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Population Viability Analysis of Captive and Released Bearded Vulture Populations

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Abstract: *With the computer program VORTEX I ran a series of simulations of the Bearded Vulture (*Gypaetus barbatus*) population held in captivity in European zoos and of the population released in the Alps. The simulations showed that the risk of extinction of the captive population with the extraction rates currently in use is low. It seems possible to maintain the current release rate of two fledglings per year at each of the four release sites in the Alps, but it does not seem possible to increase the release rate by expanding the project to other European mountains without dangerously depleting the captive population. The models showed that the most effective way to increase the release rate without increasing the captive population size is by improving hatching success in captivity. The information on the demographic parameters of the Bearded Vulture population released in the Alps was not good enough to predict the ultimate fate of the present population or to allow for recommendations on how long the population should continue to be supplemented. Although it will be necessary to wait some years to see if Bearded Vultures are able to breed in the wild in the Alps and to estimate fecundity rates, it should be possible to improve the monitoring of the individuals released to obtain more-precise survival estimates. The models of the captive and released population also showed that it should at least be possible to have an artificially supplemented Bearded Vulture population in the Alps, but because this is not the goal of the present reintroduction project, the organizations involved should decide whether this is a politically or economically desirable goal.*

Análisis de viabilidad de poblaciones para las poblaciones cautiva y liberada de quebrantahuesos

Resumen: *Realicé una serie de simulaciones de la población de Quebrantahuesos (*Gypaetus barbatus*) cautiva en zoológicos europeos y de la población liberada en los Alpes con el programa VORTEX. Las simulaciones muestran que el riesgo de extinción de la población cautiva, con las tasas de extracción empleadas actualmente, es bajo. Parece posible mantener la tasa de liberación actual de dos pollos por año en cada uno de los cuatro puntos de suelta en los Alpes, pero no parece posible incrementarla para extender el proyecto a otras montañas europeas. Los modelos muestran que la manera más efectiva para aumentar la tasa de extracción sin aumentar el tamaño de la población cautiva sería mejorar el éxito de eclosión en cautiverio. La información a cerca de los parámetros demográficos de la población de Quebrantahuesos liberada en los Alpes no es lo suficientemente buena para predecir el destino final de esta población o para permitir hacer recomendaciones a cerca del tiempo que más debería continuar siendo suplementada. Aunque será necesario esperar algunos años más para ver si los Quebrantahuesos son capaces de criar en libertad en los Alpes y estimar su fecundidad, es posible mejorar el seguimiento de los ejemplares liberados para obtener estimas más precisas de su supervivencia. Los modelos de la población cautiva y liberada muestran, así mismo, que al menos sería posible mantener en los Alpes una población de Quebrantahuesos en libertad suplementada artificialmente; pero dado que este no es el objetivo final del proyecto de reintroducción actual las organizaciones implicadas deben plantearse si éste puede ser un objetivo deseable desde un punto de vista político o económico.*

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Introduction

Captive breeding of endangered species to reintroduce them to areas where they have disappeared or to supplement existing populations is frequently employed as a management tool (Newton 1979; Barclay 1987). These management actions are expected to increase the number of populations, their size, or the genetic variability within populations of the species concerned in order to decrease the probability of extinction.

Decisions on which species should have priority in reintroduction programs are usually subjective and based on politics, convenience, or public opinion pressure, although more-objective criteria are available. Once a reintroduction project is started and goals have been defined, it is possible to evaluate whether the management plan can meet the goals in a defined time frame. Money for conservation is limited, and funds employed in one project are sometimes withdrawn from others. Accordingly, it is important that the necessary information to evaluate whether goals are or will be accomplished be collected and analyzed.

Population viability analyses can be used as an objective tool to evaluate the risk of various management scenarios, to identify the demographic parameters to which the populations are more sensitive, and to indicate where research is more urgently needed to provide the information necessary for management of the population.

The Bearded Vulture (*Gypaetus barbatus*) is a cliff-nesting, accipitrid vulture inhabiting mountain ranges in Europe, Asia, and Africa and feeding predominantly on bones (Cramp & Simmons 1980; Brown & Plug 1990). Its breeding range in Europe has suffered a progressive reduction during the nineteenth and twentieth centuries. It is restricted now to the Pyrenees, the Southern Balkans, and the Islands of Corsica and Creta (Hiraldo et al. 1979; Frey 1994*b*).

The Bearded Vulture disappeared from the Alps, the northern limit of its historical range in Europe, in the nineteenth century (Cramp & Simmons 1980). Although it has been suggested that the cooling of the climate after the Middle Ages could have been responsible for the decline (Haller 1983), it is generally assumed that direct persecution—killing of adults and robbery of eggs and chicks—and indirect mortality caused by poison baiting of carnivores helped to eliminate the species (Hiraldo et al. 1979).

The idea to reintroduce the Bearded Vulture to the Alps was first suggested by Oskar Heinroth in 1924 (Géroudet 1979). In the early 1970s there was an initial attempt to introduce birds taken from the wild; three birds from Afghanistan were released in the French Alps. Because of difficulties in obtaining a regular supply of wild birds for release, the high mortality suffered by the birds, and the success of captive breeding by the Alpenzoo Innsbruck since 1973, the initial plan was changed to a captive breeding project (Géroudet 1979; Walter 1979). The Bearded Vulture Reintroduction Project started as an international project in 1978 and initially involved 17 zoological gardens and 10 nature conservation organizations from Austria, France, Germany, and Switzerland.

In 1978, with a captive population of 30 wild-caught individuals (Frey & Walter 1989), efforts were directed to increasing the captive population through breeding and by trying to incorporate into the project all the birds kept by different zoos. In 1986 the first four Bearded Vultures born in captivity were released in Hohen Tauern National Park, Austria. By 1993 the captive population within the project included approximately 100 individuals, 53 of which were wild-caught, and 50 captive-born birds had been released into the Alps.

According to Frey and Bijleveld (1993), the project objective is "the establishment of a [Bearded Vulture] breeding population [in the Alps] totally independent of human management intervention." Released birds have not reproduced yet, although individuals seem to have survived to breeding age (more than 6 years). It is assumed that releases will continue at least until birds start breeding successfully in the wild, if they ever do, but there are no clear statements on how it will be determined that the wild population requires no further management and that releases can be stopped. Considering that money for conservation is limited, it seems reasonable to ask how long it will be necessary to release birds into the Alps; if the information being gathered on the released birds is adequate to answer this question; if it would be possible—were an independent wild population not self-sustainable and the project objective was changed accordingly—to continue releases from the captive population at the present rate; and, because there is a continuing demand for Bearded Vultures for other reintroduction projects in areas where the species has recently disappeared, such as the Cantabric Mountains and the Cazorla and Segura Mountains in Spain (Heredia 1981) or the Balkans (Grubac 1994; Negus 1994), would the captive population be able to supply birds for these demands in a reasonable period of time.

I have used a population viability analysis (PVA) of the captive and released Bearded Vulture populations to try to answer these questions with the information available. The PVA did not indicate what the fate of the captive and released Bearded Vulture populations would be, but it gave an objective evaluation of the risk of present and future management actions, indicated which information is more urgently needed to improve the models and help in management decisions, and suggested points on which to focus research effort.

Methods

I used the computer program VORTEX 5.1 (Lacy 1993) to simulate deterministic and stochastic factors affecting the 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 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, the sex of the offspring, and which of two alleles at a genetic locus are transmitted from each parent to each chick.

I used a simulation model instead of a deterministic one because both the captive and released Bearded Vulture populations were small and they could face a significant risk of extinction due to demographic, environmental, or genetic stochasticity or due to catastrophic events even in situations in which the populations had a positive growth rate. I selected VORTEX because it is a well-known and well-tested program that could model reasonably well the Bearded Vulture population dynamics. Two populations were simulated, the captive population maintained in zoos and the population released in the Alps.

Simulations of the Captive Population

The demographic parameters used for the simulation model of the captive population (Table 1) were the average values observed in captivity between 1978 and 1993 and were calculated from the data published in the reports of the Bearded Vulture Reintroduction Project (Gypaetus Barbatus bulletin nos. 1 to 15; Bearded Vulture Annual Report 1993). The annual cycle was initiated at the time of egg laying, so hatching success (46.76%), nestling survival (78.93%) and first-year post-fledging survival (92.43%) were included in the estimate of first-year mortality (65.9%). I used an adult lifespan of 7 to 31 years in the models because females in captivity laid their first egg at the median age of 6.5 years ($n = 10$) and their last egg at a median age of 31 years ($n = 7$), excluding those that died in the same year they laid eggs for the last time. There were no reasons to suspect differences in age at maturity or lifespan between males and females. Observed annual mortality rate is three times higher in adult birds than in immature birds, probably because inexperience, which causes higher mortality rates among immature birds in the wild, does not affect mortality in captivity and because the adult age class probably includes senile individuals suffering higher mortality rates. There were no significant differences in mortality rates between males and females, so I used an average mortality rate for both sexes. Although females in the wild lay a maximum of two eggs, females in captivity have laid up to four eggs, even though efforts have been taken not to force double clutching within the captive breeding program. Initial age structure and population size (50 males and 39 females) were those of the captive population in January 1993. Adult males ($n = 9$) and females ($n = 5$) of unknown age were given an age at random between 7 and 31 years. Three individuals of unknown sex (they had not bred and were 1, 8, and 12 years old) were given at random the sex of male, female, and male respectively. There is no information on the risk of a catastrophe. I thought it reasonable to assume that there could be a 1% probability of a fire or an epidemic in The Vienna Breeding Unit (Austria) that holds 30% of the captive population and approximately 50% of the successful breeding pairs, and that this could result in the mortality of half the birds (0.85 multiplicative effect on survival) and no breeding at the Vienna Breeding Unit in that year (0.5 multiplicative effect on reproduction). There were another 27 zoos collaborating in the project in 1993, each keeping between one and six Bearded Vultures. Matings in the project are not at random as assumed by VORTEX, which makes the program inadequate to simulate the genetics of the captive popu-

Table 1. Summary of initial values for VORTEX for the captive population of Bearded Vultures.

Type of mating system: monogamous
Age of first reproduction: 7 years
Age after which adults do not reproduce: 31 years
Sex ratio at birth (proportion of males): 0.5
Fecundity Rates
  Maximum clutch size: 4 eggs
    Females laying 0 egg: 28.14%, SD = 16.88%
    Females laying 1 egg: 21.82%
    Females laying 2 egg: 46.16%
    Females laying 3 egg: 3.48%
    Females laying 4 egg: 0.39%
  No density dependency in fecundity rates
Mortality Rates
  Juveniles (0-1 year): 65.90%,[a] SD = 25.06%
  Immatures (2-6 year): 1.11%, SD = 4.03%
  Adults (7-31 year): 3.33%, SD = 3.07%
No correlation between mortality and fecundity annual rates
No inbreeding depression
Probability of a catastrophe: 1%[b]
  Multiplicative effect on fecundity: 0.5
  Multiplicative effect on mortality: 0.85
Initial population: 50 males and 39 females more than 1 year old[c]
Carrying capacity: projected at 200 individuals

[a] *Includes 46.76% hatching success, 78.93% nestling survival, and 92.43% first-year, post-fledging survival.*
[b] *See methods for justification.*
[c] *Initial age distribution was that of the captive population in January 1993.*

lation. Inbreeding has been avoided, and until now there has been no pairing between related individuals. There were initially 30 wild-caught founders in the captive population, and another 23 wild-caught individuals were incorporated between 1978 and 1993. Individuals born in captivity have been transferred among zoos to avoid inbreeding (Frey 1993). I thought it best not to include inbreeding depression in the models because the ways VORTEX could model it were too unrealistic. I considered that the captive population could be simulated as a whole panmictic unit because individuals have been regularly transferred among zoos to form breeding pairs. Although VORTEX gives values of observed and expected level of heterozygosity remaining after the simulation, I did not use those estimates in the conclusions because the assumptions of random mating, equal probability of breeding of all adults, and reshuffling of the breeding pairs every year do not apply to the captive population. Because the cost of the captive breeding project increases with population size, and 43% of the costs of the project are for keeping the birds in captivity (Patchlatko 1991), I assumed there would be a limit to population size. The maximum captive population size was limited in the models to 200 individuals (double the present size).

Populations were projected for 200 years, and each projection was run 500 times. Extraction rates of fledglings to be released to the wild were simulated under two scenarios.

In scenario 1 there was a fixed extraction rate: a fixed number of fledglings (the same number of males and females) were released every year, provided that at least that number was born into the captive population. The aim of the captive breeding project is to release at least two fledglings every year at each of the four release sites in the Alps (eight fledglings per year). The number of birds released was varied from three males and three females to seven males and seven females per year. The actual mean extraction rate from 1986 to 1993 was 5.9 fledglings per year.

In scenario 2 there were proportional extraction rates: a certain proportion of the birds born each year is released to the wild. This is a more realistic scenario than scenario 1. The project tends to keep at least some of the birds born to maintain the captive population, and it can be assumed that the number of birds released would be reduced if the captive population declined. Proportional extraction rates were simulated in VORTEX by increasing first-year mortality accordingly. The proportion of birds released was varied from 40% to 80% of the chicks fledged each year. The actual extraction rate from 1986 to 1993 from the captive population was 60%.

Finally, I tested the sensitivity of the model to some demographic parameters by analyzing the relative effect on the population growth rate and on the number of chicks that could be released by improving each parameter. I ran simulations in which each demographic parameter at a time was improved by 10% and 100% of its biologically possible maximum improvement. I studied the effect of improving hatching success, nestling survival, first-year survival, immature survival, adult survival, and proportion of females that reproduce each year.

Simulations of the Population Released in the Alps

Because captive birds are released at the time of fledging and because the fecundity rate available for wild populations is the number of young fledged per breeding female, I started the annual cycle of the simulation of the released population at the time juveniles fledge. Estimates of demographic parameters are nonexistent or not as good as those for the captive population. The parameters used in the models came from different sources and are given in Table 2. For age at first breeding and for lifespan I used the same values as in captivity, although these might be optimistic. For mortalities and fecundities I used an optimistic and a pessimistic estimate for each parameter. Bearded Vultures have not reproduced in the Alps yet, so for fecundity rates I used an optimistic estimate of 0.67 fledglings per female—the mean recorded productivity in the southern slopes of the Pyrenees between 1987 and 1991, $n = 168$ reproductions (Heredia 1991)—and a pessimistic estimate of 0.35 fledging per female—the mean recorded productivity in the northern slopes of the Pyrenees between 1986 and 1990, $n = 65$ reproductions (Terrasse 1991). I calculated first-year mortality based on the 6 fledglings out of 41 (the 9 juveniles released in 1993 were excluded) that were recaptured, died, or disappeared with certainty before the end of the first year (14.6% mortality), and I considered this as an optimistic estimate. The 95% upper confidence limit for this estimate, assuming a binomial distribution, is 29%, and I used this as the pessimistic estimate for first-year mortality in the models. To estimate mortality rate after the first year I assumed a constant hazard rate and I adjusted the recorded ages at death to an exponential distribution (Crawley 1993). Individuals that outlive the duration of a study and will die at an unknown time in the future are said to be "censored." They contribute to our knowledge of the survivor function but not to our knowledge of the age at death (Crawley 1993). Birds assumed by the project to be alive were right-censored in September 1993. I did not right-censor the birds at the last published observation because I knew these were incomplete. Mean hazard (mortality) rate was 3.1%, and the 95% upper confidence limit was 9.4%. These estimates were used in the simulations as optimistic and pessimistic mortality rates after the first year (2–31 years of age). If each bird had been right-censored at the last published observation, the mean mortality rate and the upper limit would have been 5.7% and 17.6%. VORTEX assumes that the initial

Table 2. Summary of initial values for VORTEX for the population released in the Alps

- Type of mating system: monogamous
- Age at first reproduction: 7 years[a]
- Age after which adults do not reproduce: 31 years[a]
- Sex ratio at birth (proportion of males): 0.5[a]
- Fecundity Rates[b]
  - Maximum brood size at fledging: 1
    - Females raising 0 fledgling: 65.0-33.0%[c]
    - Females raising 1 fledgling: 35.0-67.0%
  - No density dependency in fecundity rates
- Mortality Rates[d]
  - Juveniles (1st year): 14.6-29.0%[c]
  - Immatures and adults (2-31 year): 3.1-9.4%
- Correlation between mortality and fecundity annual rates
- Inbreeding depression: Recessive lethal model
- Probability of a catastrophe: 1%
  - Multiplicative effect on fecundity: 0.5
  - Multiplicative effect on mortality: 0.75
- Initial population: 16 males and 24 females more than 1 year old[e]
- Carrying capacity: projected at 500 individuals

[a] *From the captive population.*
[b] *From the Pyreneean population (Heredia 1991; Terrasse 1991).*
[c] *Maximum and minimum rates used in the simulations (see methods).*
[d] *From the population released in the Alps.*
[e] *Maximum number still alive in September 1993.*

population is formed by unrelated individuals and that individuals that are supplemented are unrelated among themselves and to other individuals in the population (Lacy 1993). Actually, individuals in the released population are not unrelated. Many are offspring of the same breeding pairs, and offspring of these same pairs will continue to supplement the population in the future. Because I have no information on the degree of inbreeding depression in the Bearded Vulture, I used a recessive lethal model in all simulations, which is probably an optimistic simulation of the possible effect of inbreeding. Also, I have no information on the types and probabilities of catastrophes for the Bearded Vulture population in the Alps, so I decided to keep the default values of VORTEX in all simulations (see Table 2).

I projected the released population for 200 years and repeated each simulation 500 times. I simulated the population under four different scenarios: (1) low mortality and high fecundity, (2) low mortality and low fecundity, (3) high mortality and high fecundity, and (4) high mortality and low fecundity (Table 2). In each scenario I simulated that the population was supplemented for 0, 2, 5, 10, and 15 years with four males and four females more each year.

I also studied the effect of annual variability in the parameters due to environmental variability. Environmental variance (EV) in productivity based on the annual estimates for the Pyrenees (Heredia 1991; Terrasse 1991) and Corsica (Fasce et al. 1989) ranges from 0.9 to 1.4 times demographic variance (DV)—the effect of binomial sampling around the mean in a small population. Unfortunately there are no data available to estimate environmental variance in mortality. Because the Alps are the northern limit of the historical distribution of the Bearded Vulture in Europe, I expected that environmental variance could be at least as high as that of other areas. At the two scenarios with low mortality (1 and 2) I studied the effect of a low (1 × DV), medium (1.5 × DV), high (3 × DV), and very high (5 × DV) environmental variance in the parameters. In the simulations no new individuals were supplemented to the population. Initial population size and age structure were that of the birds assumed to be alive in 1993.

Results

Captive Population

The aim of the simulation was to study which extraction rates could be safely employed on the captive population, arbitrarily considering as such those that gave a

Table 3. Population viability analysis of the captive Bearded Vulture population under different extraction rates.

Scenario	*Extraction rate*[a]	*Probability of extinction (%)* ($\bar{x} \pm SE$)	*Years to extinction* ($\bar{x} \pm SE$)	*Observed heterozygosity (%)* ($\bar{x} \pm SE$)	*Observed growth rate (5)* ($\bar{x} \pm SE$)
Fixed extraction rate	3M3F[b]	1.6 ± 0.6	88 ± 4.5	93.5 ± 0.1	5.0 ± 0.03
	4M4F	8.6 ± 1.3	70 ± 3.0	93.4 ± 0.1	4.2 ± 0.03
	5M5F	22.8 ± 1.9	71 ± 2.5	93.8 ± 0.1	2.9 ± 0.04
	6M6F	52.6 ± 2.2	64 ± 1.6	93.9 ± 0.2	0.9 ± 0.05
	7M7F	74.4 ± 2.0	62 ± 1.5	94.0 ± 0.2	−1.4 ± 0.06
Proportional extraction rate	40	0.0 ± 0.0	—	93.6 ± 0.1	3.3 ± 0.03
	50	0.4 ± 0.3	108 ± 30.0	92.9 ± 0.1	2.1 ± 0.03
	60	20.2 ± 1.8	135 ± 4.0	87.6 ± 0.6	0.1 ± 0.04
	70	71.2 ± 2.0	116 ± 2.2	84.5 ± 1.2	−2.1 ± 0.05
	80	99.2 ± 0.4	72 ± 1.6	69.5 ± 16.4	−4.4 ± 0.09

[a] *M = males; F = females.*
[b] *Percentage of fledglings released each year is shown for the proportional extraction rate scenario.*

Table 4. Response of the captive Bearded Vulture population to improvement in a demographic parameter.

	10% improvement		*100% improvement*	
Parameter improved	*Observed growth rate (%) ($\bar{x}$ ± SE)*	*Extraction rate* fledglings/year ($\bar{x}$ ± SE)*	*Observed growth rate (%) ($\bar{x}$ ± SE)*	*Extraction rate* fledglings/year ($\bar{x}$ ± SE)*
Hatching success	2.8 ± 0.03	15.0 ± 0.34	7.5 ± 0.03	25.2 ± 0.22
Nestling mortality	2.2 ± 0.03	12.7 ± 0.39	3.7 ± 0.03	16.9 ± 0.29
First-year, post-fledging mortality	2.1 ± 0.03	12.1 ± 0.41	2.6 ± 0.03	13.5 ± 0.30
Immature mortality	2.1 ± 0.03	12.3 ± 0.38	2.5 ± 0.03	13.8 ± 0.33
Adult mortality	2.3 ± 0.03	12.5 ± 0.35	4.2 ± 0.03	15.2 ± 0.14
Females breeding (%)	2.3 ± 0.03	12.9 ± 0.39	4.2 ± 0.04	18.3 ± 0.35

**Number of fledglings released with a 50% release rate and a stable population of 200 individuals in captivity.*

probability of extinction of the captive population not greater than 5% in the next 200 years. If a fixed extraction rate was used, no more than three males and three females could be safely released each year, with a probability of extinction lower than 5% (Table 3). Releasing four males and four females gives a probability of extinction of 8.6%. The lower limit of the 95% confidence interval around the estimate, using a binomial distribution, was 6%, which is over the 5% limit. Higher release rates also gave probabilities of extinction significantly over 5%. If a proportional extraction rate was employed, a proportion of up to 50% of the fledglings could be released every year with a risk of extinction not greater than 5%.

If the criterion to select an extraction rate from the captive population was the maximum extraction rate maintaining a slightly positive growth rate in captivity it would be possible to release up to 12 birds per year, or 60% of the birds fledged.

Table 5. Population viability analysis of the Bearded Vulture population released in the Alps, with effect of different mortality and fecundity rates and number of years releases are continued.

		High survival		*Low survival*	
	No. of years[a]	*High fecundity ($\bar{x}$ ± SE)*	*Low fecundity ($\bar{x}$ ± SE)*	*High fecundity ($\bar{x}$ ± SE)*	*Low fecundity ($\bar{x}$ ± SE)*
Probability of extinction (%)					
	0	0.0 ± 0.0	0.4 ± 0.3	61.4 ± 2.2	100 ± 0.0
	2	0.0 ± 0.0	0.2 ± 0.2	48.6 ± 2.2	100 ± 0.0
	5	0.8 ± 0.4	0.0 ± 0.0	33.4 ± 2.1	100 ± 0.0
	10	0.2 ± 0.2	0.8 ± 0.4	19.4 ± 1.8	100 ± 0.0
	15	0.0 ± 0.0	0.2 ± 0.2	11.4 ± 1.4	99.8 ± 0.2
Years to extinction					
	0	—	27 ± 14	99 ± 3.0	52 ± 1.0
	2	—	69 ± 0.0	107 ± 3.0	59 ± 1.0
	5	134 ± 15	—	123 ± 3.0	67 ± 1.0
	10	63 ± 0.0	85 ± 23	134 ± 4.0	81 ± 1.0
	15	—	73 ± 0.0	148 ± 5.0	89 ± 1.0
Observed heterozygosity (%)					
	0	96.5 ± 0.07	95.5 ± 0.14	79.2 ± 1.36	—
	2	97.2 ± 0.06	97.0 ± 0.08	83.4 ± 1.11	—
	5	97.7 ± 0.05	97.7 ± 0.05	85.5 ± 0.97	—
	10	98.0 ± 0.04	98.2 ± 0.04	89.8 ± 0.60	—
	15	98.1 ± 0.04	98.4 ± 0.04	92.7 ± 0.37	100 ± 0.0
Final population size[b]					
	0	484 ± 1.6	456 ± 2.8	156 ± 11.1	—
	2	483 ± 1.5	455 ± 3.0	200 ± 10.6	—
	5	487 ± 1.4	458 ± 3.0	209 ± 9.1	—
	10	486 ± 1.5	458 ± 3.1	237 ± 4.0	—
	15	484 ± 1.7	456 ± 2.8	267 ± 7.8	5 ± 0.0
Observed growth rate (%)					
Without releases		8.2 ± 0.03	3.7 ± 0.03	−1.0 ± 0.05	−5.8 ± 0.11
With releases		12.3 ± 0.10	10.2 ± 0.10	7.3 ± 0.11	5.8 ± 0.11

[a] *Four males and four females released every year during that number of years.*
[b] *Carrying capacity fixed at 500 individuals.*

Table 6. Population viability analysis of the Bearded Vulture population released in the Alps, with effect of environmental variability.

		High survival	
	Environmental variance[a]	*High fecundity* *($\bar{x}$ ± SE)*	*Low fecundity* *($\bar{x}$ ± SE)*
Probability of extinction (%)			
	Low (1 × DV)	0.0 ± 0.0	0.4 ± 0.3
	Moderate (1.5 × DV)	0.0 ± 0.0	2.0 ± 0.6
	High (3 × DV)	0.8 ± 0.4	5.0 ± 0.9
	Very high (5 × DV)	19.2 ± 1.8	25.4 ± 2.0
Years to extinction			
	Low (1 × DV)	—	27 ± 14.0
	Moderate (1.5 × DV)	—	105 ± 21.0
	High (3 × DV)	102 ± 33	79 ± 10.0
	Very high (5 × DV)	100 ± 5.0	86 ± 5.0
Observed heterozygosity (%)			
	Low (1 × DV)	96.5 ± 0.07	95.5 ± 0.14
	Moderate (1.5 × DV)	96.3 ± 0.09	94.6 ± 0.29
	High (3 × DV)	95.8 ± 0.16	93.2 ± 0.44
	Very high (5 × DV)	93.9 ± 0.42	93.3 ± 0.42
Final population size[b]			
	Low (1 × DV)	484 ± 1.6	456 ± 2.8
	Moderate (1.5 × DV)	475 ± 2.3	438 ± 4.0
	High (3 × DV)	445 ± 2.3	379 ± 6.1
	Very high (5 × DV)	416 ± 6.1	345 ± 8.4
Observed growth rate (%)			
	Low (1 × DV)	8.2 ± 0.03	3.7 ± 0.03
	Moderate (1.5 × DV)	8.1 ± 0.04	3.7 ± 0.04
	High (3 × DV)	7.8 ± 0.05	3.4 ± 0.06
	Very high (5 × DV)	7.5 ± 0.07	3.3 ± 0.07

[a] *DV = demographic variance.*
[b] *Carrying capacity fixed at 500 individuals.*

The effect of improving the demographic parameters of the captive population is given in Table 4. Hatching success is clearly the parameter that, if improved, would give both a greater mean growth rate for the population and a higher number of fledglings to release per year with a limited population size.

Released Population

If the mortality rates of the population were as low as our minimum mortalities, the released population would have a probability of extinction under the 5% limit (Table 5), even if no further releases were conducted and the population had a relatively low fecundity. If mortality rates were as high as the maximum values used in the simulations, even if the population had a relatively high fecundity and releases were continued for 15 years, the probability of extinction of the population would be over the 5% limit. In the worst of all scenarios simulated, the population would become extinct almost with certainty if releases were discontinued after 15 years.

The released population takes a relatively long time to become extinct. In the worst scenario—low survival and low fecundity rates—the population would take a mean of 52 years to become extinct if no more releases were conducted (Table 5).

According to the simulations, the heterozygosity that remains in the population after 200 years, if it does not become extinct, is relatively high. Only with a low survival and a high fecundity would the population lose more than 5% of the original genetic variability.

The released population would show a positive growth rate under all scenarios if birds from the captive population continue to be released every year at the present rate (four males and four females on average). In the scenarios with low survival, the growth rates were negative (the population declined) if the population was not supplemented (Table 5).

The effect of environmental variability on the probability of extinction would be important only if it was high or very high (more than three times the variability attributed to demography; Table 6).

Discussion

Although VORTEX was able to simulate realistically most of the situations and management options of the

Bearded Vulture populations, there are some important aspects that need further comment. Unfortunately, VORTEX is not able to model the long-term monogamy typical of large birds of prey or to consider that all breeding pairs in the population will not have equal probability of reproducing successfully every year. (Pairs that breed successfully one year have a higher probability of breeding successfully the next year, both in captivity and in the wild.) This means that VORTEX, in general, will overestimate the number of genes transmitted to the next generation and will underestimate the extent of inbreeding. On the other hand, VORTEX always considers random mating, which is not applicable if pairing within the captive population is performed in trying to avoid inbreeding, as was the case. VORTEX is also unable to take account of the fact that the individuals in the initial population are related or that individuals released to the wild will be related among themselves or to the initial population, as is the case with the Bearded Vultures released to the Alps. This underestimates the risk of inbreeding depression. Also, the little information on the effect of inbreeding depression in birds and the lack of any data on the effect of inbreeding depression in large, long-lived raptors makes any values for the effect of inbreeding depression in the models highly speculative. Better models and more information on the effects of inbreeding depression would allow a more realistic modeling of this aspect.

The results of the simulation show that it is possible to extract fledglings from the captive population of Bearded Vultures to use them for reintroduction projects without a significant risk to the captive population, provided that extraction rates are kept relatively low, no higher than three males and three females per year or no more than 50% of the chicks fledged in a particular year. The Bearded Vulture Reintroduction Project aims to release a minimum of two birds per release site, and four release sites are currently used in the Alps. This release scheme may be slightly over the safe extraction rate, but considering that in reality releases would be stopped if the captive population declined, these numbers can be considered safe. It would be dangerous to increase the extraction rate to start new reintroduction projects in other areas in the near future.

If the only criterion for selecting an extraction rate was the maximum extraction rate that allowed for a slightly positive growth rate in the captive population, it would be possible to release up to six males and six females per year, or 60% of the chicks fledged. But this probably would not be wise before the Alpine population can be guaranteed to be self-sustainable.

Only if the size of the captive population were substantially increased or its present demographic parameters improved would it be possible to start new reintroduction projects in the next few years. From an economic point of view, improving some demographic parameters would be cheaper in the long term because most of the funds for the reintroduction project are spent on maintenance of the captive population (Patchlatko 1991).

It is obvious that the improvement of any demographic parameter in the captive population would allow higher rates of release to the wild. The mortality rates of all age classes are relatively low, and it would probably be difficult to reduce them further. Even with zero mortality in certain age classes, its relative effect on the rate of release would be small. Hatching success is the parameter with the highest possibilities of increasing the growth rate of the captive population or the rate of release to the wild because of the greater sensitivity of the population to this parameter and because it can be improved to a greater degree. The present hatching success in the captive population (46.8%) is very low compared to the hatching success of birds of prey in the wild or in captivity, which range from 60% to 95% (Newton 1979). Hatching success has not significantly improved since the project started (there is not a significant positive correlation with time from 1978 to 1993, $r_s = -0.1697$, $p = 0.51$). Research focusing on why hatching success in the captive population is so abnormally low and testing ways to improve it would be the strategy with the greatest possible benefits in the Bearded Vulture Reintroduction Project. If hatching success was improved up to 70%—the hatching success of the California Condor (*Gymnogyps californianus*) captive breeding project (Hartt et al. 1994) is below average hatching rates of birds of prey (Burnham 1983; Carpenter et al. 1987)—it would be possible to start soon reintroductions to areas outside the Alps (Bustamante et al. 1994).

The lack of adequate data on the demographic parameters of the population released in the Alps means that almost any result is possible in the range of scenarios in which the population was simulated. Our simulations suggest that it would at least be possible to maintain an artificially supported population in the Alps if the present rate of release of captive birds was maintained. But this is not the present aim of the reintroduction project and the organizations involved in the project would have to decide if this was an economically or politically desirable aim.

Because Bearded Vultures in the Alps have not reproduced yet it is not possible to know what their fecundity rates will be. There is some information about mortality, which could be improved if the fates of all the birds released were known exactly. The only marking procedure currently allowed by the reintroduction project, apart from metal rings, is bleaching of flight feathers. This allows recognition of individuals for up to 1.5–2.5 years after release, depending on the positions of the markings and the rate of molt of flight feathers (Coton 1994). The project considers that recapturing individuals for remarking or using other longer-lasting marking methods is too dangerous or too costly (Frey & Niebuhr 1994) and that enough information is obtained without more sophisticated procedures (radio tracking or longer-lasting marks). The project states that 38 Bearded Vultures more than 1 year old of the 50 released could theoretically have been living free in September 1994 (Frey 1994*a*). The 12 vultures missing have been recaptured (2 birds) or found dead (5 birds) or are considered definitively lost by the release team (5 birds). Observations during 1994 identified a minimum of 25 different individuals more than 1 year old alive—the identity of all of them not exactly known (Kurzweil 1994). Comparing the figure of vultures theoretically free with the minimum number observed alive reveals that for a minimum of 13 individuals released (26%) it is not possible to say whether they are alive or dead. Considering that the total number of birds missing in the wild could add up to 25, the project would have been able to find only 28% of the birds missing (5 dead and 2 recaptured), and the approximate time of disappearance from the population would be known in 48% of the individuals missing (5 dead, 2 recaptured, and 5 lost). If the marking method allowed identification for a longer period of time or if radio transmitters were employed, these figures could be improved and the precision in the mortality estimates would improve accordingly. Different trapping methods, longer-lasting marks, and radio transmitters have been employed on wild Bearded Vultures in the Pyrenees (Sunyer 1991; Gil Gallús & Díez Sánchez 1993) and in South Africa (Brown 1988, 1990*a*, 1990*b*) with great success and without a significant risk to the marked individuals. The importance of good estimates is that without them it will be impossible to tell if the population can be self-sustainable and for how long the releases in the Alps should continue. To continue releasing birds it is necessary to breed them in captivity, which costs time and money (Patchlatko 1991). Both of these resources would be withdrawn from other possible conservation projects.

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