Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Prioritizing among removal scenarios for the reintroduction of endangered species: insights from bearded vulture simulation modeling

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Keywords
adaptive management; demographic effects; long-lived species; population viability; reintroductions; vultures; simulation modeling; translocations.

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Editor: John Ewen

Received 09 March 2019; accepted 15 October 2019

doi:10.1111/acv.12549

Abstract

Translocations are an increasing feature of threatened species conservation plans, but the impact of removal of individuals on the source population is seldom studied. Using computational Population Dynamics P System models and the Pyrenean Bearded Vulture population as a case study we looked at: the effect on the source population of alternative strategies for removal of individual birds for use in reintroduction projects; and the trade-offs between the various management options. According to our models (over a 30 year prediction horizon) the removal of one clutch, juvenile or non-territorial adult each year over an 11 year period, results in an annual loss of 1.57, 3.71 and 0.97 territories, respectively. We forecast the impact of a plausible removal scenario for the Pyrenees source population (the removal of five clutches and five non-territorial adults each year over 11 years), leading to a predicted loss of 16 breeding territories. Nevertheless, changes in demographic parameters, mainly in productivity and adult survival, could substantially affect these predicted results. With the current demographic parameters, the removal scenarios that were estimated to not affect population size after 30 years (95% CI) are limited to: (1) the removal of five clutches and five non-territorial adults during a single year; (2) the annual removal of five non-territorial adults during a 6 year period; and (3) the annual removal of five clutches during a 6 year period. Our results suggest that removals from the Pyrenean Bearded Vulture source population should be performed with caution due to uncertainties arising from stochastic changes in survival and productivity.

Introduction

The search for innovative and effective methods to improve and optimize species conservation programs is a key issue for managers, conservationists and policy-makers responding to biodiversity loss. The translocation of individuals to formerly occupied habitats is a widespread and increasingly used tool in conservation programs to restore wild populations of endangered species (Seddon, Armstrong & Maloney, 2007; Pérez *et al.*, 2012; Seddon *et al.*, 2014; Brichieri-Colombi & Moehrenschlager, 2016; Swan, Lloyd & Moehrenschlager, 2018). Because the economic and time costs of population replenishment and reintroduction projects can be limiting factors (Smith *et al.*, 2011), reliable assessments of the effectiveness of various management options are essential in choosing the best course of action (McCarthy, Armstrong & Runge, 2012). In the case of threatened species, population size of donor population can be an additional limiting factor. As a result, researchers and practitioners need to evaluate the likely trade-offs among the ex situ (e.g. captive breeding) and in situ (e.g. threat management) options available to improve reintroduction outcomes (Dolman *et al.*, 2015).

There are many studies of translocation projects and the success of reintroductions, including settlement, survival and reproduction of translocated individuals and their effects on the viability of the reintroduced population (e.g. Sarrazin & Legendre, 2000; Armstrong & Seddon, 2008; Le Gouar *et al.*, 2008; Mihoub *et al*, 2013; Robert *et al.*, 2015; Bertolero, Pretus & Oro, 2018). However, there is less information regarding the impacts of translocations on the source or donor population (see McCleery, Hostetler & Oli, 2014; Margalida *et al.*, 2015).

This is especially relevant when translocated individuals are extracted from endangered populations, as in the threatened Bearded Vulture *Gypaetus barbatus*.

Bearded Vulture reintroduction projects have been carried out in several European countries since the mid-1980s to counter the population declines and local extinctions of this species during the 19th and the beginning of the 20th centuries. The ambitious and successful reintroduction project conducted in the Alps is the most noteworthy (Schaub *et al.*, 2009). Birds have been bred in captivity and subsequently released not only in the Alps (France, Italy, Austria, Switzerland), but also in the Massif Central (France), Andalucia (Spain) and elsewhere, specifically in Corsica (5 pairs) and Crete (5 pairs) to reintroduce the species or to reinforce threatened subpopulations.

The Pyrenees (Spain, France and Andorre), with 164 breeding territories, holds the most important European population of Bearded Vultures. There are currently three active Bearded Vulture reintroduction projects in Spain: Andalusia (started in 2006), Asturias (Picos de Europa, started in 2012) and, most recently, Maestrazgo (Castellón, started in 2018). To date, captive bred individuals have been used in the Andalusia and Maestrazgo projects (European Endangered Species Programme) while the Asturias project has used birds raised from eggs taken from clutches removed from nests in the Aragonese Pyrenees. There is also a new proposal for an experimental reintroduction project involving the translocation and release of non-territorial adults taken from the Pyrenean population. To date, two non-territorial Pyrenean adults have been captured and released in November 2018 as part of the Maestrazgo project to reinforce the hacking of captive reared birds, but one returned to the Pyrenees after 6 days (authors unpubl. data).

Because the size of the Pyrenean Bearded Vulture population is regulated by a density-dependent effect on fecundity and its geographic expansion is slow (Carrete, Donázar & Margalida, 2006; Margalida *et al.*, 2008) managers and policy-makers have proposed that more individuals be extracted from the non-territorial population to strengthen and/or reintroduce new populations elsewhere. It is therefore imperative to assess the effects of translocation on the population dynamics of the source population to establish future guidelines for reintroduction or population reinforcement projects. So far, the only study to forecast the impact of different translocation management scenarios (removal of eggs, chicks or fledglings) on Spanish Bearded Vulture populations (Margalida *et al.*, 2015) was based on only a part of the Pyrenean population (Spanish Pyrenees) and used demographic records up to 2006 only (see Oro *et al.*, 2008). Any quantitative study of the entire Pyrenean chain (Spain, France and Andorra) on the effects of different extraction scenarios on the source population dynamics will ideally use computational Population Dynamics P System (PDP) models: an important advance in estimating the population dynamics of threatened species in relation to climatic, energetic (trophic availability) or anthropogenic variables that provides a more rigorous and objective alternative to traditional models of population viability (Colomer *et al.*, 2011; Margalida & Colomer, 2012; Margalida *et al.*, 2018).

We applied PDP models to estimate the effects of different management actions on the Bearded Vulture population trend using data from the long-term monitoring of the entire Pyrenean Bearded Vulture population (1987–2016) and updated demographic parameters for the whole Pyrenean chain (A. Margalida, J. Jiménez, J. M. Martínez, J. A.Sesé, D. García, A. Llamas, M. Razin, M. A. Colomer, B. Arroyo, in prep). Specifically, we modelled the population impact (number of breeding territories) over a 30-year prediction horizon of different extraction scenarios for reintroduction purposes: removal of clutches; first year juveniles; and non-territorial adults >10–20 years old. In addition we modelled the effects of changes in demographic parameters on the simulation forecasts. Our goal was to provide accurate information for managers and policy-makers in order to establish conservation guidelines for translocation management which would not compromise the source Pyrenean Bearded Vulture population.

Materials and methods

Study species

The Bearded Vulture is the most threatened European vulture species. They can breed from 6 years of age, although most start breeding at between 9 and 12 years old (Antor *et al.*, 2007; Lopez-Lopez *et al.* 2013; A. Margalida, J. Jiménez, J. M. Martínez, J. A. Sesé, D. García, A. Llamas, M. Razin, M. A. Colomer, B. Arroyo, unpubl. data). One or two eggs are laid per nest but only one chick ever fledges as a result of siblicide (Margalida *et al.*, 2004). The chick-rearing period is about 121 days (Margalida *et al.*, 2003) and after fledging the young enter a dispersal phase until they settle as territorial adults at between 5 and 7 years old (Antor *et al.*, 2007).

In the Pyrenean study area, breeding ocurs in about 60% of territories each year (each occupied either by a pair or a polyandrous trio) and the annual productivity ranges between 0.30 and 0.40 chicks/pair/year (Margalida, Colomer & Oro, 2014). However, this population is regulated according to the site-dependency hypothesis: as the population increases, average productivity decreases as progressively poorer quality territories are used. In addition, productivity is negatively correlated to the proximity to the nearest conspecific breeding pair (due to crowding) and to the proximity to the nearest supplementary feeding point where floaters congregate (Carrete *et al.*, 2006).

Population modeling

Our methodology first estimated the population parameters based on historical records. Next, a PDP model was constructed to perform 'virtual experiments' to evaluate the effect of removals of clutches and floating individuals of different ages. In order to study the effects of various life history parameters and extractions on the population trends, we used a surface response model (Box–Behnken). We combined the extreme range values of some demographic parameters (productivity and juvenile, subadult and adult survival) in a second Box–Behnken model to assess the potential effects of changes in these parameters on the population's dynamics.

Data collection and parameter estimates

The Pyrenean (Spain and France) Bearded Vulture population has been intensively monitored since the 1980s, including field surveys to monitor population trends, breeding parameters, and survival rates (including a specific capture-mark-resighting sub-programme) (Oro *et al.*, 2008; Margalida *et al.*, 2014, 2015). Between 1987 and 2016, all known breeding Pyrenean territories were visited several times each month to record reproductive parameters. Productivity (number of fledglings per pair/trio per year) and breeding success (number of fledglings per territory with egg-laying) were estimated (Margalida *et al.*, 2014). The ranges of these observed parameters were used to populate our models, assuming an even sex ratio at birth (Bretagnolle *et al.*, 2004). From 1987 to 2016, a total of 151 individuals of known age were identified using rings and wing-marks and were radio- or satellite-tracked in the study area. This has allowed the estimation of demographic parameters such as age of first reproduction, survival and age structure using Integrated Population models (IPM) which integrate capture and recapture methods and counts in a multistate Bayesian approach (Oro *et al.*, 2008; Margalida *et al.*, 2014, 2015; A. Margalida, J. Jiménez, J. M. Martínez, J. A.Sesé, D. García, A. Llamas, M. Razin, M. A. Colomer, B. Arroyo, in prep.). We distinguished three age classes according to the most parsimonious age-model obtained in previous analyses (Oro *et al.*, 2008; Margalida *et al.*, 2014): juveniles (1–2 year old), subadults (3–5 years old) and adults (>6 years old). Given that productivity and survival rates have decreased over the years (Margalida *et al.*, 2014), we used the range of values obtained during the last 5 years (2012–2016), gathered from various demographic studies (Table 1, Supporting Information Table S1). Maximum carrying capacity of the region has been estimated at 1000 breeding individuals (500 breeding territories) based on estimates of natural (i.e. without artificial feeding) food biomass availability, which is more than twice the current population size (Margalida & Colomer, 2012; Margalida, Pérez-García & Moreno-Opo, 2017*a*).

PDP model

Population Dynamic P Systems are computational models inspired by the functioning of cells that operate in parallel at both the individual and process levels, and are capable of modeling processes that interact with each other and animals that compete for resources of different types. The components of a PDP are: environments, membrane structure, initial work alphabet and evolution rules (Colomer, Margalida & Pérez-Jiménez, 2013). The number of environments is usually associated with the number of different zones in the ecosystem to be modelled (i.e. subpopulations inhabiting different regions). The initial alphabet is the input of the model (in our case the objects associated with each individual at the start of the model run, for example, population size, demographic parameters). The rules of evolution use some parameters (e.g. demographic parameters) and aim to describe the processes and process changes that each individual will undergo.

Table 1. Values of demographic parameters obtained from our own empirical data (for details, see Methods) used to calculate the viability of the Pyrenean Bearded Vulture population

Parameter	Value
End juvenile stage	2
End sub-adult stage	5
Life expectancy	30
Age first breeding attempt	6
Number of descendents	1
Productivity ratio low density[a]	0.45
Productivity ratio high density[a]	0.25
Maximum density (pairs)	500
Annual mortality age 1–2 year	0.066
Annual mortality age 3–5 year	0.035
Annual mortality age ≥ 6 year	0.036

[a] Values are taken from the high and low end of the productivity distribution that was estimated across all densities, and assigned to low- and high-density, respectively.

Here we use a PDP model related to the population's dynamics, the density-dependent reproductive process, and the possible effects of extraction of clutches, juveniles >1 year old (hereafter juveniles), and non-territorial adults of ≥10–20 years old (hereafter adults). The results of the model were compared with a baseline non-intervention scenario, based on the demographic rates considered. In the density-dependent model, we take into account the variations in fecundity according to the population size. Our model incorporated negative density-dependence effects on fecundity (Carrete *et al.*, 2006), applying the equation used in *Vortex*: $P(N) = \left(P(0) - (P(0) - P(K)) \cdot \left(\frac{N}{K}\right)^{B}\right) \cdot \frac{N}{N+A}$, where $P(N)$ is the percentage of females that breed at population size N, $P(K)$ is the percentage of females that breed when the population is at carrying capacity (K) and $P(0)$ is the percentage of females that breed when the population is close to zero. In the extractions model, we subdivided the fecundity variables into subcategories (the percentage of pairs that lay eggs and both the hatching and reproductive success) to explore the population effects of the different intervention scenarios (clutches, juveniles and adults) on productivity and population size (breeding fraction).

Description of the PDP model

The model takes into account all the items described previously such as: the population density and the processes of mortality; reproductive parameters; and the removal interventions (clutches or individuals of different age classes) to be performed (Fig. 1) each year. These items were sequenced in order to simplify the model, although this simplification does not affect the final results. The PDP defined is formed by three membranes with the following structure: $\mu = [[]_1[]_2]_0$

(see Colomer *et al.*, 2013). The main, or skin membrane (labelled 0), contains two inner membranes labelled 1 and 2, respectively. Most processes are carried out between the skin membrane and membrane 1. Membrane 2 serves to save the information on the removals that will be extracted from the ecosystem each year and to restore the initial configuration at the end of the cycle, to reset the model at beginning of the following year.

The objects that appear in the initial configuration in the membrane labeled by 0, that is, the model inputs, are as follows:

$$\mu_0 = \left\{XS_j^{qs_j}, 1 \le j \le g_3,\right\} \cup \left\{XP_j^{qp_j}, g_4 \le i \le g_3\right\}$$
$$\cup \left\{XT_j^{qt_j}, g_4 \le i \le g_3\right\} \cup \{NES^{Eg_1}, CHI^{Chi_1}, D, ANY_1,$$
$$ANY_1^{\prime g_3}\} \cup \{b_i, 1 \le i \le g_3\}.$$

A XS_j object is associated to each non-territorial animal of age *j*, while territorial animals are associated to a XP_j or XT_j object, depending on whether they form a pair or trio, respectively. qs_j is the number of objects XS_j (number of non-territorial individuals of age *j*), qp_j the number of objects XP_j (territorial individuals that form pairs of age *j*) and qt_j the number of objects XT_j (territorial individuals that form trios of age *j*). The model allows the removal of clutches, chicks and floating individuals of different age-classes. In this study, we only considered the removal of clutches and non-territorial individuals (juveniles and adults). The number and type of extraction depend on the year. For each year, the quantity of NES objects that are generated equals the number of clutches that are extracted from nests that year. The number of CHI objects is the number of chicks to be removed from nests (not used in the current model). *D* is an object that generates a counter (R_1) in the first step, which allows control of the model and avoids inconsistency in the application of the rules. In addition, *D* generates other objects that allow control of the maximum carrying capacity in the study area. The object ANY_i stores the year that is being simulated in its index. Finally, the objects ANY'_i and b_j allow the generation of FLY_j objects, which are used to extract *i* non-territorial individuals of age *j* in the simulation.

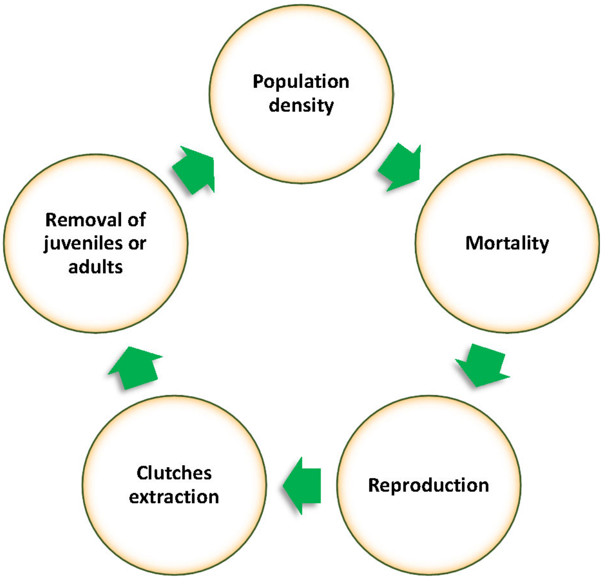

Figure 1 Representation of the modeling process carried out with the Population Dynamics P System. The input of the model is the population size at the start of the process (0) and the output is the population size in the year *t* using the parameters showed in Table 1.

The starting point is the census of animals of each age estimated through the IPM. The definitions of the parameters of the model are shown in Table 1. The model assumes that productivity varies according to the number of breeding territories as a result of density-dependent effects on fecundity (Carrete *et al.*, 2006; Oro *et al.*, 2008). The probability that an individual mates and reproduces depends on its age. The reproductive success is density-dependent and depends on the size of the population (Carrete *et al.*, 2006). The probability of mortality depends on the age of an individual, and the probablility of survival was estimated using observations during the last 5 years for the three age classes considered.

Box–Behnken design

We used a response surface (number of breeding territories) approach to estimate the size of the Bearded Vulture population in the Pyrenees over a 30-year period, depending on the mean values of the parameters considered (Table 1) as well as a range (maximum and minimum) of demographic parameter values and removal timeframes (Table 2). The response surface designs are a subset of the experimental designs used to model the relationship between the independent variables or factors (x_1, x_2, … x_n) and the response variable (Box & Behnken, 1960), using linear models and quadratic or higher order models.

To study the effect of removals on Bearded Vulture population dynamics we constructed a Box–Behnken design using four factors: clutch extractions (range 0–10); removal of 1 year old juveniles (range 0–10); removal of non-territorial adults ≥10–20 years old (range 0–10) and the time of extractions (range 1–11 years). This results in a total of 28 experiments examining 25 different scenarios and four repetitions.

Since some demographic parameters, such as productivity and survival are subject to progressive decreases (in productivity) or annual fluctuations (in survival), we subsequently created another Box–Behnken design to consider the possible

Table 2. Range (minimum–maximum values) of demographic parameters and extraction timeframes used to calculate the viability of the Pyrenean Bearded Vulture population

Factor	Low level	High level
Productivity	0.25	0.45
Juvenile mortality (age 1–2 year)	0.046	0.086
Subadult mortality (age 3–5 year)	0.015	0.055
Adult mortality (age ≥ 6 year)	0.015	0.055
Years extraction	5	11

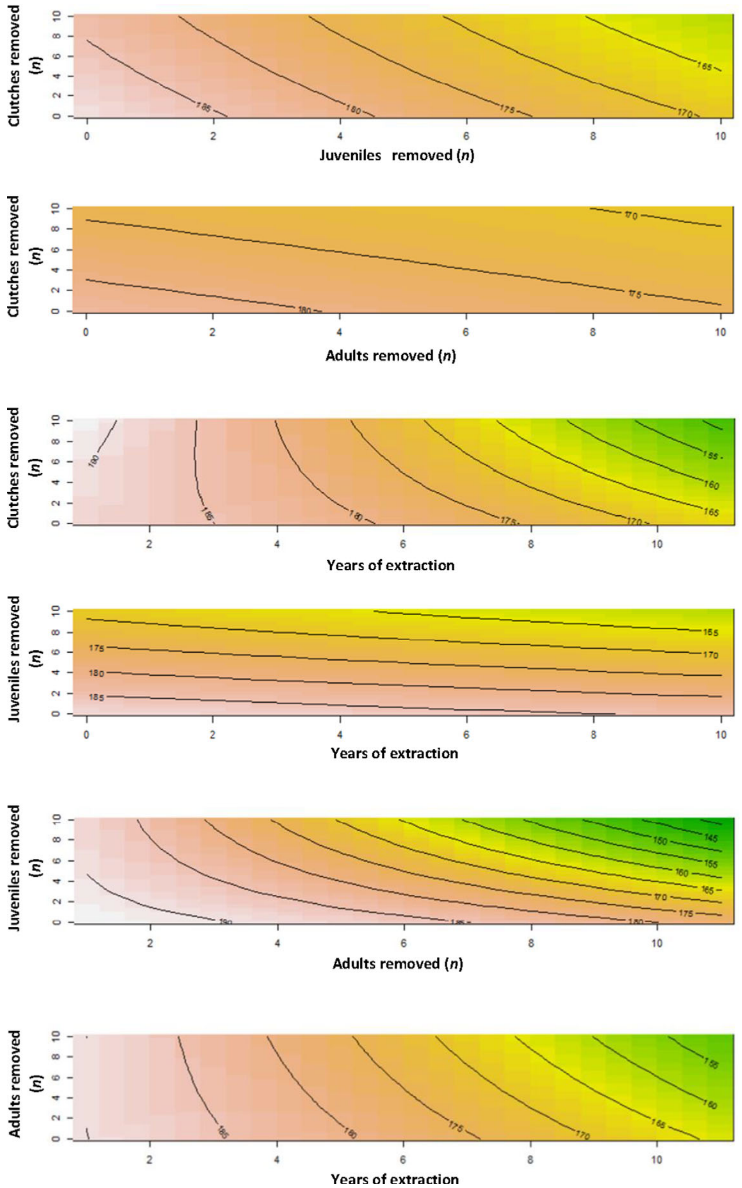

Figure 2 Response surface (number of breeding territories) obtained using the current estimates of the population demographic parameters. The colours represent the number of breeding territories: brown represents the higher values and green the lower ones. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

variations (Table 2). In this case, the number of experiments was 44 with a total of 41 different scenarios with four repetitions.

For the design and the statistical analyses we used DoE.-base, a package in the R program (R 3.5.2.) R Core Team, 2018.

Results

All of the four factors considered (clutches, juveniles, non-territorial adults and years) had a significant effect on the number of breeding territories (Fig. 2; Table 3). In addition, the interactions among clutches, juveniles and adults and the timing of extractions were also significant. The removal of one clutch, juvenile or non-territorial adult each year over an 11 year period, resulted in an annual loss of 1.57, 3.71 and 0.97 territories, respectively. Therefore, an annual extraction of five clutches lead to the loss of 10 breeding territories over 11 years, compared with 20 territories lost due to an annual extraction of five juveniles and seven territories lost due to an annual extraction of five adults. The annual extraction of five clutches and five adults over an 11-year period is a plausible scenario in the Pyrenees and would lead to the loss of 16 breeding territories after 30 years.

As shown in Fig. 3 and Table 4, there were nine removal scenarios that did not result in a significant change (95% CI)

Table 3. Coefficient values of the response surface (number of breeding territories) and significance levels of the variables and interactions that were tested using mean demographic parameter values (Table 1)

	Estimate	SE	*t* value	*P*
Intercept	174.947	0.865	202.194	**0.0001**
Clutches	−3.792	0.499	−7.590	**0.0001**
Juveniles	−10.947	0.499	−21.915	**0.0001**
Adults	−3.138	0.499	−6.282	**0.0001**
Years	−16.181	0.499	−32.391	**0.0001**
Clutches × juveniles	−0.657	0.865	−0.760	0.461
Clutches × adults	0.585	0.865	0.676	0.511
Clutches × years	−5.452	0.865	−6.302	**0.0001**
Juveniles × adults	−0.735	0.865	−0.849	0.410
Juveniles × years	−9.025	0.865	−10.431	**0.0001**
Adults × years	−3.110	0.865	−3.594	**0.003**
Clutches^2	0.299	0.706	0.423	0.679
Juveniles^2	0.640	0.706	0.906	0.381
Adults^2	0.156	0.706	0.221	0.828
Years^2	−1.250	0.706	−1.769	0.100

Juvenile refers to individuals 1-year-old and adults to non-territorial adults 10–20 years old. Statistically significant results are shown in bold type.

in the population trend over 30 years compared to the non-intervention scenario (Fig. 3). The only combinations lying inside this confidence interval were extractions performed during 1 year (7 scenarios) and 6 years (2 scenarios) (Table 4).

What would happen if the demographic parameters change?

Bearing in mind that productivity and survival rates may vary, another Box–Behnken design was constructed, evaluating the importance and effect of variations in these demographic parameters in combination with several types of extractions.

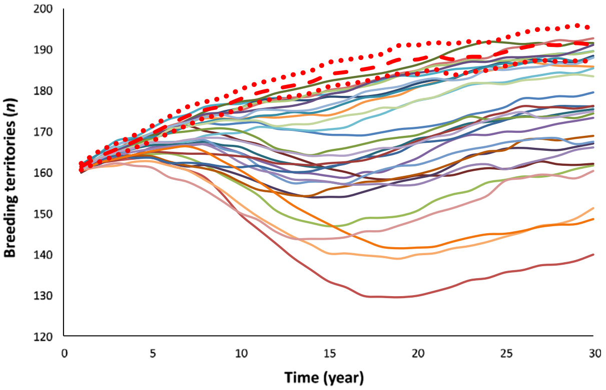

Figure 3 Projections of the number of Bearded Vulture territories in the Pyrenees over time as predicted under different combinations of extraction scenarios, using the currently estimated (mean values) for demographic parameters (Table 1). The red line shows the population trend without any intervention. The dashed line is the 95% CI. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

The results show that all four factors (productivity, juvenile survival, subadult survival and adult survival) had a significant effect on the number of breeding territories, with the most significant effects resulting from variations in productivity and adult survival rates (Fig. 4; Table 5). The duration of the intervention had no statistically significant effect due to the overwhelming effects of the other factors. According to our results, an increase in juvenile mortality (up to 0.086) resulted in a breeding population loss of seven breeding territories after 30 years. If an increase in mortality occurred in the subadult age-class (up to 0.055), the impact would be a loss of 20 breeding territories. Finally, in the case of adults (up to 0.055) 66 breeding territories would be lost. On the contrary, if the survival rates of all age-classes are maintained at the current levels (Table 1), but productivity falls (to 0.25 chicks/pair/year), 57 breeding territories would be lost after 30 years.

Table 4. Extraction scenarios that do not have a significant impact (95% CI) on the Pyrenean Bearded Vulture source population trend over a 30-year scenario

Removal scenario			
Clutches	Juveniles	Adults	Years
5	0	5	1
0	5	5	1
10	5	5	1
5	5	0	1
5	5	10	1
0	0	5	6[a]
5	10	5	1
5	0	0	6[a]
0	5	5	1

[a] The five removals happen annually.

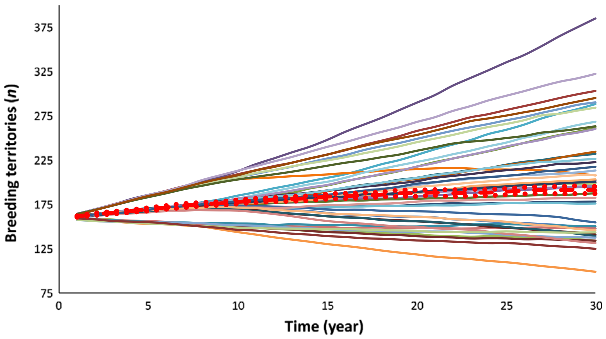

Figure 4 Projections of the number of Bearded Vulture territories in the Pyrenees over time as predicted under different combinations of demographic parameters and extraction scenarios, using the range (minimum–maximum) of demographic parameter values and extraction timeframes (Table 2). The red line shows the population trend without any intervention. The dashed line is the 95% CI. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

Discussion

For threatened species, removal of individuals from the wild for reintroduction projects or to create a captive population could compromise the source population both due to the loss of the individuals extracted and because the population becomes more vulnerable to stochastic events (Margalida *et al.*, 2015; Heinrichs *et al.*, 2018; Heinrichs *et al.*, 2019). The simulations presented here offer sufficient evidence to assist managers and policy-makers to adopt the most rigorous and effective management measures for the restoration of European Bearded Vulture populations, without undue harm to the source population. These models, linked to various removal scenarios, could enable managers and policy-makers to develop objective-based conservation trade-offs in current conservation projects to reinforce or reintroduce sub-populations of the species.

Until now, the Pyrenean Bearded Vulture population has been managed using two types of extractions: (1) the regular removal of clutches, started in 2008 and still ongoing (about five clutches are currently removed annually); and (2) the extraction of non-territorial adults, started in 2018 (when two adults were removed). To explore a broader spectrum of possible extraction scenarios we added a third option as an alternative: the extraction of trapped 1 year old juveniles. This new simulated scenario could provide an alternative to reintroductions using fledglings derived from captive rearing projects which are then hacked out into the wild.

With 164 breeding territories, the Pyrenees harbour the most important population of wild Bearded Vultures in Europe. This population is characterized by a progressive increase in breeding territories and, in parallel, a density-dependent decrease in productivity (Carrete *et al.*, 2006). In addition, there has been an increase in the fraction of non-territorial but potential breeders (i.e. mature floaters > 6 years of age), from 39% in 2006 to 68% in 2015 (Antor *et al.*, 2007; Margalida *et al.*, 2015). This situation prompted a technical-scientific debate regarding the need and opportunity to remove clutches and floating individuals for use in reintroduction programs (Ferrer *et al.*, 2014; Margalida *et al.*, 2015; Margalida *et al.*, 2017*b*).

Table 5. Coefficient values of the response surface (number of breeding territories) and significance levels of the variables and interactions that were tested using a range (minimum–maximum) of demographic parameter values and extraction timeframes (Table 2)

	Estimate	SE	*t* value	*P*
Intercept	200.170	2.479	80.731	**0.0001**
Productivity	56.946	1.240	45.934	**0.0001**
Juvenile mortality	−7.144	1.240	−5.762	**0.0001**
Subadult mortality	−19.869	1.240	−16.027	**0.0001**
Adult mortality	−80.053	1.240	−64.573	**0.0001**
Years	−2.071	1.240	−1.670	0.108
Productivity × juvenile mortality	−6.962	2.479	−2.808	**0.010**
Productivity × subadult mortality	−7.617	2.479	−3.072	**0.005**
Productivity × adult mortality	−32.075	2.479	−12.936	**0.0001**
Productivity × years	1.477	2.479	0.596	0.557
Juvenile mortality × subadult mortality	1.622	2.479	0.654	0.519
Juvenile mortality × adult mortality	2.315	2.479	0.934	0.360
Juvenile mortality × years	0.925	2.479	0.373	0.712
Subadult mortality × adult mortality	8.437	2.479	3.403	**0.002**
Subadult mortality × years	−1.030	2.479	−0.415	0.682
Adult mortality × years	0.340	2.479	0.137	0.892
Productivity^2	−1.203	1.825	−0.659	0.516
Juvenile mortality^2	−0.590	1.825	−0.323	0.749
Subadult mortality^2	1.202	1.825	0.659	0.516
Adult mortality^2	13.627	1.825	7.468	**0.0001**
Years^2	1.184	1.825	0.649	0.523

Statistically significant results are shown in bold type.

Our results show that of the three scenarios modeled, juvenile removal has twice the impact on the source population compared with the extraction of clutches or non-territorial adults. This is due to the fact that juveniles preserve intact their probabilities of beginning reproduction (from 6 years old onwards) whereas non-territorial adults (≥10 years), have lost part of their potential reproductive probabilities. However, reintroduction using juveniles is the principle management strategy used to reintroduce the species in Europe (i.e. hacking fledgling individuals from captive breeding) and is the most successful in many different European projects (see Schaub *et al.*, 2009), although our results show that, in the wild, its impact on the source population is substantial. Therefore, from a conservation point of view, the extraction of clutches and non-territorial adults is preferable to the removal of juveniles. In the case of clutch removal, the extraction should be focused on low quality territories with low breeding success to reduce the demographic impact on the source population. In this sense, in future work it would be necessary to estimate the number of removals that could occur (Margalida *et al.*, 2017*b*) without a negative impact if the removals were to be from these low quality territories (i.e. with low breeding success). This could potentially be an optimal management approach because releasing juveniles into the reintroduction site may be of benefit to the reintroduced population (i.e. potentially higher release site fidelity and high reproductive potential) with relatively low impact on the source population.

The next question is how many clutches and/or non-territorial adults could be removed from the Pyrenean population for use in reintroduction projects elsewhere in Europe without affecting the source population. There are several ways to view this question. First, from a conservation biology perspective, there is an argument that the Pyrenean population should be conserved through management programs and not subject to the removal of individuals. As such, reintroduction programs should focus on species recovery in existing reintroduction areas, but do not justify extractions from source nuclei. Expanding the species' range should prioritize alternative reintroduction methods such as captive breeding, management of supplementary feeding sites and so on and the removal of wild birds from existing populations should not be the first option. Second, we need to be cautious regarding the projections forecast here because some scenarios show no impact at the 95% CI (Table 4), indicating the pronounced influence of stochastic variations. The demographic parameters that we used in the models (survival and productivity) may be considered optimistic and their true values may well be lower (e.g. the falls in productivity resulting from density-dependent factors) and mortality values could increase as a result of non-natural factors such as illegal poisoning (Margalida, 2012). In this regard we can confirm that the observed mean values of subadult and adult survival rates (*c.* 0.96) are the most accurate so far obtained for this species in our study area and are higher than the 0.88 reported by Oro *et al.,* (2008) and comparable to that of reintroduced populations in the Alps (0.96, Schaub *et al.*, 2009). The current mean values of productivity in our density-dependent model are c. 0.38 chicks/pair/year; higher than those recorded during the previous 5 years (0.32 chicks/pair/year) and on the southern side of the Pyrenees (0.29; Margalida *et al.*, 2014). Therefore, all of the model projections based on rates of survival and productivity higher than the current observations (Table 2) can be considered relatively unlikely (Fig. 4). To assess the effects of parameter variations we constructed a second Box–Behnken design which showed that population size is very sensitive to productivity rate. A decrease in productivity to 0.25 chicks/pair/year suggests that 57 pairs would be lost from the breeding population after 30 years. An increase in subadult and adult mortality predicts a substantial slowing of population growth. For example, an increase in subadult mortality (up to 0.055), predicts a loss of 20 breeding territories and similarly in adults, a loss of 66 breeding territories. Our results therefore suggest that even in a long-lived species such as the Bearded Vulture, population size and viability are very sensitive to changes in adult mortality (Saether & Bakke, 2000) but also productivity. Productivity also seems to exert a very strong effect on population viability in other species (see Genovart, Oro & Tenan, 2018). In addition, since population growth is very sensitive to adult survival rate, the extraction of floating adults should also have substantial demographic effects. It is therefore important to know the true effect of extractions in order to avoid levels which would leave a population vulnerable to damage from stochastic increases in mortality or reductions in productivity. It should be noted that our models assume that extractions of floating adults are homogenous across all age classes between 10 and 20 years. Therefore, some of the individuals extracted from the Pyrenean population could be potential breeders (mainly those between 10 and 14 years old), while others (from 15 to 20 years old) could be extracted with less demographic impact. However, because the priority of reintroductions is to establish a viable or self-sustaining population at the new site, it seems imperative to evaluate trade-offs between objectives, and the benefits through a structured decision-making framework when faced with such complex decisions (Seddon *et al.*, 2007; Converse *et al.*, 2013). For example, the experimental reintroduction of non-territorial 15- to 20-year-old individuals would have less demographic impact on the source population but these individuals would have low probability of breeding at the release site. The post-release dispersal behavior of individuals released as adults is unknown, and there is a possibility they could return immediately to the natal site. As such, there could be benefit in reintroducing 15–20 year old birds to improve knowledge about management options available to maximise site fidelity.

How many clutches and non-territorial adults could be removed?

Focusing on management by the removal of clutches and non-territorial adults, our results suggest that there are only three scenarios inside the 95% CI (i.e. those that do not affect the source population size after 30 years): (1) the removal of five clutches and five non-territorial adults during a single year; (2) the annual removal of five non-territorial adults during a 6-year period; and (3) the annual removal of five clutches during a 6-year period. We identify a limiting temporal removal scenario of 6 years in which two removal actions are combined (i.e. clutches and non-territorial adults) rather than extractions concentrated into a single year. All the rest of the combinations modelled will have detrimental effects on the dynamics of the source population, although some of the forecast trajectories showed population growth. This is because selective harvesting can indirectly increase recruitment, thereby potentially impacting population growth rate (Milner, Nilsen & Andreassen, 2007). Furthermore, our simulations show that the effects of extractions will not be detectable until 10–15 years after the start of such interventions. Therefore, applying the precautionary principle, interventions in the Pyrenean Bearded Vulture source population should be performed with caution. As an experimental project, the extractions could focus on floating individuals >15 years, which should have a lower demographic impact and allow an increase in the number of extractions without undue population effects. A next step would be to use GPS transmitters to monitor the behavior of translocated individuals and their success in settling into their new locations in order to fine-tune future management procedures. With respect to clutch extractions, we suggest there would be value in future work to evaluate the impact of removing clutches from high-quality versus low-quality habitat. For example, removal of clutches from low quality habitat potentially has a lower demographic impact (Margalida *et al.*, 2017*b*) and would allow an increase in the number of extractions without undue population effects.

Concluding remarks

Our simulation approach provides a vital tool for planning the management and conservation of a threatened long-lived population and for making objective decisions regarding trade-offs in future reintroduction projects (Converse *et al.*, 2013; Lloyd *et al.*, 2019; Panfylova, Ewen & Armstrong, 2019). Quantitative modeling provides explicit predictions about future population trends and the uncertainty surrounding forecast population trajectories under different extraction regimes and allows the pros and cons of different removal alternatives to be assessed. Our results will be of value to decision-makers, allowing them to anticipate and avoid detrimental impacts on source populations. However, due to the inevitable stochastic changes in demographic parameters and the potential limitations of computational models, it is essential to constantly update future model replications with current observed parameter values when using theoretical models to implement management actions for threatened species, in order to increase credibility, efficiency and objectivity (Thiele & Grimm, 2015; Margalida *et al.*, 2018).

Acknowledgements

We thank R. Heredia, L.M. González, R. Moreno-Opo, GEPT, FCQ, J. Larumbe, P. Muñoz, M. Alcántara, R. Casanovas, D. Garcia, J. Ruiz-Olmo, I. Afonso, D. Campión, J.A. Sesé and M. Razin for providing data. The comments of two anonymous reviewers improved the manuscript. Andy Richford reviewed the English. This study was supported by Ministerio para la Transición Ecológica and by Ministerio de Economía y Competitividad (CGL2015-66966-C2-1-R2).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Definition of the parameters used in the PDP model.