Hungary, as

167 well as recoveries from neighbouring countries. See *Results* for a summary of the number of

168 ringed, resighted, and recovered birds.

169

170 **Data analysis by Integrated Population Modeling**

171 We developed an integrated population model (IPM) within a Bayesian inferential framework,

172 jointly analyzing population survey, productivity, and mark-recapture-recovery datasets (Figure

173 1) to estimate juvenile and adult survival, productivity, recruitment, and age-specific population

174 size from 1997 to 2023.
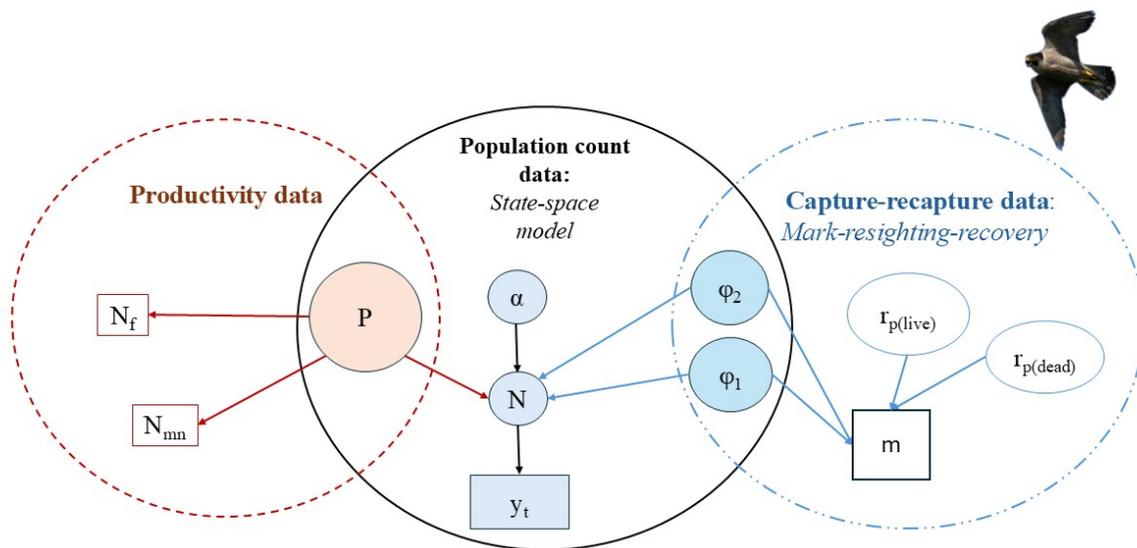
**Figure 1.** Schematic showing the data sources providing information about the parameters in the integrated population model. Data are shown in rectangles, estimated parameters are shown in circles, and arrows represent dependencies. Nodes of the graph are the following: m -- mark-recapture data; $r_p$ -- recapture (both live resighting and dead recovery) probability; $\varphi_1$ -- juvenile survival, $\varphi_2$ -- adult survival; α – recruitment parameter; N -- population size; $y_t$ -- population count data; ρ – productivity; $N$ -- number of fledglings; $N_{mn}$ -- monitored nests. Priors in the Bayesian model are omitted (based on Schaub & Abadi 2011).

The core of the IPM is a stochastic stage-structured population model that reflects the life cycle of the Peregrine (Schaub and Kéry 2022). Our stage-structured model was female-based, assumed an even sex ratio, and was constructed following a pre-breeding "census" formulation (Caswell, 2001). We distinguished five stage classes: juveniles or one-year-olds ($N_1$), first-year non-breeders ($N_2$), second-year non-breeders ($N_3$), second-year breeders ($N_4$), and third-year and older birds, which were all assumed to be breeders ($N_5$; Figure 2). Note that we define both a breeder and a nonbreeder stage for two-year-olds ($N_2$ and $N_3$). We did so because we had field evidence that a few females began reproducing before three years of age, although we had no

192    explicit data to estimate the proportion of 2-yr-old females that recruited into the breeding

193    population. This proportion (α) was therefore estimated as a hidden parameter using the shared

194    indirect information contained in the different ecological datasets used, as is commonplace in

195    IPMs (Schaub & Kéry, 2022). Demographic stochasticity was incorporated using Poisson (for

196    modelling the yearly numbers of live juveniles) and binomial distributions for the remainder of

197    the population stages.
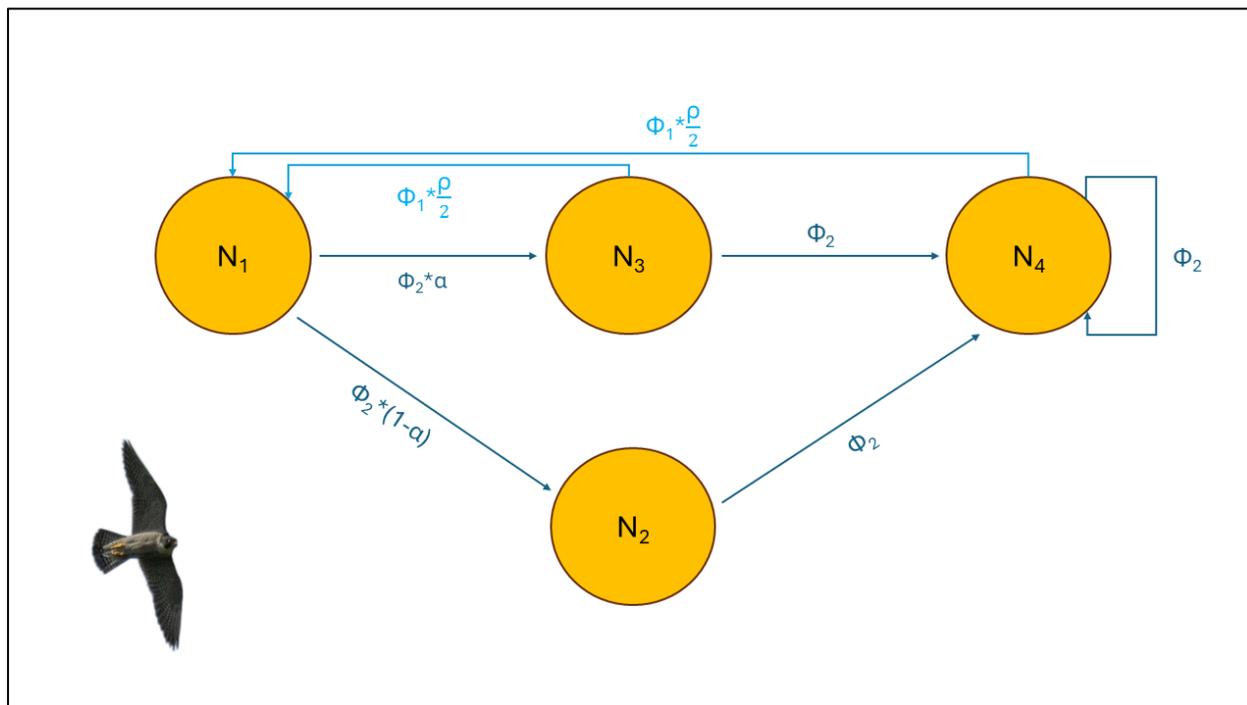
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199    **Figure 2.** Pre-breeding, female-based stage-structured population model. Stage classes are: $N_1$=
200    first-year (juvenile) non-breeders; $N_2$ = second-year non-breeders (floaters), $N_3$ = second-year
201    first time breeders; and $N_4$ = three-year old or older breeders. Dark blue arrows indicate survival
202    and stage transitions ($\varphi_1$ = first year survival, $\varphi_2$ = annual survival of older stages); α indicates the
203    recruitment probability into breeding at age 2 years; and light blue arrows leading from $N_3$ and
204    $N_4$ back to $N_1$ represent reproduction, where productivity ($\rho$) is combined with first year survival.
205

206    The main part of the model can succinctly be summarized by the following equations:

207 $$N_{1,t+1} \sim Poisson\left((N_{3,t} + N_{4,t}) * \frac{\rho_t}{2} * \varphi_{1,t}\right)$$

208 $$N_{2,t+1} \sim Binomial(\varphi_{2,t} * (1 - \alpha), N_{1,t})$$

209 $$N_{3,t+1} \sim Binomial(\varphi_{2,t} * \alpha, N_{1,t})$$

210 $$N_{4,t+1} \sim Binomial(\varphi_{2,t}, (N_{2,t} + N_{3,t} + N_{4,t}))$$

211 where $\rho_t$ is productivity in year $t$, $\varphi_{1,t}$ and $\varphi_{2,t}$ are survival probabilities from $t$ to $t+1$ of juveniles

212 and individuals older than 1 year, respectively, $\alpha$ is the probability that a two-year-old female is

213 recruited into the breeding population (i.e., recruitment rate), and $N_{a,t}$ is the age-specific

214 population size in year $t$. The estimated number of breeding females in year $t$ is given by the sum

215 $N_{3,t} + N_{4,t}$.

216 The population count data were modeled as a state-space model (Figure 1), where the state-

217 process model is the above-defined stage-structured population model. The observation model

218 related the estimated stage-structured numbers of individuals to the yearly counts of breeding

219 females $y_t$ using a normal distribution, whose precision parameter $\tau$ was defined with a vague

220 prior. The observation model is used to accommodate some counting error, but also functions as a

221 residual in the IPM (Schaub and Kéry 2022):

222 $$y_t \sim Normal(N_{3,t} + N_{4,t}, \tau).$$

223 As a derived parameter, we calculated the annual number of floaters as the sum of individuals

224 that had not yet started breeding (i.e., individuals aged 1 and 2; Schaub & Kéry, 2022).

225 The mark-resighting-recovery data were analyzed using a multistate capture-mark-recapture

226 (CMR) model implemented with a multinomial likelihood (Schaub and Kéry 2022). The state-

transition model consisted of five different states: (1) alive as a fledgling; (2) alive as a 1-year-old; (3) alive as an adult (at least 2-years old); (4) recently dead; and (5) dead for good. The state-transition probabilities were functions of age-specific survival and recruitment probabilities. The specification of two dead states (4 and 5) facilitates estimation of recovery probability which can only occur in the year of death ("recently dead"; Barker, 1997). The observation model links the true states with the observations ('seen alive', 'found dead' and 'not encountered') via the resighting and the recovery probabilities.

We assumed the effort devoted to finding dead individuals was consistent throughout the study period; hence, we modelled recovery probabilities as constant over time. However, we structured resighting probabilities by age (1y vs. adults) to account for the likely heterogeneity in detection probabilities arising from their different behavioral patterns (nomadic vs. territorial, respectively; Badia-Boher et al., 2025).

Yearly productivity ($\rho$) was modelled using a Poisson regression model where the yearly number of fledglings ($J_t$) of the monitored broods was the product of the number of monitored broods in year $t$ ($B_t$) and the productivity parameter in year $t$, $\rho_t$:

$$J_t \sim Poisson(B_t * \rho_t)$$

Both annual age-specific survival and productivity were modelled using temporal random effects (i.e., random effect of year):

$$logit(\varphi_{t,age}) \sim Normal(\mu_{\varphi_{age}}, sd_{\varphi_{age}})$$

$$log(\rho_t) \sim Normal(\mu_\rho, sd_\rho).$$

**Model fitting**

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249 We used Bayesian posterior inference and fitted our model using JAGS (Plummer 2003), run

250 from R using package jagsUI (Kellner 2024). The model was run with 4 chains over 180,000

251 iterations, of which the first 100,000 were discarded as a burn-in, and the remainder was thinned

252 by 1 in 160. Model fit was assessed using posterior predictive checks for productivity and count

253 data (Schaub and Kéry 2022). We used vague Beta(1,1) priors, assigning equal probability to all

254 possible values for our parameters and vague uniform(0,5) priors for the mean productivity rate

255 in natural scale for the standard deviations of the temporal random effects of survival and

256 productivity. See the Appendix for a complete description of the model in the BUGS language.

257 We report posterior means, along with 95% credible intervals (CRI).

258

**Population projections under hypothesized survival and productivity scenarios**

260 We used an IPM-PVA to assess the potential effect of Eagle Owl predation on the mountain-

261 dwelling segment of the Peregrine population. An IPM-PVA is basically an IPM that in addition

262 projects demographic rates and the resulting population sizes into the future (Schaub & Kéry

263 2022). Our IPM-PVA used the same structure as described above, i.e., it included demographic

264 and environmental stochasticity, but no density-dependence. We projected the Peregrine

265 population 20 years into the future, where we used different combinations of decreased values of

266 survival and productivity (simulating the effect of Eagle Owl predation in the study population).

267 We computed the resulting population growth rate ($\lambda$) as the dominant eigenvalue of the stage-

268 structured projection matrix under each combination of survival and recruitment parameters.

269     To simulate the negative impact of predation, we used as reference values the mean juvenile

270    survival, adult survival, and productivity estimates derived from the IPM results for the mountain

271    population. To establish realistic values for productivity in the presence of Eagle Owls, we

272    referenced data from northern Hungary (1.29 ± 0.12 young per pair; Prommer, M. *unpublished*

273    *data.*), Germany (1.10; Lindner 2018), and the Italian and Swiss pre-Alps (0.77 ± 0.25; Brambilla

274    et al. 2006) where the Eagle Owl is found or suspected to negatively impact Peregrine

275    productivity. Given the available evidence, we considered as realistic a potential reduction from 0

276    to 40% in productivity due to Eagle owl predation. There are no specific data or studies

277    quantifying the impact of Eagle Owl predation on adult and juvenile survival, but field

278    observations suggest it may be common in areas where both species co-occur. Therefore, we

279    assumed Eagle Owl predation would reduce juvenile survival of the mountain Peregrine

280    population (N = 100) from 0 to 30% (equivalent to an average of 8 dead juvenile females per year

281    at 30% reduction) and adult survival from 0 to 15% (equivalent to an average of 15 dead adult

282    females per year at 15% reduction). The number of dead individuals per population stage that we

283    show is calculated over the population size estimated in the last year of data (2023), so, right

284    before the start of the forecasts. After setting these ranges, we generated sequences of ten values

285    for each parameter (e.g., 0% – 1.5% – 3% – 4.5% up to 15% for adult survival, and similarly for

286    other parameters). This approach yielded 11 possible values for each of the three parameters,

287    resulting in 1,331 combinations of productivity, juvenile survival, and adult survival.

288     Then, we evaluated in more detail the outputs of four specific projections (hereafter

289    '*scenarios*'). The '*best-case*' scenario was the result of the projection using the actual

290    productivity and survival estimates obtained in our IPM of mountain-dwelling Peregrines (1997-

291    2023); this scenario assumed no wider and stronger effect of Eagle Owl predation than already

292   present in the north-northeast region. The '*worst-case*' scenario was the projection resulting from

293   the combination of the lowest values for each demographic parameter (i.e., a 40% reduction in

294   productivity, 30% reduction in juvenile survival, and 15% reduction in adult survival). In the

295   '*random*' scenario, we arbitrary selected productivity, juvenile survival, and adult survival values,

296   to model an unforeseeable situation that may emerge, and that may influence demographic

297   parameters in an unpredicted way. Lastly, the '*mean*' scenario used the average values of the

298   decreased parameters from the above scenarios (20% reduction in productivity, 15% reduction in

299   juvenile survival, and 7.5% reduction in adult survival).

300       We calculated quasi-extinction probabilities for each projection year and scenario. The quasi-

301   extinction threshold was set at 10 breeding females, corresponding to a small fraction (11%) of

302   the mountain population size (90 pairs in 2023). This threshold was chosen deliberately as an

303   early-warning trigger rather than a definition of biological extinction, reflecting a population

304   level at which conservation action would still be feasible, whereas lower thresholds (e.g. five

305   breeding pairs) would likely represent a stage at which effective intervention would already be

306   severely constrained.

307

308

309   **RESULTS**

310

311   **Summary of monitoring data and population trends**

312   The estimated number of occupied territories in the whole Hungarian population agreed well with

313   the observed counts, suggesting the absence of lethal lack of fit of our model. The population

314   increased from 3 (95% CRI 2-5) occupied territories in 1997 to a maximum of approximately 120

315   (95% CRI: 116-122) in 2023.

316        During this study period, of the 855 nestlings ringed with standard aluminum rings, 61 birds

317   were resighted 138 times, and 25 recovered dead. No individual observed alive was later

318   recovered as dead, resulting in 163 total encounters of 86 unique birds. These encounter histories,

319   combined with productivity and count data, provided complementary demographic information

320   for the integrated population model.

321

**Demographic parameters of the overall population**

323   Juvenile apparent survival ($\varphi_1$) averaged 0.50 (0.35–0.69) across the study period and showed

324   substantial year-to-year variability (Figure 3a). Uncertainty was greatest during the early years of

325   recolonization, when the number of marked juveniles was relatively low.

326   Adult apparent survival ($\varphi_2$) was considerably higher and was estimated with greater precision,

327   with an overall mean of 0.79 (0.73–0.85) and fairly low temporal variation (Figure 3b). This

328   reflects both the larger sample size and the higher detectability of territorial individuals.

329   Productivity ($\rho$) averaged 1.92 fledglings per successful breeding attempt (1.44–2.53), with

330   moderate interannual variation (Figure 3c). Precision increased over the duration of the study as

331   monitoring intensity grew and a higher proportion of breeding attempts were documented,

332   leading to narrower credible intervals in later years.

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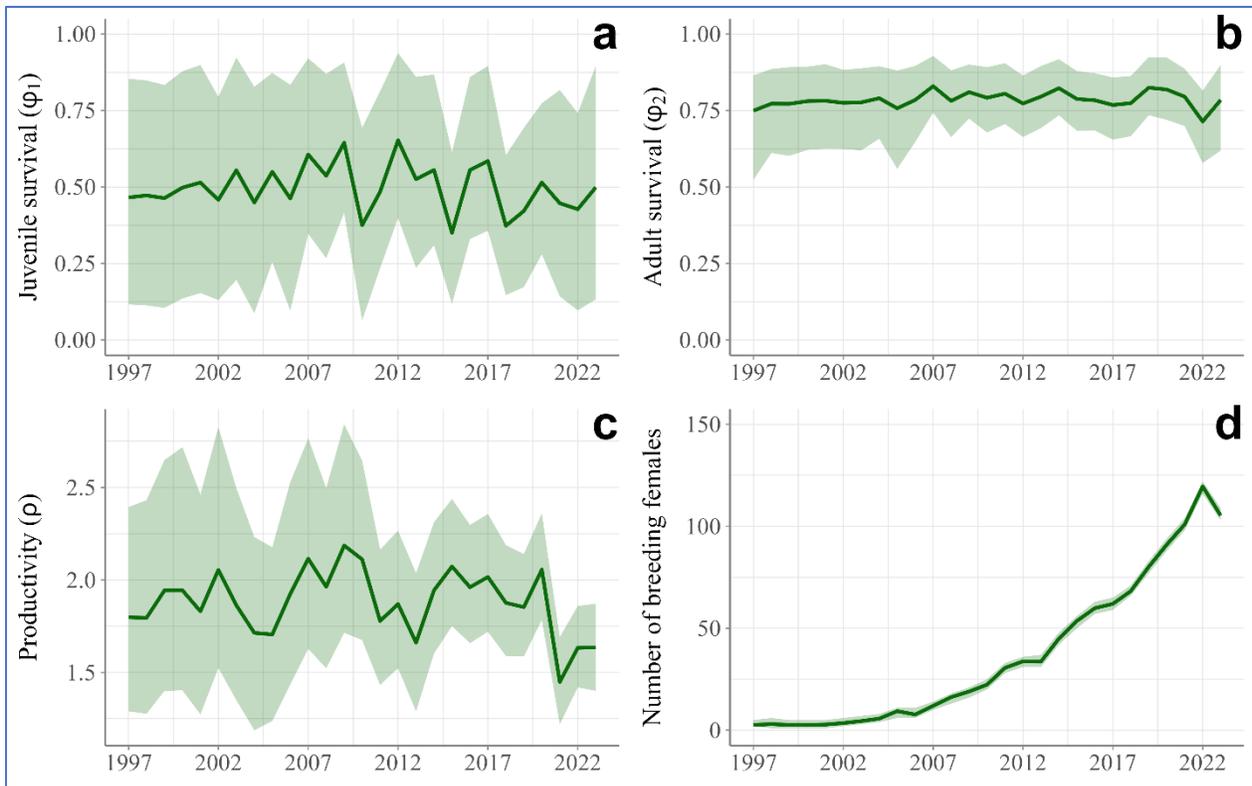
**Figure 3.** Demographic parameters of the Peregrine population in Hungary from 1997 to 2023. Demographic parameters are: (**a**) juvenile survival ($\varphi_1$), (**b**) adult survival ($\varphi_2$), and (**c**) productivity ($\rho$). Panel (**d**) shows the observed number of breeding pairs/females during the monitoring period. Shaded areas represent 95% credible intervals.

The recruitment probability of two-year-old females ($\alpha$), a parameter inferred from the joint likelihood across datasets, was estimated at 0.76 (0.39–0.98). This indicates that every year, three quarters of all two-year Peregrines transitioned into the breeding population, consistent with occasional field observations of birds breeding prior to age three.

Posterior estimates of stage-specific abundances are shown in Figure 4. The number of one-year-olds increased substantially during the period of rapid population growth. The two-year-old nonbreeding floater class also increased steadily, indicating a growing pool of potential recruits. First-time breeders and established adult breeders increased in parallel with overall population

348 growth and represented the majority of individuals once the population stabilized at higher

349 numbers.
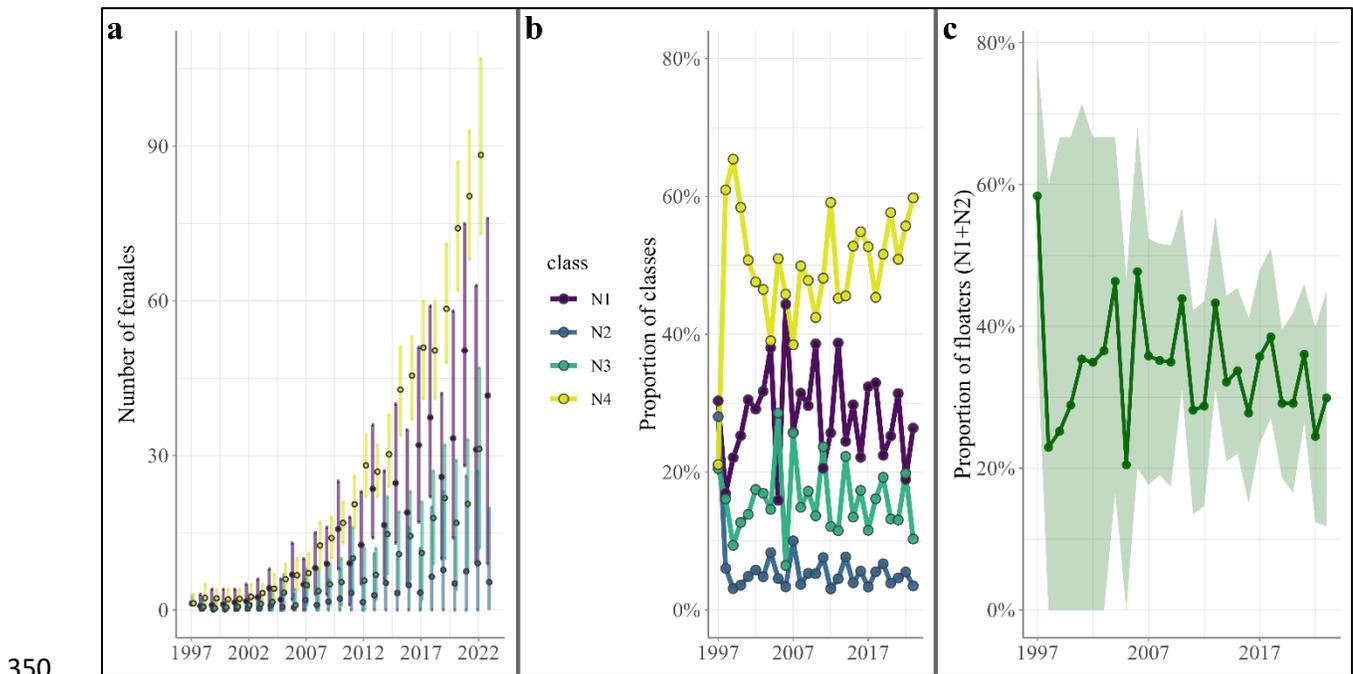


**Figure 4.** The estimated number (**a**) and proportion (**b**) of females in different age classes: juveniles ($N_1$), non-breeding two-year-olds ($N_2$), breeding two-year-olds ($N_3$), and three-year-old and older breeders ($N_4$) from 1997 to 2023, as estimated by the integrated population model. Panels (**c**), with shaded areas indicating the 95% confidence intervals.

**Demographic parameters of the mountain population**

The estimates of demographic parameters for the mountain population were somewhat different than those for complete Hungary: juvenile survival ($\varphi_1$) was slightly lower ($\varphi_1 = 0.46$ (0.30-0.64), adult survival ($\varphi_2$) was similar ($\varphi_2 = 0.79$ (0.74-0.85)), and productivity ($\rho$) was slightly higher ($\rho = 1.97$ (1.62-2.36)). Breeding probability of second-year birds ($\alpha$) was lower ($\alpha = 0.63$ (0.27-0.97)).

**Population viewability analysis for the mountain population**

To simulate the effect of Eagle Owl predation or other factors depressing survival and productivity on $\lambda$ in the mountain-dwelling Peregrine population, we calculated $\lambda$ for 1,331 possible combinations of juvenile survival, ($\varphi_1$) adult survival ($\varphi_2$), and productivity ($\rho$) (11 values each for $\varphi_1$, $\varphi_2$ and $\rho$). Results of these analyses are presented as contour plot of $\lambda$ as a function of $\varphi_1$ and $\varphi_2$ for each hypothesized value of $\rho$ (Figure 5). The results indicate that if $\rho$ falls below approximately 1.15 young per breeding attempt, $\lambda$ will be less than 1, regardless of the values of juvenile and adult survival parameters within the hypothesized range. Additionally, the results show that changes in adult survival cause a larger change in $\lambda$ than equivalent changes in juvenile survival,. These results suggest that the Peregrine population would be strongly and adversely affected if Eagle Owl predation reduces survival of adult Peregrines more than anything.
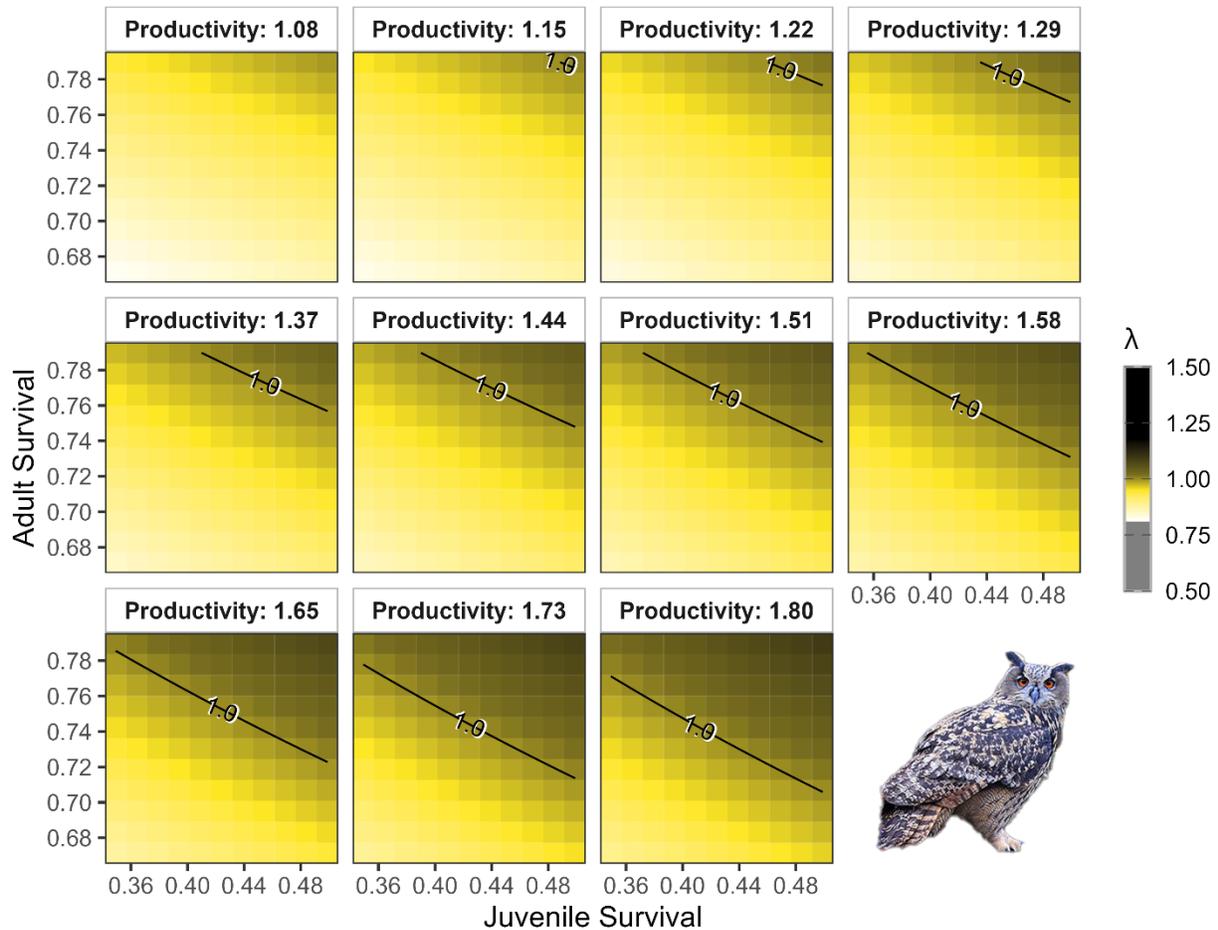
**Figure 5.** Estimates of population growth rate ($\lambda$) of the mountain-dwelling population for various combination of juvenile ($\varphi_1$; x-axis) and adult ($\varphi_2$; y-axis) for 11 different productivity ($\rho$) scenarios (1.08 to 1.80 young per breeding attempt, mimicking a gradually reduced productivity by 40%). Grey to yellow areas indicate population decrease ($\lambda < 1$), while green areas show population increase ($\lambda > 1$). The equilibrium, representing a stable population, is marked along the border between the green and yellow areas, with the contour showing ($\lambda = 1$).

## Population projection under predation scenarios

Out of the 1331 scenarios, we further examined four representative scenarios (Figures 6 and 7).
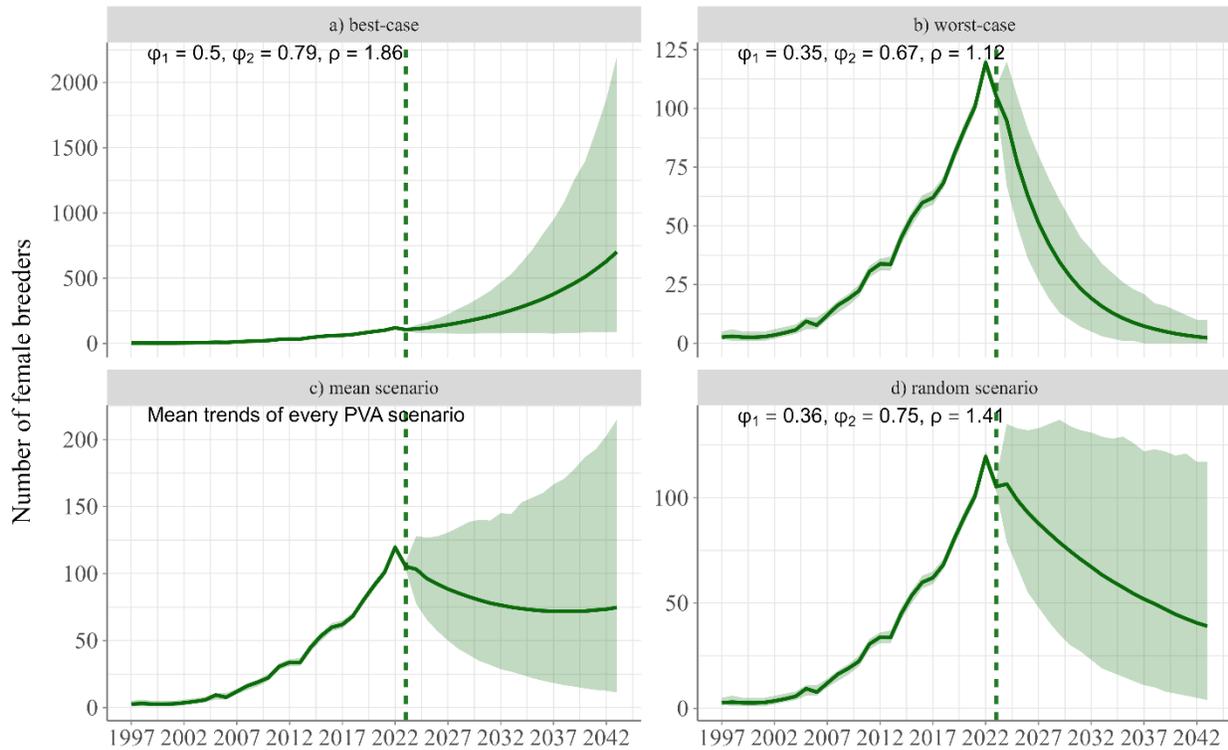
**Figure 6.** Projected growth of the mountain population of Peregrine Falcons under four hypothesized scenarios regarding Eagle Owl predation. Projected number of female breeders under four hypothetical scenarios from 1997 to 2043: (**a**) "best-case" scenario with current levels of predation pressure (and data-based estimates of demographic parameters); (**b**) "worst-case" scenario simulating high predation pressure on all demographic parameters across the entire population; (**c**) "mean scenario", representing mean trends of all PVA scenarios; (**d**) "random scenario" with random survival and productivity values reflecting an uneven effect of predation pressure on demographic parameters. Shaded areas represent 95% credible intervals. The vertical dashed line shows 2023, which is the last year in the dataset.

**Best-case scenario.** This scenario used the current demographic estimates obtained from the mountain subpopulation and assumed no additional predation pressure beyond what is reflected in the IPM-estimated parameters. Under these conditions, the projected population growth rate was $\lambda = 1.1$ (1.03-1.17). All simulated trajectories were stable or increasing, and the cumulative probability of quasi-extinction (<10 breeding females) by 2043 was null.

21

401    **Worst-case scenario.** This scenario applied the largest plausible concurrent reductions: 40%

402    in productivity, 30% in juvenile survival, and 15% in adult survival. Under this combination, $\lambda$

403    declined to 0.82 (0.78–0.87), producing the steepest projected declines among all scenarios and a

404    cumulative quasi-extinction probability of 0.98 by 2043.

405    **Mean scenario.** The mean scenario used the average proportional reductions across the full

406    grid: 20% reduction in productivity, 15% in juvenile survival, and 7.5% in adult survival. This

407    parameter combination generated a projected growth rate of $\lambda = 0.94$ (0.89–1.00). Although less

408    severe than the worst-case scenario, the mean scenario nevertheless produced substantial declines

409    in many simulated trajectories, resulting in a nonzero but very low (0.02) quasi-extinction risk by

410    2043.

411    **Random scenario.** In this scenario, we arbitrarily selected a representative but uneven parameter

412    combination ($\varphi_1 = 0.36$, $\varphi_2 = 0.75$, $\rho = 1.41$) meant to mimic a plausible yet unpredictable pattern

413    of predation pressure. The resulting growth rate was $\lambda = 0.95$ (0.90–1.00). Greater process

414    variance—driven by reduced juvenile survival combined with moderate productivity—generated

415    more declining trajectories than in the mean scenario, resulting in the second-highest cumulative

416    quasi-extinction probability (0.09).

417

418    Across all four scenarios, cumulative quasi-extinction probabilities ranged from 0.00 (best-

419    case) to 0.98 (worst-case), underscoring the potential vulnerability of the mountain subpopulation

420    when key demographic rates are reduced (Figure 7).
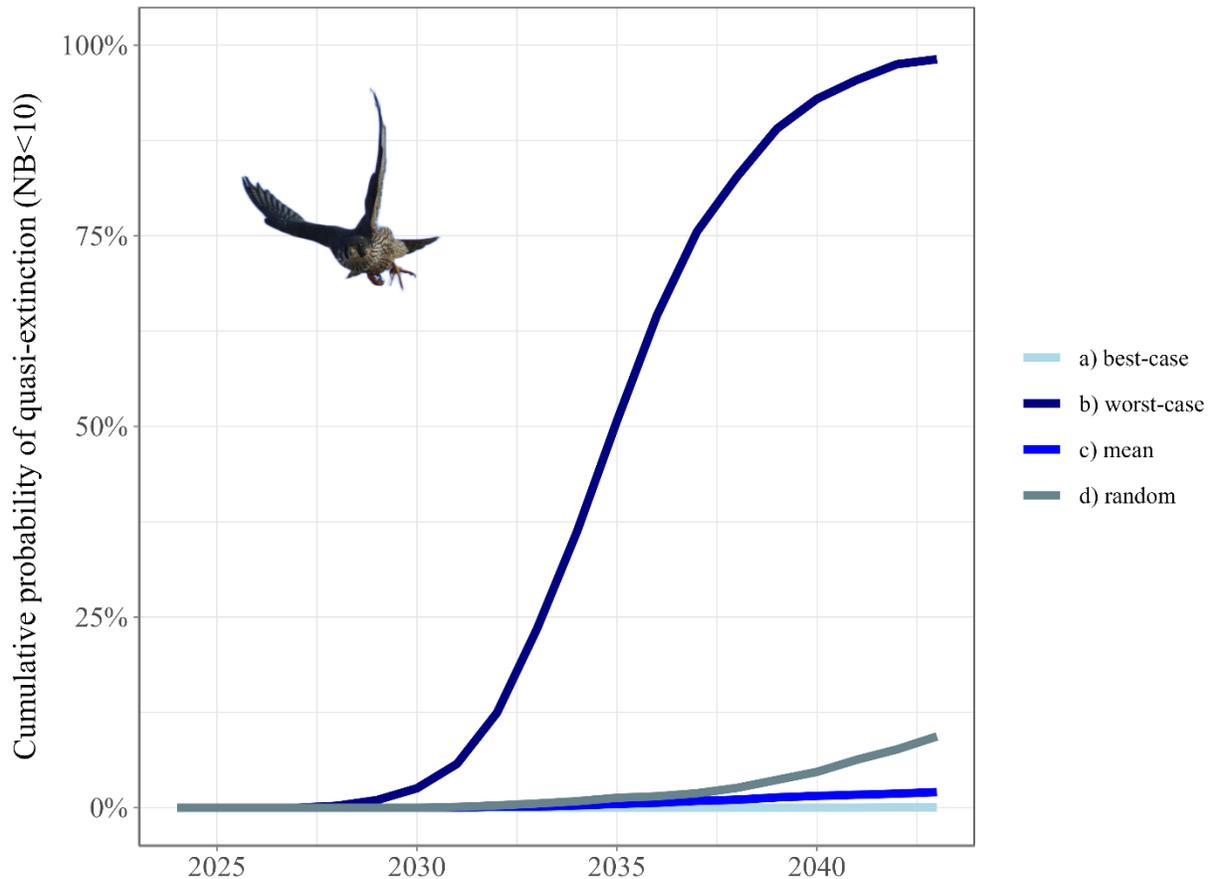
**Figure 7.** Cumulative probability of quasi-extinction of the mountain Peregrine population: (**a**) high survival of both juveniles and adults, and high productivity, the "best-case" scenario reflecting no additional predation pressure; (**b**) low juvenile and adult survival, and low productivity, the "worst-case" scenario, simulating high predation pressure affecting all demographic parameters; (**c**) mean trends of all PVA scenarios, "mean" scenario; (**d**) "random" scenario with random survival and productivity values reflecting an uneven effect of predation pressure (low juvenile survival–high adult survival) on demographic parameters.

## DISCUSSION

### Demographic patterns

Our integrated population model revealed a demographic pattern typical of long-lived raptors (high adult survival, moderate juvenile survival, and stable productivity), illustrating how these parameters interacted to shape the recolonization and persistence of Peregrines in Hungary. Mean

435    juvenile and adult survival and productivity were similar to values reported for other European

436    and North American Peregrine populations (Smith et al. 2015; Robinson and Wilson 2021; Kéry

437    et al. 2021; Nygård et al. 2019; Oli et al. 2023) and fall within the range similar-sized raptors

438    (Millsap 2018; Schaub et al. 2024b; Newton et al. 2016). These results suggest broadly that the

439    Hungarian population exhibits demographic characteristics consistent with global patterns of

440    Peregrine recovery following pesticide-induced declines (Cade et al. 1968; Fyfe et al. 1976;

441    Newton 1979, 1988; Kéry et al. 2018; Monneret et al. 2018, Altwegg et al. 2014, Kéry et al.,

442    2025).

443        Comparable recovery trajectories have been documented in other Peregrine populations,

444    where increases in adult survival and productivity produced rapid growth followed by

445    stabilization (Smith et al. 2015; Kéry et al. 2018; Nygård et al. 2019). In long-lived species,

446    proportional changes in adult survival exert far greater influence on population growth rate ($\lambda$)

447    than equivalent changes in fecundity or juvenile survival (Sæther and Bakke 2000; Stahl and Oli

448    2006). Our scenario-based projections revealed patterns consistent with this expectation:

449    relatively small changes in adult survival resulted in substantial variation in $\lambda$.

450

451    **Demographic mechanisms and ecological drivers**

452    Although overall population growth has characterized the Hungarian Peregrine's recovery in

453    recent years, our projections identified potential vulnerabilities. Simulated reductions in adult

454    survival below 0.70 or productivity below 1.3 fledglings per nesting attempt caused the

455    population to decline, indicating that persistence depends on maintaining both parameters above

456    these thresholds. Among potential mechanisms affecting these rates, predation and interference

457    from the expanding Eagle Owl population appear especially consequential (Mearns and Newton

458    1988; Prommer et al. 2025). Eagle Owls can affect Peregrines directly by killing adults or young

459 and indirectly by reducing productivity through nest abandonment. This is likely to happen in

460 Hungary particularly in mountainous areas where the two species overlap spatially (Brambilla et

461 al. 2006; Lindner 2018; Monneret 2010). Similar asymmetric interactions have been reported

462 elsewhere among large raptors, such as between Bonelli's Eagles and Golden Eagles (Lourenço et

463 al. 2011; Béres et al. 2022).

464 Beyond interspecific interactions, climatic variability, changes in prey composition,

465 agricultural intensification, and increasing urbanization may also affect productivity by altering

466 foraging efficiency or prey delivery rates. Comparative studies of urban versus rural populations

467 reveal marked variation in productivity linked to anthropogenic food availability and disturbance

468 (Kettel et al. 2019; Caballero et al. 2016). Including environmental covariates with strong

469 population-level effects in future IPMs would clarify mechanistic drivers and enhance predictive

470 accuracy (Abadi et al. 2010; Tenan et al. 2021).

471 Recruitment was estimated as a latent parameter in our model, showing that three quarters

472 of all two-year-old females are already breeders, which is more than reported elsewhere (Zabala

473 & Zuberogoitia 2015; Smith et al. 2025). However, our estimate is likely inflated because

474 immigration was not explicitly modeled, and the parameter therefore captures both local

475 recruitment and immigration from neighboring regions, particularly Slovakia (Plard et al., 2021).

476 Ring-recovery evidence supports cross-border movement during early recolonization, which

477 likely declined as the available nesting habitat saturated, and local recruitment became dominant.

478 Similar transitions from immigration-driven to locally sustained population growth have been

479 observed in other recovering raptor populations (Altwegg et al. 2014; Kauffman et al. 2003).

480

481 **Integrating inference and forecasting for conservation**

482   The Hungarian Peregrine's recolonization represents a clear conservation success, yet our

483   analyses reveal demographic fragility beneath apparent stability. Even modest reductions in adult

484   survival or productivity could reverse population growth. The IPM–PVA developed here

485   demonstrates how data from diverse monitoring programs can be analyzed within a Bayesian

486   hierarchical IPM to estimate survival, recruitment, and productivity, and to project the population

487   into the future to evaluate viability under a range of future scenarios of conservation interest. This

488   seamless integration of estimation, inference, and forecasting transforms long-term and diverse

489   monitoring data into a forward-looking conservation tool capable of identifying quantitative

490   demographic thresholds associated with population vulnerability and persistence (e.g., adult

491   survival $>0.70$ and productivity $>1.3$ fledglings per attempt).

492       By coupling demographic estimation with stochastic simulation, this framework enables

493   conservation practitioners to test "what-if" scenarios, evaluate management options, and quantify

494   population persistence under alternative environmental conditions. In doing so, it provides a

495   transparent and data-driven foundation for adaptive management (McCarthy and Possingham

496   2007; Allen and Gunderson 2011; Canessa et al. 2016). Because the approach relies on standard

497   data types (population counts, productivity, mark–recapture–recovery), it can be readily applied

498   to other bird species to generate rate-specific management triggers and identify decision

499   thresholds. In long-lived raptors, improving adult survival typically yields the greatest long-term

500   conservation return (Steenhof and Newton 2007; Sergio et al. 2006; Tavecchia et al. 2016;

501   McClure et al. 2025).

502       The integrated IPM–PVA workflow developed here is flexible and generalizable,

503   providing a framework extendable to other bird species. Future research should incorporate finer-

504   scale environmental covariates (e.g., prey abundance, local climatic anomalies, predator

505   densities) to mechanistically link demographic variation to environmental change. Embedding

506  these models within adaptive management frameworks (Nichols and Williams 2006; Runge et al.

507  2011) will enable evaluation of alternative management strategies under uncertainty and ensure

508  conservation resources are directed toward the most influential demographic processes.

509      In conclusion, the recovery of Peregrines in Hungary underscores both the promise and

510  fragility of demographic resilience in a rapidly changing world. The IPM-PVA framework

511  exemplifies how population ecology can move beyond description to prediction: anticipating

512  vulnerability, quantifying resilience, and informing proactive management initiatives. This

513  integrative approach converts monitoring data into actionable guidance and establishes a robust

514  foundation for conservation planning that keeps pace with accelerating environmental change and

515  the complex realities of species recovery.

516

528    Michael P. Moulton (University of Florida) for their advice and constructive comments on the

529    manuscript.

530

537

538    **Ethics statement**

539    The monitoring and ringing activities during this study were carried out in accordance with the

540    principles and rules of Law LIII/1996 '*on the Conservation of Nature*', the raptor research permit

541    PE-KTFO-507-16-2019 issued for MME-BirdLife Hungary, and the ethical code of the

542    Hungarian Bird Ringing Center.

543

544    **Conflict of interest statement**

545    The authors declare no conflict of interests.

546

547    **Author contributions**

548    M..P. conceived the idea, conducted research in most of the study period (2006-2023), collected

549    data, developed methods and analyzed data, contributed substantial materials, and wrote the

550  paper; J.A.B-B. developed methods for data analysis, analyzed data, and edited the paper; M.K.

551  and M.S. supervised method development methods and edited the paper; J.B. conducted data

552  collection in the early phase of research (1997-2005); M.K.O. supervised research especially for

553  data analysis, and edited the paper.

554

555  **Data availability**

556  Analyses reported in this article can be reproduced using the data provided by Prommer et al.

557  (2025).

558

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771

**APPENDIX**

!

U#INTEGRATED POPULATION MODEL ####

# Hungarian Peregrines: 1997-2023

# ----------------------------

#Data: breeding census, productivity, mark-resighting-recovery

#Female-based IPM

# Component data likelihoods

# ============================================

```
####### PVA objects######

#By which percentage will each parameter decrease in each
   scenario. These parameters should be multiplied to the
   estimates in the population dynamics model

surv.1.mod <- seq(from = 1, to = 0.7, length.out = 11)

surv.2.mod <- seq(from = 1, to = 0.85, length.out = 11)

prod.mod <- seq(from = 1, to = 0.6, length.out = 11)

#Write all possible combinations in a data frame
percs <- expand.grid(data.frame(surv1 = surv.1.mod, surv2 =
   surv.2.mod, prod = prod.mod))

names(percs) <- c("s1", "s2", "prod")

#Bundle the data
jags.data <- list(

  #Mark-recapture
  marr = marr,
```

```
802    nyears = ncol(mmm),

803    rel = rowSums(marr),

804    ns = ns,

805    zero = matrix(0,ns,ns),

806    ones = diag(ns),

807

808    #Count

809    y = as.numeric(count_matrix[,2]),

810

811    B = as.numeric(productivity_matrix[,2]),

812    J = as.numeric(productivity_matrix[,3]),

813

814    pNinit = dUnif(1,5), #1,70 is definitely too much for a
815      population that started with 3 pairs. I go from 1 to 5, which
816      is more or less the same ratio as 1-70 for 50, or even more
817      (twice above, twice below)

818

819    #PVA

820    percs = as.matrix(percs[-1,]), #matrix data frame with all
821      combinations of parameters to be tested

822    nscenarios = nrow(percs[-1,]), #Remove the first combi (1,1,1)

823    nyf = 20 #Number of forecasted years

824  )

825

826  str(jags.data)

827

828  # 12.5 The integrated population model

829  # ==================================

830

831  # IPM1: temporal random effects on the demographic rates
```

```
832   # ''''''''''''''''''''''''''''''''''''''''''''''''''''''''''''

833

834   # Write JAGS model file

835   cat(file = "modelpva.txt", "

836   model {

837      # Priors for detection and recovery probabilities

838

839        mean.p1 ~ dbeta(1,1)

840        mean.p2 ~ dbeta(1,1)

841        mean.r ~ dbeta(1,1)

842

843        #Recruitment component, assumed constant

844

845        mean.alpha ~ dbeta(1,1)

846

847     # Priors and random effect in survival

848      for (t in 1:(nyears-1+nyf)){

849        logit.s[1,t] ~ dnorm(l.mean.s[1], tau.s[1])

850         s[1,t] <- ilogit(logit.s[1,t])

851        logit.s[2,t] ~ dnorm(l.mean.s[2], tau.s[2])

852         s[2,t] <- ilogit(logit.s[2,t])

853       }

854      for (u in 1:2){

855        mean.s[u] ~ dunif(0, 1)                          # Priors for
856       mean age-dep. survival

857        l.mean.s[u] <- logit(mean.s[u])

858        sigma.s[u] ~ dunif(0, 5)

859        tau.s[u] <- pow(sigma.s[u], -2)

860       }
```

```
861
862   #Priors and constraints for productivity
863      for (t in 1:(nyears+nyf)){
864         log.rho[t] ~ dnorm(l.mean.rho, tau.rho)
865         rho[t] <- exp(log.rho[t])
866
867         #Detection and recovery probability
868         p1[t] <- mean.p1
869         p2[t] <- mean.p2
870         r[t] <- mean.r
871
872      }
873
874   # Prior for mean productivity
875
876      mean.rho ~ dunif(0, 5)
877      l.mean.rho <- log(mean.rho)
878      sigma.rho ~ dunif(0, 5)
879      tau.rho <- pow(sigma.rho, -2)
880
881
882      # Population count data (state-space model)
883      # Model for the initial population size: discrete uniform
884       priors
885      for (a in 1:4){
886         N[a,1,1] ~ dcat(pNinit)
887      }
888
889      # Process model over time: our model of population dynamics
```

```
890   for (t in 1:(nyears-1+nyf)){

891

892     N[1,t+1,1] ~ dpois(rho[t] / 2 * s[1,t] * (N[3,t,1]+N[4,t,1]))
893    #One-year-olds

894     N[2,t+1,1] ~ dbin(s[2,t]*(1-mean.alpha), N[1,t,1]) #Two-year-
895    olds, nonbreeders

896     N[3,t+1,1] ~ dbin(s[2,t]*mean.alpha, N[1,t,1])  #Two-year-
897    olds, breeders

898     N[4,t+1,1] ~ dbin(s[2,t], N[2,t,1]+N[3,t,1]+N[4,t,1]) #Three-
899    year-olds and older, breeders

900

901   }

902

903   #Projections

904

905   #Fixing sizes for past years

906

907   for (t in 1:nyears){

908     for(ns in 2:(nscenarios+1)){

909

910       N[1,t,ns] <- N[1,t,1]

911       N[2,t,ns] <- N[2,t,1]

912       N[3,t,ns] <- N[3,t,1]

913       N[4,t,ns] <- N[4,t,1]

914

915

916     }

917   }

918

919   #Projecting into the future
```

```
920
921    for(t in nyears:(nyears-1+nyf)){
922      for(ns in 2:(nscenarios+1)){
923

924       N[1, t+1, ns] ~ dpois((rho[t]*percs[ns-1,3]) / 2 *
925    (s[1,t]*percs[ns-1,1]) * (N[3,t,ns]+N[4,t,ns]))
926       N[2, t+1, ns] ~ dbin((s[2,t]*percs[ns-1,2]*(1-mean.alpha)),
927    N[1,t,ns])
928       N[3, t+1, ns] ~ dbin((s[2,t]*percs[ns-1,2]*mean.alpha),
929    N[1,t,ns])
930       N[4, t+1, ns] ~ dbin(s[2,t]*percs[ns-1,2],
931    N[2,t,ns]+N[3,t,ns]+N[4,t,ns])
932

933      }
934    }
935

936  #Model for the counts
937    sigma.y ~ dunif(0.5, 100)
938    tau.y <- pow(sigma.y, -2)
939

940    # Observation model
941    for (t in 1:nyears){
942     NB[t] <- N[3,t,1] + N[4,t,1]
943     y[t] ~ dnorm(NB[t], tau.y)
944

945     # GOF for population count data: mean absolute percentage
946    error
947     y.pred[t] ~ dnorm(NB[t], tau.y)
948     disc.y[t] <- pow(((y[t] - NB[t]) / y[t]) * ((y[t] - NB[t]) /
949    (y[t] +
```

```
 950       0.001)), 0.5)     # Add a small number to avoid potential
 951    division by 0

 952     discN.y[t] <- pow(((y.pred[t] - NB[t]) / (y.pred[t] + 0.001))
 953     *

 954       ((y.pred[t] - NB[t]) / (y.pred[t] + 0.001)), 0.5)

 955    }

 956    fit.y <- 100 / nyears * sum(disc.y)

 957    fitN.y <- 100 / nyears * sum(discN.y)

 958

 959    # Mark-recapture data (multinomial model)

 960   #Define state-transition and observation probabilities

 961     for(t in 1:(nyears-1)){

 962

 963    psi[1,t,1] <- 0

 964    psi[1,t,2] <- s[1,t]

 965    psi[1,t,3] <- 0

 966    psi[1,t,4] <- 1-s[1,t]

 967    psi[1,t,5] <- 0

 968

 969    psi[2,t,1] <- 0

 970    psi[2,t,2] <- 0

 971    psi[2,t,3] <- s[2,t]

 972    psi[2,t,4] <- 1-s[2,t]

 973    psi[2,t,5] <- 0

 974

 975    psi[3,t,1] <- 0

 976    psi[3,t,2] <- 0

 977    psi[3,t,3] <- s[2,t]

 978    psi[3,t,4] <- 1-s[2,t]
```

```
979     psi[3,t,5] <- 0

980

981     psi[4,t,1] <- 0

982     psi[4,t,2] <- 0

983     psi[4,t,3] <- 0

984     psi[4,t,4] <- 0

985     psi[4,t,5] <- 1

986

987     psi[5,t,1] <- 0

988     psi[5,t,2] <- 0

989     psi[5,t,3] <- 0

990     psi[5,t,4] <- 0

991     psi[5,t,5] <- 1

992

993     po[1,t] <- 0

994     po[2,t] <- p1[t]

995     po[3,t] <- p2[t]

996     po[4,t] <- r[t]

997     po[5,t] <- 0

998

999     }

1000

1001    #Calculate probability of non-encounter (dq) and reshape the
1002    array for the encounter probabilities

1003

1004    for(t in 1:(nyears-1)){

1005    for(s in 1:ns){

1006

1007    dp[s,t,s] <- po[s,t]
```

```
1008    dq[s,t,s] <- 1-po[s,t]

1009

1010    } #s

1011

1012    for(s in 1:(ns-1)){
1013    for(m in (s+1):ns){

1014

1015    dp[s,t,m] <- 0
1016    dq[s,t,m] <- 0

1017

1018    }
1019    }

1020

1021    for(s in 2:ns){
1022    for(m in 1:(s-1)){

1023

1024    dp[s,t,m] <- 0
1025    dq[s,t,m] <- 0

1026

1027    } #s

1028    }#m

1029    }#t

1030

1031    # Define the multinomial likelihood
1032  for (t in 1:((nyears-1)*ns)){
1033  marr[t,1:(nyears *ns-(ns-1))] ~ dmulti(pi[t,], rel[t])
1034  }

1035

1036  # Define cell probabilities of the multistate m-array
```

```
# Matrix U: product of probabilities of state-transition and non-
    encounter (needed because
# there is no product function for matrix multiplication in JAGS)
for (t in 1:(nyears-2)){
U[(t-1)*ns+(1:ns),(t-1)*ns+(1:ns)] <- ones
for (j in (t+1):(nyears-1)){
U[(t-1)*ns+(1:ns),(j-1)*ns+(1:ns)] <- U[(t-1)*ns+(1:ns),(j-
    2)*ns+(1:ns)] %*% psi[,t,] %*%
dq[,t,]
} #j
} #t
U[(nyears-2)*ns+(1:ns), (nyears-2)*ns+(1:ns)] <- ones
for (t in 1:(nyears-2)){

# Diagonal
pi[(t-1)*ns+(1:ns),(t-1)*ns+(1:ns)] <- U[(t-1)*ns+(1:ns),(t-
    1)*ns+(1:ns)] %*% psi[,t,] %*%
dp[,t,]

# Above main diagonal
for (j in (t+1):(nyears-1)){
pi[(t-1)*ns+(1:ns),(j-1)*ns+(1:ns)] <- U[(t-1)*ns+(1:ns),(j-
    1)*ns+(1:ns)] %*% psi[,j,] %*%
dp[,j,]
} #j
} #t
pi[(nyears-2)*ns+(1:ns),(nyears-2)*ns+(1:ns)] <- psi[,nyears-1,]
    %*% dp[,nyears-1,]

# Below main diagonal
```

```
1067    for (t in 2:(nyears-1)){
1068    for (j in 1:(t-1)){
1069    pi[(t-1)*ns+(1:ns),(j-1)*ns+(1:ns)] <- zero
1070    } #j
1071    } #t
1072    # Last column: probability of non-recapture
1073    for (t in 1:((nyears-1)*ns)){
1074    pi[t,(nyears*ns-(ns-1))] <- 1-sum(pi[t,1:((nyears-1)*ns)])
1075    } #t
1076
1077      # Productivity data (Poisson regression)
1078      for (t in 1:nyears){
1079        J[t] ~ dpois(B[t] * rho[t])
1080
1081        # GOF for productivity data: deviance
1082        J.pred[t] ~ dpois(B[t] * rho[t])
1083        J.exp[t] <- B[t] * rho[t]
1084        dev[t] <- J[t] * log(J[t] / J.exp[t]) - (J[t] - J.exp[t])
1085        devN[t] <- J.pred[t] * log(J.pred[t] / J.exp[t]) - (J.pred[t]
1086      - J.exp[t])
1087      }
1088      fit.J <- sum(dev)
1089      fitN.J <- sum(devN)
1090    }
1091    ")
1092
1093    # Initial values
1094    inits <- function(){list(mean.s=runif(2, 0.6, 0.8),
1095                        mean.p1 = runif(1,0,1),
```

```
1096                                   mean.p2 = runif(1,0,1)#,
1097                                   #N = Ninits
1098
1099
1100   )}
1101
1102   # Parameters monitored
1103   parameters <- c("s", "rho", "mean.r", "N", "fit.y", "fitN.y",
1104      "fit.DR", "fitN.DR", "fit.J", "fitN.J", "sigma.y", "mean.p1",
1105      "mean.p2", "mean.alpha", "mean.s", "mean.rho")
1106
1107   # MCMC settings
1108   ni <- 180000; nb <- 100000; nc <- 4; nt <- 160; na <- 5000
1109
1110   # Call JAGS from R (ART 100 min) and check convergence
1111   pvares <- jags(jags.data, inits, parameters, "modelpva.txt",
1112      n.iter=ni, n.burnin=nb, n.chains=nc, n.thin=nt, n.adapt=na,
1113      parallel=TRUE)
1114
1115   #Save object
1116   save(pvares, file = "pvarec_fromappendix_binom_final.RData")
1117
```