

Use of simulation models to plan species reintroductions: the case of the bearded vulture in southern Spain

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(Received 12 December 1997; accepted 16 April 1998)

Abstract

I used VORTEX to make a prior evaluation of the planned reintroduction project of the endangered bearded vulture (*Gypaetus barbatus*) in the mountains of southern Spain. The minimum size of a captive population needed to ensure the release of two bearded vulture fledglings per year is 30 individuals. If breeding success was improved, this minimum captive population could be reduced to 10 individuals. As the cost of the project is proportional to the size of the captive population, some research effort should be devoted to improving breeding success in captivity. The current size of the captive population — four individuals — is not enough to start the releases, even if the vultures were already breeding. The first step for the project should be to increase the size of the captive population. If on average one individual per year was added to the captive population, it would take 15 years to reach 30 individuals. If breeding in captivity was improved, it would take only three to seven years to reach the minimum captive population of 10 individuals. Once releases were started, the project would need on average 20 years to reach a goal of 15 adult pairs in the Cazorla mountains. Both the success of the project and the time necessary to reach this stated goal are very sensitive to the mortality rates in the wild. There is little known about these rates, and better estimates are urgently needed to improve the predictions of the models.

INTRODUCTION

Computer simulation models have become a popular tool for estimating the probability of extinction, time to extinction, population trajectory and loss of genetic variability of small populations (Lindenmayer, Cunningham, Tanton & Smith, 1990; Lindenmayer, Cunningham, Tanton, Nix *et al.*, 1991; Armbruster & Lande, 1993; Haig, Belthoff & Allen, 1993; Swart, Lawes & Perrin, 1993; Doak, Kareiva & Klepetka, 1994; Possingham *et al.*, 1994; Akçakaya, McCarthy & Pearce, 1995; Lindenmayer & Lacy, 1995; Maguire, Wilhere & Dong, 1995; Gaona, Ferreras & Delibes, in 1998). Although they have been used to predict the future fate of certain populations, their main strength is in their ability to evaluate different management alternatives in small populations. They can be used to provide estimates of the probability of success, the time necessary to succeed (or cost of different management actions) and a quantitative evaluation of the different alternatives (Maguire & Lacy, 1990; Maguire, Lacy, *et al.*, 1990; Lindenmayer & Possingham, 1996; Gaona *et al.*, 1998).

Sensitivity analysis of the models can indicate how dependent the conclusions are on the parameters used (Armbruster & Lande, 1993; Doak *et al.*, 1994; McCarthy, Burgman & Ferson, 1995; Bustamante, 1996). So population viability analyses (PVAs) can be used as a tool to guide research efforts in the conservation biology of endangered species (Hamilton & Moller, 1995; Bustamante, 1996; Gaona *et al.*, 1998).

Computer simulation models have been used for *post hoc* evaluation of species reintroduction projects. They have been used to determine whether current practices are still adequate, whether the projects could be improved, or whether the reintroduction should continue (Bustamante, 1996; Green, Pienkowski & Love, 1996; Nolet & Baveco, 1996). The novel aspect of this study is that I used simulation models to make a prior evaluation of a reintroduction project to quantify the project goals and time scale, to evaluate management alternatives, and to identify where research effort is urgently needed.

The bearded vulture

The bearded vulture (*Gypaetus barbatus*) is a cliff-nesting accipitrid vulture inhabiting the mountain ranges in Europe, Asia and Africa, and feeds predominantly on

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bones (Cramp & Simmons, 1980; Brown & Plug, 1990). Its breeding range in Europe has suffered a progressive reduction during the 19th and 20th centuries, and it is now restricted to the Pyrenees, southern Balkans and the Islands of Corsica and Crete (Hiraldo, Delibes & Calderón, 1979; Frey, 1994).

The causes of the bearded vulture decline in Europe have been direct persecution, e.g. the killing of adults and the stealing of eggs and chicks, and indirect mortality caused by poison baiting (Hiraldo *et al.*, 1979; Cramp & Simmons, 1980). The population in the mountains of southern Spain declined as a result of direct human persecution during the 20th century (Hiraldo *et al.*, 1979). It became extinct in 1987, when the last territorial adult in the Cazorla mountains disappeared (Donazar, 1993; Frey, 1996). The species is legally protected in Spain and direct human persecution is no longer a problem in the reintroduction area.

Bearded vulture reintroduction projects

The bearded vulture is presently being reintroduced in the European Alps (Frey & Walter, 1989; Frey & Bijleveld, 1993). This is an international project that started in 1978 with a captive population of 30 individuals (Frey & Walter, 1989). In 1986 the first four bearded vultures born in captivity were released in Austria. By 1995 the captive population within the project comprised 96 individuals and a total of 60 captive-born birds had been released into the Alps (Frey, 1995a, b).

The *Consejería de Medio Ambiente de la Junta de Andalucía* (environmental agency of the regional government of Andalusia) started a reintroduction project to re-establish the species in its former range in the mountains of southern Spain in 1996. A captive breeding station was built in the Cazorla Protected Area and started operation in 1997 with four captive bearded vultures. It is planned that birds born in captivity from this population will be reintroduced to the wild, beginning in the Cazorla mountains. The first goal of the Cazorla Project is to re-establish the bearded vulture population of the Cazorla mountains, which was estimated by J. A. Donazar, F. Hiraldo and J. Bustamante (unpub. data) at 15 breeding pairs. This would be the first step in re-establishing the former bearded vulture metapopulation in the mountain ranges of southern Spain. The Alpine experience shows that re-establishing a bearded vulture population is a slow and costly process. Considering that money for wildlife conservation is limited and that time, money and effort invested in one project are withdrawn from other projects, it is important to estimate how much investment is necessary in the Cazorla Project to guarantee its success. Models can be a very useful tool for this. They (1) force us to define quantitative goals in the project, (2) allow us to estimate the probability of reaching those goals in a certain time frame, (3) allow us to compare alternative management actions by assessing their ability to reach the project goals or to reduce project costs, (4) allow us to evaluate whether the information available for the models is sufficient, especially

concerning the demographic parameters which have more influence on the success of the project.

In the present paper I used simulation models to answer the following questions regarding the Cazorla Project. (1) What should be the minimum size of a captive population before releases to the wild can be started? (2) How long would it take for the captive population to reach this size? (3) If demographic parameters in the captive population were improved, what would be the effect on the previous questions? (4) For how long would it be necessary to release bearded vultures in Cazorla to reach a population of 15 breeding pairs? (5) Is the information available on demographic parameters of the bearded vulture sufficient to answer these questions?

METHODS AND MATERIALS

I used the computer program VORTEX v 7.00 (Lacy, 1993) to simulate deterministic and stochastic factors affecting the population dynamics of bearded vultures. VORTEX, a Monte Carlo simulation of demographic events, models population processes as discrete, sequential events, with probabilistic outcomes determined by a pseudo-random number generator. VORTEX simulates birth and death processes and the transmission of genes through generations by generating pseudo-random numbers to determine whether each animal lives or dies, which adult female pairs with each adult male, whether a paired adult female produces a brood of a given size each year, offspring sex, and which of two alleles at a genetic locus are transmitted from each parent to each chick. I used stochastic models instead of deterministic ones because the populations I was interested in were small and could be very much affected by demographic, environmental or genetic stochasticity or by catastrophic events. I used VORTEX instead of building my own simulation model because VORTEX can simulate the population dynamics of bearded vultures and has been extensively tested (Akçakaya, 1992; Lacy, 1993; Lindenmayer, Lacy *et al.*, 1993; Kurzweil, 1994; Bustamante, 1996).

Three simulation models were built using VORTEX.

Model 1

To estimate the minimum captive population necessary for the reintroduction project, I simulated captive populations of variable founder size (4–100 individuals) with a constant harvest rate (release to the wild of two fledglings per year) and without supplementation during the simulations. I considered two scenarios. The first scenario used the demographic parameters from the population held in captivity in European zoos between 1973 and 1993 for the Alpine Project (Bustamante, 1996). The second scenario considered the possibility of improving the breeding rate in captivity by increasing hatching success to 70% and performing 'egg-pulling' so that females that lay produce one egg more per year on average (Table 1).

Table 1. Summary of VORTEX initial values in Model 1: captive population of variable initial size with constant releases and no supplementation.

Type of matching system: monogamous			
Age at first reproduction: 7 years			
Age after which adults do not reproduce: 31 years			
Sex ratio at birth (proportion of males): 0.5			
Fecundity rates			
	Scenario 1	Scenario 2	SD
Maximum clutch size	4 eggs	5 eggs	
Females laying 0 egg:	28.14%	28.14%	17%
Females laying 1 egg:	21.82%	0.00%	
Females laying 2 eggs:	46.16%	21.82%	
Females laying 3 eggs:	3.48%	46.16%	
Females laying 4 eggs:	0.40%	3.48%	
Females laying 5 eggs:	—	0.40%	
No density dependency in fecundity rates			
Mortality rates			
	Scenario 1	Scenario 2	SD
Juveniles (0–1 year) ^a	65.90%	48.93%	25.00%
Inmatures (2–6 years)	1.11%	1.11%	4.03%
Adults (7–31 years)	3.33%	3.33%	3.07%
No correlation between mortality and fecundity annual rates			
Inbreeding depression: recessive lethal model			
Probability of a catastrophe: 1% ^b			
Multiplicative effect on fecundity: 0.25			
Multiplicative effect on survival: 0.50			
Initial population: variable size with stable age distribution.			
Population sizes modelled (4, 6, 8, 10, 15, 20, 25, 30, 35, 40, 50, 60, 75 and 100 individuals)			
Carrying capacity: projected at 100 individuals			
Releases: 1 juvenile male and 1 juvenile female per year			
1000 simulations of 100 years			

^a Includes: 46.76% hatching success in scenario 1 (70.00% hatching success in scenario 2) plus 78.93% nestling survival and 92.3% first year, post-fledgling survival.

^b Risk of an epidemic or a fire in captive breeding facilities.

Model 2

To estimate how long it would take to reach a certain captive population size, I simulated populations of a fixed founder size (four individuals), without harvest, and supplemented with external birds. Supplementation rate varied from zero to four individuals per year. I considered four scenarios: (1) the demographic parameters of the captive population of the Alpine Project, (2) the breeding rate improved only by 'egg-pulling', (3) the breeding rate improved only by increasing hatching success to 70%, and (4) both improvements combined (Table 2).

Model 3

To estimate how long it will take to re-establish 15 breeding pairs in Cazorla I simulated wild populations supplemented at a rate of two fledglings per year. The breeding rate for the wild populations was that recorded for territorial females in the southern slopes of the Pyrenees, Northern Spain, between 1973 and 1993 (Heredia, 1991; Table 3). Mortality rates varied between scenarios and were based on mean and maximum estimates from captive-born bearded vultures reintroduced in the Alps (Bustamante, 1996) and mortality estimates from individually marked wild birds in the Pyrenees

Table 2. Summary of VORTEX initial values in Model 2: captive population of fixed initial size, no releases and variable supplementation rate.

Fecundity rates			
	Scenario 1 and 3	Scenario 2 and 4	SD
Maximum clutch size	4 eggs	5 eggs	
Females laying 0 egg:	28.14%	28.14%	17%
Females laying 1 egg:	21.82%	0.00%	
Females laying 2 eggs:	46.16%	21.82%	
Females laying 3 eggs:	3.48%	46.16%	
Females laying 4 eggs:	0.40%	3.48%	
Females laying 5 eggs:	—	0.40%	
Mortality rates			
	Scenario 1 and 2	Scenario 3 and 4	SD
Juveniles (0–1 year)	65.90%	48.93%	25.00%
Inmatures (2–6 years)	1.11%	1.11%	4.03%
Adults (7–31 years)	3.33%	3.33%	3.07%
Initial population: 4 individuals with stable age distribution.			
Supplementation rate: variable (0, 0.5, 1, 2 and 4 individuals per year)			
1000 simulations of 30 years			

Parameters not mentioned remain as in Table 1

Table 3. Summary of VORTEX initial values in Model 3: reintroduced population with a constant annual release rate in different demographic scenarios.

Fecundity rates^a				SD	
Maximum brood size at fledging :				1	
Females raising 0 fledgling :				33.0%	
Females raising 1 fledgling :				67.0%	
Mortality rates^b					
	Pyrenees	Alps (optimistic)	Alps (pessimistic)	SD	SD
Juveniles (1st year)	7.2%	13%	14.6%	15%	29.0%
Inmatures (2–6 years)	7.2%	13%	3.1%	6%	9.4%
Adults (7–31 years)	6.0%	6%	3.1%	6%	9.4%
Annual correlation between fecundity and mortality rates					
Probability of a catastrophe: 6.6% ^c					
Multiplicative effect on fecundity: 1 (no effect)					
Multiplicative effect on survival: 0.50 and 0.75					
Initial population: 2 individuals in their 1st year					
Carrying capacity: projected at 500 individuals					
Extractions: no extractions					
Supplementations: 1 male and 1 female in their 1st year are released annually					
1000 simulations of 100 years					

^a Annual cycle started when chicks fledge.

^b Mortality estimates from the Pyrenean population (R. J. Antor, pers. comm.) and an optimistic and pessimistic estimate from reintroduced birds in the Alpine Project (Bustamante, 1996).

^c Mortality risk from poisoned baits for carnivores simulated with two different mortality intensities.

Parameters not mentioned remain as in Table 1

(R. J. Antor, pers. comm.). The catastrophic effect of the illegal use of poisoned baits was also varied between simulations.

Justification of parameters used in the models

I assumed that the demographic parameters of the captive population of the Cazorla Project would not differ initially from those of the population kept in European zoos for the Alpine Project, for which there are extensive and well documented records (Frey, Knotzinger & Llopis Dell, 1995). The breeding rate in captivity potentially could be

improved (Bustamante, 1996). I considered as a reasonable scenario that hatching success could be increased to 70% (a conservative rate considering hatching rates in captivity for other raptors (Burnham, 1983; Carpenter, Gabel & Weinmeyer, 1987; Hartt *et al.*, 1994). It could also be possible to perform 'egg-pulling' (taking the first egg of the clutch after it is laid, to force the female to lay a second egg). This technique is currently used in other raptor captive breeding programs (Carpenter *et al.*, 1987). I assumed that this would increase by one egg the average clutch size of females that lay eggs. I assumed a 1% annual risk of an epidemic or a fire in the breeding station with the effect of a 75% decrease in the year's breeding rate and a 50% decrease in survival.

I assumed that the breeding rate for vultures reintroduced in Cazorla could be similar to that of the southern slopes of the Pyrenees (Heredia, 1991). This is the best known wild population and the one closest to Cazorla. Data on mortality rates in the wild are scarce so I decided to use all available estimates. The mortality rates from the Pyrenees were estimated from 10 juveniles and subadult birds marked with wing-tags and radiotransmitters between 1987 and 1995 (R. J. Antor, pers. comm.). Adult mortality rates in the Pyrenees were calculated considering the 5.5% annual growth rate of the population as recorded in annual censuses (Heredia, 1991). Mortality rates in the Alps were estimated from the time at death and resightings of 41 reintroduced juveniles between 1986 and 1992. The lack of a long-lasting marking method for released birds makes those estimates imprecise and I have used the mean and maximum mortality estimates from these data (see Bustamante, 1996).

Illegal poisoning of carnivores occurs sporadically in Spain when small carnivore populations increase. Bearded vultures have a high risk of being poisoned if poisoned baits are used (Hiraldo *et al.*, 1979). Poisoned baits could be used illegally in neighbouring areas and bearded vultures are known to have very large home ranges, up to 700 km² (Brown, 1988; Sunyer, 1991). I have assumed a 6.6% annual risk in the use of poison (estimated from an observed 15-year interval between successive peaks in the illegal use of poison in Spain). There is no quantitative information on the effect of the use of poison on the population. Survival during periods of poison usage was varied between 50 and 75% of that during the non-poison years.

For release rates to the wild, I have used an annual release of a male and a female in all cases. This would be the minimum desirable release rate. Juvenile bearded vultures have a certain social behaviour (Sunyer, 1991) and it is assumed that presence of other juveniles is necessary for normal development (Frey & Walter, 1989; Frey & Bijleveld, 1993).

RESULTS

Model 1

I considered that an initial captive population size is 'out of danger' when the probability of extinction is less than

5% in 100 years. To be able to maintain a release rate to the wild of two fledglings per year, with current bearded vulture demographic parameters, it would be necessary to have a captive population of 30 vultures for the Cazorla Project (Fig. 1). There are other demographic estimates derived from the models that also support this criterion. The captive population growth rate also indicates the maximum possible harvest rate. Captive populations under 10 individuals with a constant release of two fledglings per year would have a negative growth rate — they would inevitably become extinct. With more than 30 individuals in captivity, population growth rate is barely affected by population size (Fig. 2). On the other hand, with less than 20 individuals in captivity in most years there would not be enough fledglings to reach the goal of releasing one male and one female per year (actual release rate would be around 1.2 fledglings per year). With over 30 individuals, the actual release rate tends to stabilize at around 1.5 fledglings per year (actual release attained would be three male–female pairs every four years). If we consider the heterozygosity of the founder population after 100 years, a population of 20 individuals would maintain 90% of the initial heterozygosity. Founder populations of more than 20 individuals would only slightly increase the genetic variability maintained after 100 years (Fig. 3).

If the demographic parameters of the captive populations are improved, by simultaneously raising hatching success up to 70% and performing 'egg-pulling', a captive population as small as eight bearded vultures could be considered 'out of danger' (Fig. 4). In this improved scenario, even a captive population of four individuals would have a positive growth rate. With over 10 individuals in captivity, the annual growth rate of the population almost reaches an asymptote of 11% (Fig. 2). The actual release rate to the wild stabilizes with captive populations over 10 individuals, at around 1.8 fledglings per year. However, it would be necessary to have at least an initial population of 30 individuals to maintain 90% of the heterozygosity for 100 years.

Model 2

A founder captive population of only four bearded vultures with no supplementation of individuals and no releases to the wild has a very high extinction risk (> 15% in 30 years). Only by simultaneously improving hatching success and performing 'egg-pulling' is this extinction risk lowered to 5% in 30 years (Fig. 5). On the other hand, a captive population of only four individuals, provided it survives, would require more than 30 years to reach a population size of 30 individuals. Improved breeding rates could reduce this time interval to 15 years (Fig. 6). If the supplementation rate of new bearded vultures to the captive population was around one individual per year (a reasonable figure considering the rate bearded vultures have been found injured in the Pyrenees in recent years), the effect would be comparable to an improvement in the breeding rate and it would

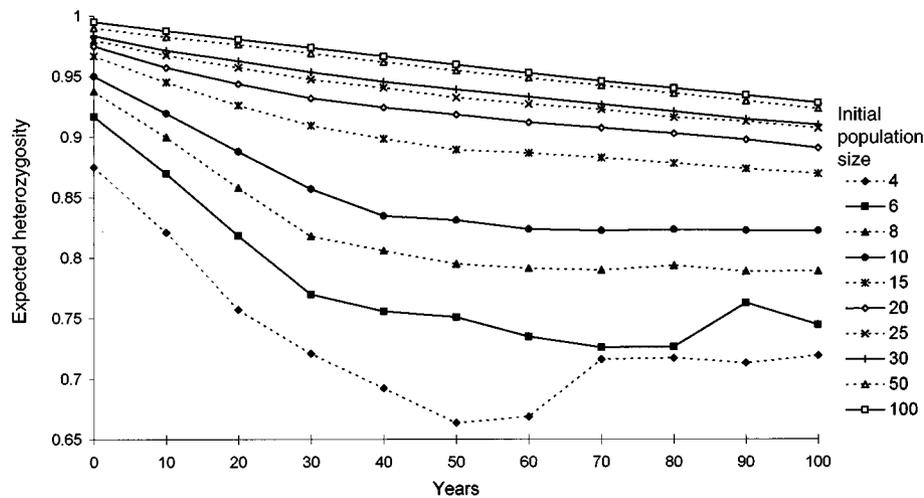


Fig. 3. Expected proportion of initial heterozygosity remaining with time in captive bearded vulture populations of different initial sizes with current demographic parameters.

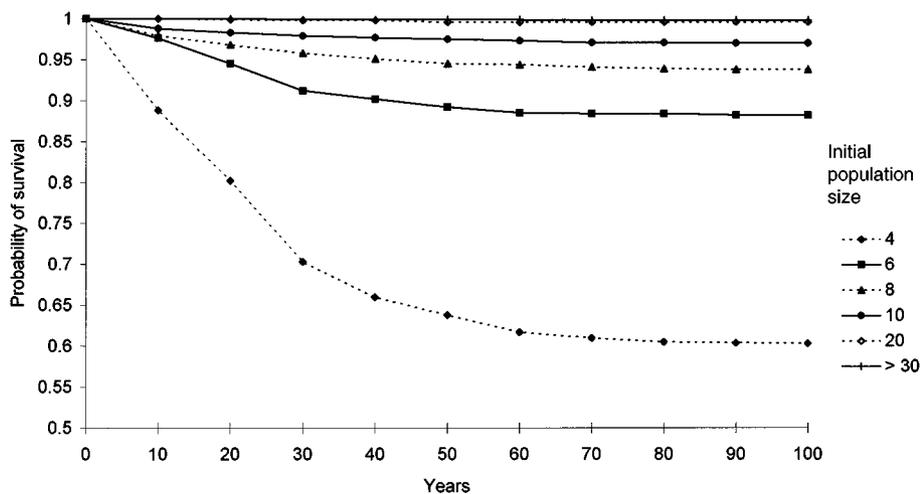


Fig. 4. Probability of survival of captive bearded vulture populations of different initial sizes with improved breeding and constant extraction of 1 male and 1 female per year for release.

of poisons on the levels simulated here has an important effect on average population trajectories.

Considering the most optimistic scenario, we would need on average more than 20 years of constant releases to reach 15 bearded vulture adult females in Cazorla. Considering the variability of the individual trajectories of the simulations we could need between 15 and 40 years to reach 15 pairs (Fig. 8). In the most pessimistic scenario we would need a minimum of 35 years to reach 15 pairs, but this scenario also includes population trajectories that do not reach 15 pairs after 100 years (Fig. 9).

DISCUSSION

Although I have estimated the genetic variability remaining in a captive population using VORTEX, these results

should be taken with caution. VORTEX is not able to simulate the fact that bearded vultures, once paired, will breed with the same partner for most of their life. On the other hand, little is known about the quantitative effect of inbreeding depression in birds and the only two bearded vulture populations studied so far have low genetic variability (Negro & Torres, 1998). With this little information I decided to use a simple recessive lethal model for inbreeding depression (Lacy, 1993). The result that improving breeding rate requires a bigger captive population to maintain the same amount of initial genetic variability is an artefact of the simulations. For the estimate of genetic variability, VORTEX uses only those populations that survive. With present breeding parameters the populations that lose variability become extinct more easily and do not contribute to the estimate

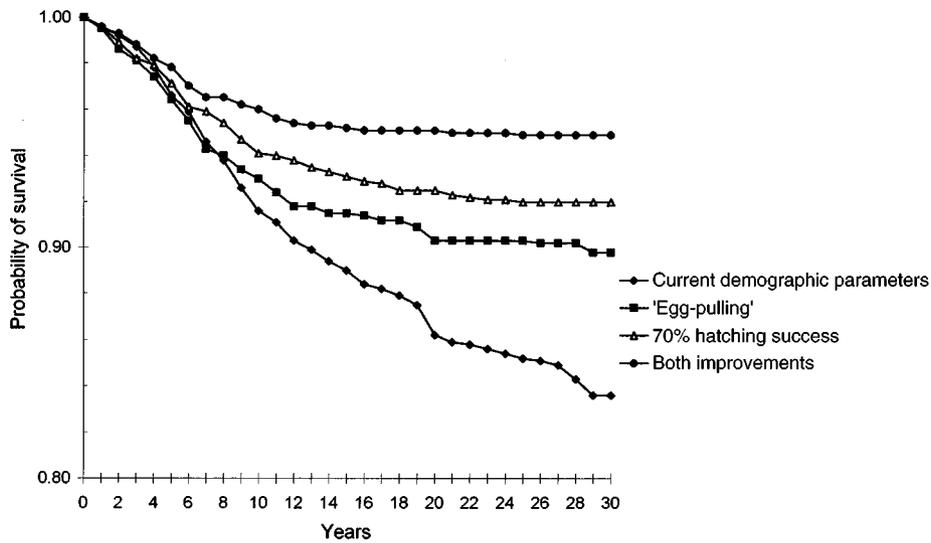


Fig. 5. Probability of survival of a captive bearded vulture population of four individuals with no supplementation and no releases in four different demographic scenarios.

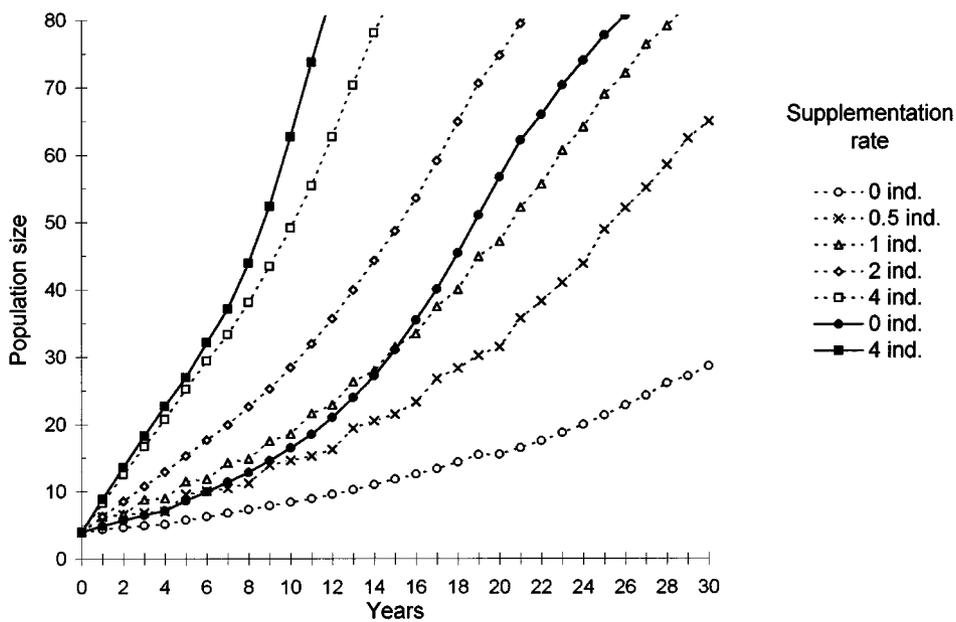


Fig. 6. Mean population trajectory of surviving captive bearded vulture populations with no releases and different annual supplementation rates. Actual demographic parameters represented by dashed lines and open symbols. Breeding improved by ‘egg-pulling’ and 70% hatching success represented by continuous lines and filled symbols.

of genetic variability retained. This explains why, when initial population size is very small, mean genetic variability retained by the populations has an apparent recovery at the end (Fig. 3).

The minimum size of a captive population to assure the release in Cazorla of two bearded vulture fledglings per year with current demographic parameters is 30 individuals. Hatching success is the demographic parameter of the captive population that can be improved to the greatest extent (see Bustamante, 1996) and ‘egg-pulling’

is a breeding technique known to work with bearded vultures but not regularly used. If hatching success was improved to 70% and ‘egg-pulling’ was used, the minimum size of the captive population necessary for the Cazorla Project could be reduced to 10 individuals. The experience of the Alpine Project shows that the main cost is maintaining birds in captivity (Patchlakto, 1991), so reducing the minimum captive population size would reduce the total costs.

The models show that the current size of the captive

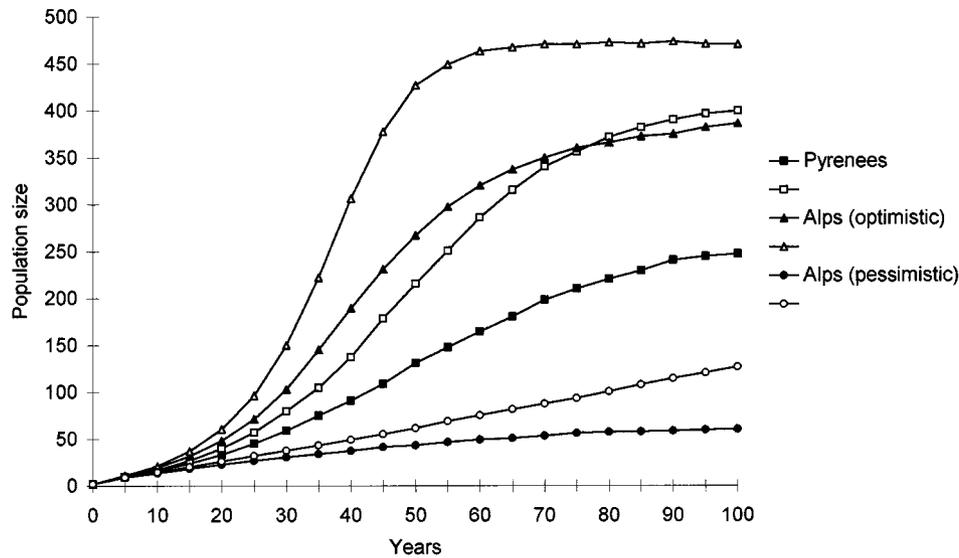


Fig. 7. Population trajectories of reintroduced bearded vulture populations with a constant release of one male and one female per year and different mortality rates. Open symbols represent a 25% reduction in annual survival due to the use of poisoned baits and filled symbols a 50% reduction.

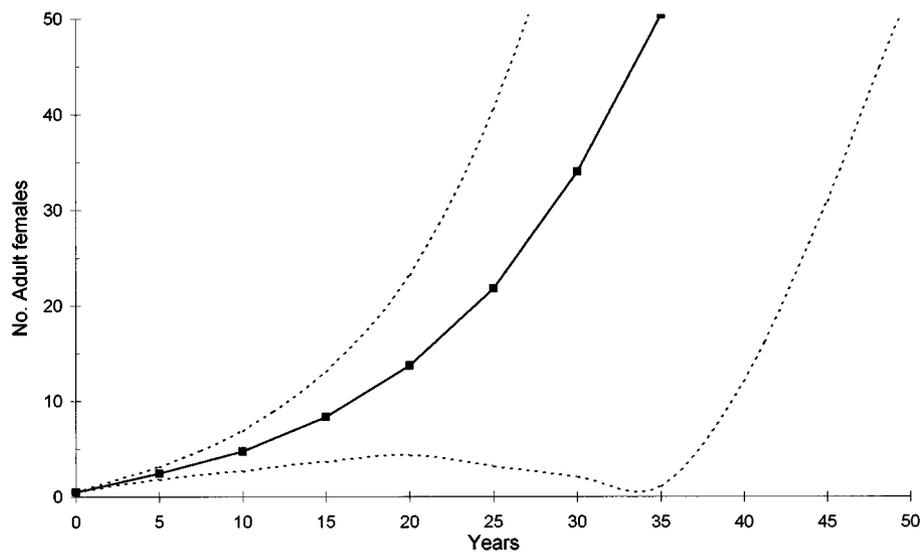


Fig. 8. Mean number of adult females in a reintroduced bearded vulture population with a constant release of one male and one female per year in the most optimistic scenario. Dashed lines represent the 95% confidence interval for individual simulation trajectories.

population in the Cazorla breeding station, four individuals, is not big enough to start releases, even if the birds were already breeding regularly. The first step should be to increase captive population size, and this can be attained in a reasonable period of time if new individuals are incorporated into the captive population. Improving breeding success has a similar effect but reaching the rates used in the simulations would already take some years. A reasonable supplementation rate would be one new individual per year, and probably could be obtained by simply adding birds from the Pyrenees that are found injured, or adding chicks that

may accidentally fall from nests to the captive population. With this supplementation rate it would take on average 15 years to reach a captive population of 30 individuals, which would be sufficient for the releases to start. If demographic parameters were improved, a captive population of 10 individuals would be enough and this could be reached in three to seven years.

Once the releases were started, the project would need on average 20 years to reach a population of 15 adult pairs in the area of Cazorla if mortality in the wild was as low as in my most optimistic scenario. Thus, the minimum duration of the project with the present demo-

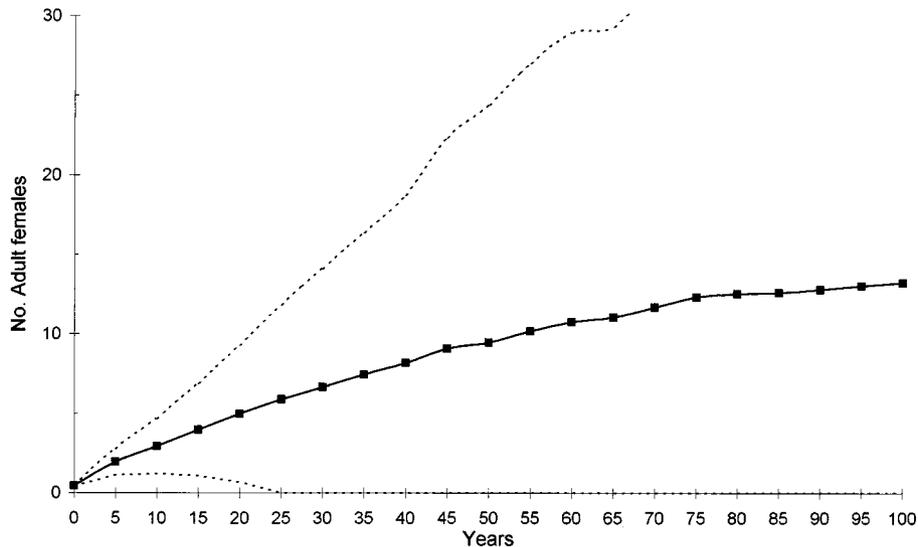


Fig. 9. Mean number of adult females in a reintroduced bearded vulture population with a constant release of one male and one female per year in the most pessimistic scenario. Dashed lines represent the 95% confidence interval for individual simulation trajectories.

graphic parameters and information actually available would be 35 years. This could be reduced to 23–27 years if the demographic parameters for the captive population were improved and this could mean a reduction of 23–34% in the costs.

The bearded vulture reintroduction project to southern Spain is a long-term project and commitment should be made to maintain investment long enough to guarantee its success. Both to reduce project costs and to guarantee its success, the size of the captive population should be increased as fast as possible and efforts to improve breeding rates should be carried out.

Demographic parameters in the wild are not well known and it is not known whether the estimates will apply to the birds released in Cazorla. The models show that population trajectories are very sensitive to mortality estimates, and the ones currently available are not precise enough. The duration of the project is very much affected by the mortality estimates, so it is very important that adequate mortality data are obtained from wild bearded vulture populations as well as from birds that will be released into the wild so that better simulation models can be used in the future.

This study shows that, even with limited knowledge on the demography of an endangered species, it is possible to set minimum time limits for successful reintroduction projects using simulation models. Also the models allow a prior evaluation of the management strategies and indicate where more information on the demography of the species is needed.

Acknowledgements

F. Hiraldo, J. A. Donázar and J. J. Negro made helpful comments on a previous draft of the paper. This study was funded by the Recovery Program for the Bearded

Vulture in Andalusia from the *Consejería de Medio Ambiente, Junta de Andalucía*, and by research projects PB93–0040 and PB96–0805 from DGICYT.

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