

Population Viability Analysis (PVA)

of the Eastern Imperial Eagle

in the Pannonian Region

Research Report for "Conservation of the eastern imperial eagle by decreasing human-caused mortality in the Pannonian Region (LIFE15/NAT/HU/000902)" project

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Introduction

Population viability analysis (PVA) is a widely used tool in conservation biology. Its aim is to identify key demographic parameters to be in the focus of conservation and to compare effectiveness of proposed management actions by modelling future population growth under different management scenarios. PVA starts with the construction of a model that aims to represent real population dynamics of the species as accurately as possible by synthesising current knowledge on demographic parameters and processes. Stochasticity of these parameter values (originating from individual heterogeneity, environmental variability, genetic drift and inbreeding, Schaffer 1981), along with the uncertainty of parameter estimates are also considered in the analysis. Investigating future growth and extinction probability of the population under different scenarios e.g., different levels of mortality or breeding success, allows us to compare the effects of different management schemes and make decisions about allocation of conservation efforts (Lacy, 2019).

Aims of study

The main objective of our study was to forecast population growth of eastern imperial eagles (*Aquila heliaca*) in the Pannonian Region for the next decades under different levels of mortality corresponding to different levels of persecution activities. We also aimed to model past population growth of the Eastern and Western subpopulations, to investigate differences in demographic parameters. The analysis comprised of the following steps:

I. Estimation of demographic parameters:

Data collected in the last four decades served as the base for estimating key demographic parameters, including breeding success, mortality rates of the different age groups, dispersal rates and carrying capacity.

II. Construction of the PVA model:

We constructed a stage-based population model using the demographic parameters estimated from the largest and most extensively monitored East-Hungarian subpopulation.

III. Validation of the PVA model:

To validate our model and parameter estimates, we compared the observed population sizes of the last decades in East-Hungary to the sizes predicted from our simulation.

IV. Modelling the Eastern and Western subpopulations:

Over the last decades, only the Eastern subpopulation - mainly due to the expansion of the East-Hungarian part of the population - showed exponential growth, while the Western subpopulation only increased slowly. This is most probably due to higher mortality rates, emerging from higher persecution rates in the Western areas. We aimed to explore the magnitude of this difference in mortality between the two subpopulations.

V. Investigating future population growth under different scenarios:

We gave predictions of future population growth for the East-Hungarian part of the population under different levels of mortality in order to investigate the consequences of possible elevations in persecution levels.

I. Estimation of demographic parameters

Breeding parameters

Breeding success and productivity of the East- and the West-Hungarian areas were estimated from the database of MME BirdLife Hungary on the breeding records of eastern imperial eagles in Hungary between 1980-2022. Furthermore, the breeding parameters of other Pannonian countries (Eastern subpopulation: East-Slovakia, Serbia, Romania, Ukraine and Western subpopulation: West-Slovakia, Austria and the Czech Republic) were also available for the same study period. Therefore, we could calculate the breeding success and the productivity for both subpopulations separately. The ratio of successful pairs (number of pairs fledging at least one chick / total number of nesting pairs) was calculated for each year, along with the ratio of 1-chick, 2-chick and 3-chick broods among successful pairs. Since breeding success and productivity showed an increase over the decades, the trends of these ratios were also considered during analysis. We fitted linear trend lines to the changing breeding parameter data and the estimates of the fitted lines were implemented into the models instead of average values.

Young individuals in the population can start breeding at a different age, depending on internal and environmental factors. Because of this observed variability in the population we estimated the probabilities of different age groups entering the breeding stage from satellite-tracking data of young birds, which were marked as chicks and followed until their first breeding attempt (n=15). Birds could start to breed first in their 3rd year, all birds were breeding by the age of 6cy (6 calendar years) and most birds started to breed in their 4th year (Figure 1). The probability of a bird starting to breed in the given age were calculated as follows:

Pi: probability of an individual starting to breed in age *i*, conditional on it is surviving until age *i*

To estimate these P*i* probabilities, we calculated the proportion of birds breeding at different ages (Figure 1) and divided these proportions by the probability that an individual does not start breeding before this specific age:

P3cy = proportion of birds breeding in 3cy = 0.20

P4cy = proportion of birds breeding in 4cy / (1-P3cy) = 0.58

P5cy = proportion of birds breeding in 5cy / [(1-P3cy) * (1-P4cy)] = 0.80

P6cy = proportion of birds breeding 6cy / [(1-P3cy) * (1-P4cy) * (1-P5cy)] = 1.00



Figure 1. The proportion of breeding birds at different ages (a), and the proportion of birds starting to breed at different ages (b) were calculated from satellite-tracking data of birds, which were followed from fledging until their first breeding attempt (n=15). Age groups are given in calendar years (cy).

Mortality rates

Mortality of the younger age groups were calculated based on satellite-tracked individuals marked as chicks (n=79). Mortality between 1cy and 2cy were 33.3% (n = 79), between 2cy and 3cy were 13.5% (n = 37), between 3cy and 4cy were 11.1% (n = 18) and between 4cy and 5cy 8.3% (n = 9). Mortality between 5cy and 6cy were estimated to be 11.1%, but we considered this estimate to be unrealistic, as mortality usually decreases by age and this estimate was based on only 7 birds. Consequently, we assumed mortality between 5cy and 6cy to be equal to 8.3%, which is the value of the preceding age group.

For the mortality of birds in the breeding stage, we used the estimate from the markrecapture analysis of breeding birds (see report for *Survival rate estimation*), mortality of 8.3% estimated from the model assuming constant survival over the years.

The standard deviation (SD) of mortality – variability between the years – was estimated to be 4.52%, based on the annual mortality estimates from the year-dependent mark-recapture model.

Dispersal

Emigration from the East-Hungarian population was estimated based on satellite-tracking and genetic monitoring data. Out of the 18 satellite-tracked birds that were followed until breeding, two started nesting in the Western subpopulation (2 / 18 = 11%). Genetic monitoring revealed 44 matches among chicks hatched between 2011-2016 (n = 543 genotyped individuals) and birds that presumably started to breed between 2016-2019 (n = 305 breeding birds that were identified first in this interval). Out of the 44 matches, three birds started to breed in the Western subpopulation (3 / 44 = 7%). The population in the Pannonian Region is closed (no migration from or into other populations) based on satellitetracking, ringing and population genetics data calculated to estimate the gene flow among European populations (Szabó et al., unpublished results). Assuming that immigration into the East-Hungarian subpopulation from other parts of the Pannonian population is just as likely as emigration from it and considering that the East-Hungarian subpopulation is ~70% of the Pannonian population, we estimated emigration from the East-Hungarian population to other parts to be 0.7 * $((7+11)/2) \sim 6\%$. Using the same estimates, when modelling demographic trends in the Eastern and Western subpopulations separately, migration from East to West and from West to East was set to $(7+11)/2 = 9^{\circ}\%$

Carrying capacity and density-dependence

Carrying capacity of the East-Hungarian population was estimated to be roughly 5000 individuals. This estimate is based on two assumptions: (1) that the potentially available habitats in East-Hungary could hold up to approx. 1000 nesting pairs based on summarizing the estimations of many local experts working throughout the distribution area of the species in East-Hungary and (2) that the total number of individuals is roughly equal to 5 times the number of nesting pairs based on field census data.

Density dependence was implemented by reducing the percentage of adult (in territorial stage, see Figure 3) females breeding as population size grows. The following function was used to describe density dependence: = $(100-((100-40)*((N/K)^4)))*(N/(0+N))$, where N is the total population size and K is the carrying capacity. At N=K only 40% of adult females are

breeding (Figure 2, red line). At the current population size (in year 2022) in East-Hungary (Figure 2, grey line) the effect of density-dependence is still negligible.



Figure 2. The density-dependent function applied to the percentage of adult females breeding. At carrying capacity (N = K = 5000), only 40% of adult females are allowed to breed (red line). The grey line indicates the East-Hungarian population size in 2022.

Defining initial population size and age distribution

Initial population size in East-Hungary was estimated to be 30 individuals based on the number of nesting pairs in 1980 (6 pairs) and the assumption of total population size = 5 x no. of nesting pairs (see above).

Initial age distribution was calculated based on estimates from field census data and on the knowledge that age distribution is usually exponential: 25% 1cy, 12% 2cy, 10% 3cy, 8% 4cy, 6% 5cy non-territorial and 39% nesting birds (in territorial stage, see Figure 3).

II. Construction of the PVA model

Stage-structured model

An outline on the basic structure of our PVA model can be seen in Figure 3. We used a stagestructured model, when stage of an individual was determined by its age and breeding status (non-territorial vs. territorial). At the end of the simulation year, all individuals that survived "aged", meaning that they progressed into the next stage (e.g., from stage 1 to stage 2). If they ended up in an immature age group (stage 3-5), then they either stayed in this non-territorial stage for the next year, or they went to stage 5 (territorial stage) with probabilities P3-P5. Instead of aging from 5cy to 6cy, individuals automatically progressed into stage 5. The same demographic parameters are applied to all the individuals within a specific stage. Individuals were allowed to disperse only once in their lifetime, at age 2cy (stage 1). In the simulation, yearly census took place after breeding, similarly to field census.



Figure 3. The outline of our stage-structured PVA model.

The PVA analysis was carried out in program VORTEX 10.0 (Lacy, 1993). The population model of VORTEX is individual-based and can also incorporate stochastic effects. Demographic rates, such as mortality or breeding success, can be defined as functions of other variables, including density or time (Lacy, 2000). We ran each simulation of population growth multiple times (100 or 50 iterations) and the mean values and standard deviations of the different demographic variables (number of individuals, number of nesting pairs etc.) estimated from these multiple runs are reported.

Input parameters for our basic model representing the East-Hungarian part of the population are listed in Supplement Table 1, along with a short description for specific parameters. Estimation of these values is explained in detail in the first section of this report. Some changes in model structure and parameters were introduced for modelling the Eastern and Western subpopulations and for the exploration of future population growth of East-Hungary - these differences are discussed later in the corresponding sections.

III. Validation of the PVA model

We validated our basic PVA model by comparing the population trends observed in East-Hungary between 1980-2022 with the trends predicted by our model for this same, 43-year period.

The means of the predicted demographic values of the population (total number of individuals, number of nesting pairs, number of successful pairs and number of fledglings) closely follow the observed trends (Figure 4-7). A minor deviation in the total number of nesting pairs can be seen around 2010, when the poisoning rate was the highest. Then, the observed population size remained constant for two years instead of increasing exponentially. The reduction in survival caused by this high persecution was compensated for in the model by applying the average annual survival estimated for the whole period including these high poisoning years. Where observed values deviated from the predicted mean, they were still included in the error bars.

Therefore, we conclude that the parameter set predicts the population dynamics well, and so we believe that no serious bias is present in our parameter estimates or in the structure of the model.



Figure 4. The observed population sizes (calculated from 5 times the observed number of nesting pairs) in East-Hungary between 1980-2022 (blue) and the population sizes predicted (mean ± SD) from the model simulating the population growth in East-Hungary for the same period (orange). The simulation was run 100 times.



Figure 5. The observed number of nesting pairs in East-Hungary between 1980-2022 (blue) and the number of nesting pairs predicted (mean ± SD) from the model simulating the population growth in East-Hungary for the same period (orange). The simulation was run 100 times.



Figure 6. The observed number of successful pairs in East-Hungary between 1980-2022 (blue) and the number of successful pairs predicted (mean \pm SD) from the model simulating the population growth in East-Hungary for the same period (orange). The simulation was run 100 times.



Figure 6. The observed number of fledglings in East-Hungary between 1980-2022 (blue) and the number of fledglings predicted (mean ± SD) from the model simulating the population growth in East-Hungary for the same period (orange). The simulation was run 100 times.

IV. Modelling the Eastern and Western subpopulations

To simulate the population trends of the Eastern (East-Hungary, East-Slovakia, Serbia, Romania and Ukraine) and Western (West-Hungary, West-Slovakia, Austria, Czech Republic) subpopulations since 1980, we considered the Eastern and Western subpopulations as two distinct populations in our model with a 9% dispersal rate between the two. Breeding parameters (breeding success, ratio of 1-chick, 2-chick, 3-chick broods) were calculated for both subpopulations using data since 1980 and were implemented in the model as trends, similarly as in our baseline model for East-Hungary. Reliable survival estimates were only available for East-Hungary and therefore we used these estimates for both subpopulations and also, we looked for such mortality values, with which we could reproduce the observed trends. Initial population size was defined the same way as in our baseline analysis (total number of individuals = 5 times the number of nesting pairs), resulting in starting sizes of 70 for the Eastern and 30 for the Western subpopulations. We set very high carrying capacities (K = 10 000 individuals for both subpopulations) because of the following reasons: carrying capacity is very difficult to estimate but neither subpopulation has reached it yet, and we were only interested in the difference of growth trends of the two subpopulations.

The simulations show that the population would have grown much faster in the Eastern and Western subpopulations as well if the mortality rates were the same as the ones estimated for East-Hungary (Figure 7).

Applying mortality rates estimated from East-Hungary to the whole of the East subpopulation, the model predicts three times the size of the observed population size. Increasing the mortality rate by 2.2 percentage points for all ages, we get the observed population trend of the Eastern subpopulation, implying that the average mortality in the East is lower than mortality in only East-Hungary. This is supported by the fact, that the population size in Serbia was stagnant over the last four decades and population sizes in East-Slovakia also increased much slower compared to East-Hungary.

Additionally, it is also visible from the results, that despite the difference in the initial population sizes, the Eastern and Western subpopulations should have similar sizes by now if there was no difference in the mortality rates between the two areas. In contrary, in 2022, the size of the Eastern subpopulation is approximately four times the size of the Western one. Increasing mortality rates in the Western subpopulation by 6.2 percentage points resulted in

the observed population trend of the West, indicating that mortality is higher in the Western subpopulation than it is in East-Hungary.





V. Investigating future population growth under different scenarios

We predicted future population growth for the East-Hungarian part of the population considering different scenarios (Figure 8). The initial population size was 1930 individuals (calculated as 5 x 386 nesting pairs) and carrying capacity was set to 5000 individuals in all cases.

For the "current" scenario (Figure 9, blue line), we used the same mortality rates as for the baseline analysis, an average mortality from the last decade. In the case of breeding parameters, an average of only the last five years was used. The reason for this, is that unlike mortality, productivity showed a strong increasing trend over the years, therefore the average of the most recent years can better represent the future parameters, than an average of the last ten years. In this current scenario, the set carrying capacity of 5000 individuals (approx. 1000 nesting pairs) is predicted to be reached in 10 years. In case productivity will continue to increase, carrying capacity will be reached even faster than it is presented here. Extinction probability of the population in this scenario is basically zero.

In the further scenarios, mortality rates for all ages were increased by specific values. The first two of these scenarios aim to represent mortality in the high poisoning years between 2011-2022 in East-Hungary (4 percentage points higher mortality, Figure 8, orange line), and the assumed mortality rates in the highly persecuted Western subpopulation (see previous section, 6.2 percentage points higher mortalities, Figure 8, red line). In both cases, the population still increases but slower than in the current scenario and it is unable to reach set carrying capacity.

With the help of the simulations, we explored how much increase in mortality would result in nearly stagnating population sizes (11 percentage points higher mortality, Figure 8, grey line) and what magnitude in mortality increase would already lead to the decline and consequently the extinction of the population within the next 50 years (15 percentage points higher mortality, Figure 8, black line).

Mortalities for all ages were increased with the same percentage point throughout the analysis. It could result in a more significant reduction in population size if survival of the younger age groups were more affected by the different mortality factors.



Figure 8. Predicted population sizes (mean ± SD) of the East-Hungarian subpopulation for the next 43 years in five possible future scenarios with different levels of mortality. Simulations were run 50 times.

Discussion

We built a PVA model to forecast population dynamics of the eastern imperial eagle in the Pannonian Region and to gain indirect estimates for the unknown demographic parameters of the Western subpopulation by comparing the growth of the two subpopulations.

We had the best demographic parameter estimates for the East-Hungarian population and with these parameters we built a baseline PVA model that successfully predicted the population trend observed in the last four decades. Also, the PVA suggests that the East-Hungarian population was able to grow exponentially without immigration from outside of the Carpathian Basin, in accordance with a lack of observed immigrant birds and population structure implying genetic isolation.

In our first future scenario, we used these demographic parameters to predict population dynamics for the next four decades ("current mortality" scenario). With these settings there was no danger of extinction, and the population size is predicted to reach carrying capacity of 5000 individuals in 10 years. However, carrying capacity and the form of density-dependence are less precisely estimated than fertility and mortality, because up until now, the population growth trend showed no effect of density-dependence and carrying capacity is difficult to judge as there are still a lot of seemingly suitable but empty habitats.

The estimated survivals showed some variation between years, the lower survivals mostly coinciding with the highest poisoning rates and the stagnation of the otherwise exponentially increasing population size. In these years mortality was estimated to be 4 percentage points higher than for the other years, so in the second future scenario we investigated the effect of such an increase in mortality on population growth and stable population size ("4 pp higher mortality" scenario). For the Western subpopulation we had no reliable mortality estimates, however, we had fertility estimates and population size estimates for the last forty years. So, by trial and error (that is running the PVA with several mortality settings) we came to know that the mortality rates in the Western subpopulation should have been higher by 6.2 percentage points than the East-Hungarian estimates (assuming that mortality increased similarly in each age group). In the third future scenario the Western subpopulation like mortality rates were applied. In both of these scenarios with elevated mortalities, the growth

of the population slowed down, and stabilized below the set carrying capacity, but extinction did not occur among the 50 simulation runs in the projected 43 years.

We determined, that if the East-Hungarian mortalities were increased by 11 percentage points then the population size would stabilize at the current level. This fourth scenario still did not predict extinction. Finally, the fifth future scenario revealed that 15 percentage points increase in mortality results in exponentially decreasing dynamics ending up in extinction.

The PVA model uses estimates of demographic parameters, including mortality, fertility, dispersal, carrying capacity and the effect of density on these parameters in order to project population growth. We had good estimates for fertilities in both for the Eastern and Western subpopulations and breeding survivals for the East-Hungarian birds, but survival of the floaters and dispersal rates are based on less data. We consider the estimate of carrying capacity and the structure of density dependence to be the most uncertain. To more accurate approximation we should collect data about prey distribution, available nesting sites and human disturbance and build a model to estimate the number of nesting pairs for the still unoccupied areas. We plan to investigate the functional form of density dependence via studying the effect of local density on breeding parameters.

In the case of imperial eagles, the number of nesting pairs in each year since the 1980s is a precisely registered demographic data, that cannot be used directly in our Vortex PVA. We could use the observed past numbers of nesting pairs only to validate the settings of the simulations, but we intend to build an integrated population model including these certain data in a Bayesian framework to get more accurate estimations for the other demographic parameters. Using these new methods and modifications we will be able to construct a PVA model that can give more reliable predictions for the demographic trends of the whole Pannonian imperial eagle population.

References:

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Supplement

Table 1. Input parameters for the basic PVA model in VORTEX representing the East-Hungarian part of the population. Some changes in model structure and parameters were applied for modelling the Eastern and Western subpopulations and the future population growth of East-Hungary - these differences are discussed in the corresponding sections. Parameters indicated by grey were irrelevant for this model structure.

Menu	Parameter	Values	Description
Scenario Settings	No. of iterations	100	
	No. of years	43	1980-2022
	Duration of years in days	365	
	Extinction definition	Only 1 sex remains	
	Number of populations	2	Second population serves only
			as a "ghost" population to
			model emigration from
			EastHU
	Order of events in a Vortex year	EV	Census after breeding includes
		Breed	6-7 week-old chicks, similarly
		Census	to field census. Event "Age" is
		Disperse	absent, since the "AGE"
		Mortality	property of individuals is
		GSUpdate	replaced by "STAGE", which
		PSUpdate	updates in the ISUpdate event.
		ISUpdate	1st year mortality is delayed
		rCalc	until event "Mortality",
			instead of event "Breed".
Species	Inbreeding depression	yes	
Description	Lethal equivalents	6.29	Default value
	Percent due to recessive alleles	50	Default value
	EV correlation between	0.5	Default value
	reproduction and survival		
	Sample EV from distribution,	no	Default value
	rather than binomial		

State Variables	Global State Variables	no	
	Population State Variables	yes	
B = Birth	PS1 / P3 - probability of 3cy	I: 0.20; T =PS1	
Function	individual (stage 2) entering the		
	breeding stage (stage 5)		
I = Initialization	PS2 / P4 - probability of 4cy	I: 0.58; T: =PS1	Estimated from satellite
Function	individual (stage 3) entering the		tracking data
	breeding stage (stage 5)		
T = Transition	PS3 / P5 - probability of 5cy	l: 0.80; T: =PS3	
Function	individual (stage 4) enters the		
	breeding stage (stage 5)		
	Individual State Variables	yes	
	IS1 / RNUM	I: =RAND; B: =RAND;	Random number generated
		T: =RAND	from the uniform distribution
			each year for each individual,
			used in the initialization and
			transition functions of ISVar
			AGE
	IS2 / AGE	B: =0	AGE Individual state variable
	IS2 / AGE	B: =0 I:	AGE Individual state variable analogous to age in a stage-
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(AGE Individual state variable analogous to age in a stage- based model. The Initialization
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age"
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0.	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5)))))	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5)))))	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of progressing from one stage to
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5))))) T:	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of progressing from one stage to the next.
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5))))) T: =IF([AGE=5]OR[AGE=	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of progressing from one stage to the next.
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5))))) T: =IF([AGE=5]OR[AGE= 4];5;IF([AGE=3]AND[AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of progressing from one stage to the next.
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5))))) T: =IF([AGE=5]OR[AGE= 4];5;IF([AGE=3]AND[RNUM<=TERP5];5;IF(AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of progressing from one stage to the next.
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5))))) T: =IF([AGE=5]OR[AGE= 4];5;IF([AGE=3]AND[RNUM<=TERP5];5;IF([AGE=2]AND[RNUM<	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of progressing from one stage to the next.
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5))))) T: =IF([AGE=5]OR[AGE= 4];5;IF([AGE=3]AND[RNUM<=TERP5];5;IF([AGE=2]AND[RNUM< =TERP4];5;IF([AGE=1]	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of progressing from one stage to the next.
	IS2 / AGE	B: =0 I: =IF(RNUM<0.25;0;IF(RNUM<0.37;1;IF(RN UM<0.47;2;IF(RNUM <0.55;3;IF(RNUM<0. 61;4;5))))) T: =IF([AGE=5]OR[AGE= 4];5;IF([AGE=3]AND[RNUM<=TERP5];5;IF([AGE=2]AND[RNUM< =TERP4];5;IF([AGE=1]AND[RNUM<=TERP3	AGE Individual state variable analogous to age in a stage- based model. The Initialization Function defines the "age" distribution in the starting population. The Transition Function describes the rules of progressing from one stage to the next.

Dispersal	Age range: Youngest	1	Individuals could disperse only
	Age range: Oldest	1	once in their lifetime, at the age
			of 2cy (stage 1).
	Dispersing sexes	both	
	% Survival of dispersers	100	
	Percent of individuals in each age c	lass that disperse	
	between each pair of populations each year:		
	from EastHU to EastHU	94	
	from EastHU to "Pop 2"	6	Estimated from satellite-
			tracking and genetic monitoring
			data
	from "Pop2" to EastHU	0	
	from "Pop2" to "Pop2"	100	
Reproductive	Reproductive System	Long-term	
System		monogamy	
	Age of first offspring females	5	
	Maximum age of female	5	
	reproduction		i a stara E tamitarial stara
	Age of first offspring males	5	_ i.e. stage 5 – territorial stage
	Maximum age of male	5	-
	reproduction		
	Maximum lifespan	6	
	Maximum no. of broods per year	1	
	Maximum no. of progeny per	3	Based on breeding data
	brood		between 1980-2022. Frequency
			of 4-chick broods are negligible
			(only one 4-chick brood is
			known between 1980-2022).
	Sex ratio at birth - in % males	50	Based on molecular sexing of
			over 700 chicks from the
			Pannon Region between 2011-
			2022
	Density dependent reproduction	no	
	% Breeding at low density, P(0)	50	Density-dependence is
	% Breeding at carrying capacity)	25	implemented in % adult female
	Alee parameter, A	1	breeding
	Steepness parameter, B	2	1

Reproductive	% adult female breeding	=(100-((100-	The percentage of breeding
Rates		40)*((N/K)^4)))*(adult (territorial, stage 5)
		N/(0+N))	females were assumed to be
			density-dependent
	SD in % breeding due to EV	0	
	Distribution of 0 broods per year	=33.65+(-0.06*Y)	Trend calculated from the
			proportion of unsuccessful (no
			chicks) broods between 1980-
			2022 in EastHU
	Distribution of 1 broods per year	=66.35+(0.06*Y)	Trend calculated from the
			proportion of successful broods
			between 1980-2022 in EastHU
	Distribution of 1 offspring per	=62.67+(-0.73*Y)	Trend calculated from the
	female per brood		proportion of 1-chick broods
			between 1980-2022 in EastHU
	Distribution of 2 offspring per	=39.73+(0.21*Y)	Trend calculated from the
	female per brood		proportion of 2-chick broods
			between 1980-2022 in EastHU
	Distribution of 3 offspring per	=-2.39+(0.51*Y)	Trend calculated from the
	female per brood		proportion of 3-chick broods
			between 1980-2022 in EastHU
Mortality Rates	Mortality from age 0 to 1 (stage 0	33.3	
	/ age 1cy to stage 1 /age 2cy),		
	both sexes		
	Mortality from age 1 to 2 (stage 1	13.5	
	/ age 2cy to stage 2 /age 3cy),		
	both sexes		
	Mortality from age 2 to 3 (stage 2	11.1	Estimated from satellite-
	/ age 3cy to stage 3 /age 4cy),		tracking data
	both sexes		
	Mortality from age 3 to 4 (stage 3	8.3	
	/ age 4cy to stage 4 /age 5cy),		
	both sexes		
	Mortality from age 4 to 5 (stage 4	8.3	
	/ age 5cy to stage 5 / age 6cy),		
	both sexes		

	Annual mortality after age 5	8.3	
	(stage 5 / breeding stage), both		Estimated from genetic
	sexes		monitoring of breeding birds
	SD in mortality (all age groups)	4.52	-
	Delay 1st year mortality until all	yes	
	annual mortality is done (rather		
	than in Breed)		
Catastrophes	No. of types of catastrophes	0	
Mate	Degree of monopolization of	100	
Monopolization	breeding opportunities - Males in		
	breeding pool (both populations)		
Initial Population	Use stable age distribution	no	Initial age distribution is defined
Size			by the Initialization Function of
			ISVar AGE
	Initial population size	30	Based on 1980 census data
			from Hungary and the
			assumption of total population
			size = 5 times the no. of nesting
			pairs
Carrying	Carrying Capacity (K)	5000	Based on the assumption of
Capacity			carrying capacity of 1000
			nesting pairs and of total
			population size = 5 times the
			no. of nesting pairs
	SD in K due to EV	0	
	Future change in K?	no	
Harvest	Population harvested?	no	
Supplement	Population supplemented?	no	
Genetics		no	