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Evaluation of the extinction risk and of conservation alternatives for a very small insular population: the bearded vulture *Gypaetus barbatus* in Corsica

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Abstract

The bearded vulture *Gypaetus barbatus* is a large, long-lived osteophagus vulture whose abundance and breeding range have drastically declined during the last century, making it one of the most endangered European bird species. We evaluated the extinction risk of the bearded vulture population in Corsica (a small, isolated breeding population of 8–10 pairs), one of the last extant populations in Western Europe, and estimated its probability of extinction to be 0.165 over the next 50 years. A sensitivity analysis to assess the influence of uncertain demographic rates showed that it is critical to estimate precisely the values of pre-adult survival. Neither the type nor the parameters of density dependence acting on fecundity and survival rates influenced much the extinction risk of the Corsican population. We evaluated the effect of four realistic conservation actions that could be implemented on the Corsican bearded vulture population and rank them in terms of their respective decrease of the current extinction risk faced by this population. We found that the release of two juveniles every other year for 12 years and the increase of fecundity due to selective food provisioning would reduce by more than one-half the current extinction risk of Corsican bearded vulture population. In contrast, even substantial increases in the carrying capacity through large supplemental feeding produced very modest decreases in the extinction risk, thus calling into question the efficacy of one of the main pan-European conservation strategies for this species. Re-establishing a population network within the Mediterranean could be a potentially better strategy, though its efficacy depends on natal dispersal among populations that is currently unknown.

Keywords: Raptors; Conservation; Vulture; Reinforcement; Artificial feeding; Birds

1. Introduction

Several species of vultures (both New and Old World vultures) have shown huge declines over the last century: California condor *Gymnogyps californianus* (Snyder and Snyder, 2000), Asian vultures (white-backed vulture *Pseudogyps bengalensis*, Indian griffon *Gyps indicus*, slender-billed vulture *Gyps tenuirostris*, and Eurasian griffon *Gyps fulvus*, Satheesan, 2000; Pain et al., 2003), and the bearded vulture *Gypaetus barbatus* (Cramp and Simmons, 1980). Vultures are thus among the most endangered raptors, partly due to their extremely low reproductive rates (clutch of 1 or 2 eggs, annual or biennial breeding, and extended breeding seasons in some species, >12 months; Newton, 1998). Consequently, vultures have been the subjects of considerable interest from conservation, with more than one third of vulture species being currently the target of management/conservation actions in the world (Houston, 1987).

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The bearded vulture (or Lammergeier), is a large (4.5–7.1 kg), territorial accipitrid scavenger inhabiting scattered mountains ranges in Eurasia and Africa that predominantly feeds on bones and carcasses of medium-sized wild and domestic ungulates (Cramp and Simmons, 1980). The numbers and breeding range of this species have dramatically declined in Western Europe over the last century, leading to its current listing as endangered in Europe (Tucker and Heath, 1994). Reduction of the breeding range of the bearded vulture in Western Europe has been associated with direct human prosecution through killing of eggs and adults (Cramp and Simmons, 1980), and to indirect causes: mortality by poison baiting, collision with electric lines, and reproductive failure related to human disturbance (Hernandez, 2003). While most of these factors related to human activity seems not to be affecting most extant bearded vulture populations anymore (Heredia and Heredia, 1991), poisoning may have increased again in Spain (Hernandez, 2003) and Greece (Xirouchakis et al., 2001). Extant western European populations totals ca. 120 breeding pairs, currently confined to the French and Spanish Pyrenees (100 pairs), Corsica (10 pairs), Crete (currently 4 pairs; Xirouchakis et al., 2001), and a recently reintroduced population in the western Alps (6 pairs). There are also isolated individuals in scattered locations across the Balkans and populations breeding in Turkey and Caucasus whose current abundances are not precisely known (Abuladze, 1998).

Corsica is an island of 8750 km^2 located at 42°N and 9°E with mountain areas higher than 1000 m covering 18.7% of its area. Remains of bearded vultures in Corsica are known from mid and late Pleistocene (Louchart, 2002; Robert and Vigne, 2002). The species has been regularly recorded since the late 19th century (Thibault and Bonaccorsi, 1999). The bearded vulture population in Corsica is however unique for two reasons. First, following the extinction of the species in Sardinia in the 1970s (Schenk, 1976), it has an extreme geographic isolation, with the closest breeding pair being ca. 600 km away. More recently however, a reintroduced population in the French Alps (Arlettaz, 1996) that started breeding in 1997 lies at ca. 300 km from Corsica. Second, the Corsican population has been remarkably stable over at least the last two decades, with 8 pairs from 1983 to 2001 (Seguin et al., 2003). With such a small size and a high degree of geographic isolation, the extinction risk of this population would be expected to be rather high.

The objectives of this article are twofold. First, we estimate the current risk of extinction faced by the Corsican population of the bearded vulture using the best available demographic information, and perform a sensitivity analysis to assess the importance of uncertain parameter estimates. Second, we evaluate the effect of four possible conservation strategies of the Corsican bearded vulture: release of juvenile birds, changes in the food supplementing program, increases of natural resources, and (re-)establishment of a population network (or metapopulation) within the Western Mediterranean basin. These conservation strategies will be assessed and ranked according to the relative decrease of the baseline extinction risk of the Corsican bearded vulture estimated above.

2. Methods

2.1. The basic model: structure and parameter estimates

We built an age-structured, post-breeding, stochastic population model (hereafter the basic model) based on all individuals of the Corsican bearded vulture population. Stochastic demographic models have become an important and increasingly used tool for assessing the degree of threat of natural populations (Burgman et al., 1993; Beissinger and McCullough, 2002; Reed et al., 2002). There are no data on survival rates from Corsica, so we used published estimates from the Pyrenees or from captive breeding programs. The age at first reproduction was set at 7 years (median age at first breeding of females in captivity: 6.5 years, $n = 10$; Bustamante, 1996) and the maximum age of reproduction at 31 years (Bustamante, 1996; there is one case in captivity at 35 years: Frey, 2000). Adult (>6 years) and immature (1–6 years) survival rates (mean and SD values) were taken from Bustamante (1998) and Antor (1999) that are the only published estimates existing for the species. To account for the observed longevity of the species, individuals had a non-zero probability of remaining at the last age class. The latter however should not be construed as assuming that the birds are immortal since the chances of remaining in the last age class diminishes each year at a rate of $(1 - S_{\text{adults}})$. Survival of last age class was arbitrarily set to 0.8 (compared to 0.94) with a standard deviation equal to that of the other adult age classes.

Estimates of fecundity (number of fledglings per pair) were obtained from the long term monitoring program in Corsica (mean = 0.183 and SD = 0.192, $n = 23$ years and 163 breeding events; Seguin et al., 2003), assuming an even sex ratio at birth (see also Meretsky et al., 2000 for California condor). Table 1 shows the mean and standard deviations of all demographic rates of the basic model. We considered that young adults (7–10 y), i.e. inexperienced adults, would show reduced fecundity (Razin and Bretagnolle, 2003; Margalida et al., 2003). We thus set the average fecundity of the first three reproducing age classes (and that of the oldest age class due to senescence) arbitrarily to one third of adult fecundity whilst their standard deviations remained identical to other adult age classes.

Table 1
Average and temporal variability (standard deviation) of the demographic rates of the basic model for the bearded vulture in Corsica

Demographic rate	Average	Standard deviation
Survival juveniles (1–6 years)	0.93	0.13
Survival adults (7–29 years)	0.94	0.06
Survival old adults (30+ years)	0.80	0.03
Fecundity young adults (7–10 years)	0.06	0.06
Fecundity adults (11–29 years)	0.18	0.19
Fecundity old adults (>30 years)	0.06	0.06

Age at first reproduction was assumed to be seven years. Ceiling density dependence was assumed to affect all demographic rates, with a constant carrying capacity estimated of $K = 40$ individuals (see main text for the sources of data). See Section 2 for additional details.

2.1.1. Stochasticity

Environmental stochasticity was modelled by drawing the values of the age-specific survival and fecundity rates from a set of lognormal distributions whose parameters (means and standard deviations) reflect the average value and the temporal variability of each demographic rates. Using the lognormal distribution to model environmental stochasticity is recommended whenever the average survival and/or fecundity rates are either close to zero or to one in order to avoid biases in the average realised rates that would be induced by using the normal distribution and truncating biologically impossible values (i.e. negative fecundity, survival higher than one) of the demographic rates (Akçakaya, 1998). The relatively long chick-rearing period of bearded vulture (Cramp and Simmons, 1980) makes it likely that breeding success and adult survival be correlated, and hence we assumed that the values of fecundity and adult survival of a population for a given year were perfectly correlated.

Demographic stochasticity was modelled by sampling the number of survivors of each age class and the number of young birds from binomial and Poisson distributions at each time step of the simulations (Akçakaya, 1998). We did not consider the role of genetic variability on population viability because there is no reason to believe that the Corsican bearded vulture population has ever been much larger in recent historic times, and thus the population is unlikely to have suffered a recent bottleneck (see Reed et al., 2002). The initial age structure (25 individuals; range 24–27) was obtained as the average from the entire Corsican population between 2000 and 2002, yielding: 1 year = 1.5; 2–4 years = 1.5; 5–6 years = 1; adults = 21 (unpublished data). These data come from exhaustive and simultaneous counts made once a year (and realised over several days) over the entire distribution range of bearded vulture in Corsica by at least 20 experienced observers each year between 2000 and 2002.

2.1.2. Density dependence

We considered two variant models for density dependence (Ceiling and Contest; see Burgman et al., 1993), a factor that is known to have potentially strong effects on population persistence (e.g. Stacey and Taper, 1992; Morris and Doak, 2002). Briefly, contest competition reflects the unequal sharing of the available resources common in territorial species whereby a few individuals always receive enough resources for survival and reproduction at the expense of others (Beverton and Holt, 1957). Ceiling density dependence (akin to density vagueness; Strong, 1986) is similar to, but simpler than, the contest model since, under the ceiling type of density dependence, the population grows exponentially until it reaches the maximum population size or ceiling. If the total population abundance increases above this ceiling K, it is truncated by multiplying the abundance of each age class by N_{tot}/K, where N_{tot} is the total population abundance at each time step (Akçakaya, 1998). Although bearded vultures defend areas around the nests, it is unclear that they also defend feeding territories; home ranges are around ca. 200–400 km^2 (Heredia and Razin, 1999; but see Brown, 1988, for larger values). Two parameters, $R_{\max}$ (set to 1.0165 i.e., 1.65% yearly rate of increase, the maximum value attainable in Corsica with current demographic rates) and the carrying capacity (K; see below), define the continuous decline of the population growth rate with increasing density. Density dependence in the basic model was assumed to affect all vital rates (fecundity and survival), as we had no prior reasons to believe that it should affect one parameter in particular. Additional analyses (not shown) showed that the behaviour of the model did not differ depending on whether either model density dependence affected only either fecundity or survival (or both).

2.1.3. Carrying capacity

Carrying capacity was evaluated in terms of resource abundance for two reasons: first, the bearded vulture is more likely to be limited by food abundance than by availability of breeding sites, since there are numerous unoccupied cavities in the area of distribution of the species in Corsica (i.e., mountain areas above 1000 m); second, there is no other vulture species in Corsica that could potentially interfere with the holding of available carcasses. The diet of the bearded vulture in Corsica is comprised of mouflon (*Ovis gmelini)* 12%, sheep/goats (*Ovis aries Capra hircus*) 36% (with goats being dominant), cattle (*Bos taurus)* 33% and suids 16% (Thibault et al., 1993). The abundance of ungulates within the potential distribution area of the Corsican bearded vulture is (see Seguin et al., 2003 for details): 20,000 sheep, 9000 goats, 9000 cattle heads and 600 mouflons (reliable estimates of the number of wild pigs were unavailable to us, but a reasonable figure would be between 500 and 1000 individuals). Most of livestock is more or less free ranging in Corsica and dead animals are left untouched (Thibault et al., 1993), thus we assumed that all dead animals were accessible to bearded vultures. Using conservative estimates of annual mortality rates of 1% for sheep/goat and Cattle (L. Hugot, unpubl. data from Corsica, E. Le Nuz, unpubl. data, Margalida et al., 1997) and of 4% for wild ungulates, mouflons in this case (Pfeffer, 1967; E. Le Nuz, unpubl. data), estimating that 20% of every carcass should be available to the bearded vultures given the absence of other vultures in Corsica (E. Le Nuz, unpubl. data, suggests a value of 25% in the Alps), and given that a breeding pair of bearded vultures requires an average of 350 kg of carcass per year (Margalida et al., 1997), annual energetic requirements of each prey type in the bearded vulture diet in Corsica are 1.300 sheep/goats, 460 cattle, 75 pigs/boars and 125 mouflons per year. The "K-values" for each prey item thus ranged from 23 (sheep/goat) to 5 (mouflon) breeding pairs. However, bearded vultures in Corsica show some diet specialisation on their home ranges (Thibault et al., 1993): for instance, only five breeding pairs in Corsica have been observed to feed on mouflon carcasses. Thus, we revised this preliminary estimate of the carrying capacity, using only sheep/goat and cattle that are shared by all breeding pairs, and setting the % in diet at 50% for each prey type. The recalculated K-values were 17 and 14 pairs for sheep/goat and cattle, respectively. We thus finally assumed a carrying capacity of 15 breeding pairs, and used a K value of 40 individuals in the basic model.

2.2. Implementation of models

All models were analysed by Monte Carlo simulation using RAMAS/Metapop (Akçakaya, 1998) using 1000 replications for each combination of parameter values for three different time horizons: 10, 25 and 50 years. Those time intervals were chosen to represent an immediate extinction risk (10 years), a period for which a conservation strategy could be used and tested (25 years), and finally, a time period that would predict the "long-term" persistence of the population (50 years, corresponding to three generations of the species). Longer periods (e.g., 100 years) were not considered because we believe that it is unrealistic that landscape would remain stable over such time spans. The results of the simulations were summarised in terms of probability of extinction during time horizon of simulations and the average population abundance at the end of the simulations (including populations that went extinct).

2.3. Sensitivity analysis

Aware of the uncertainties existing for the estimates of several parameters of the basic model, we carried out a sensitivity analysis to assess the extent to which the values of these uncertain estimates would affect model results. Specifically, we considered changes in the average adult and juvenile survival rates, the type of density dependence, the average and temporal variation in K using separate simulations for each parameter combination and time horizon.

Adult and juvenile survival rates were taken from the Spanish bearded vulture population (which are currently showing a sharp population increase, ca. 5%/year), and these values were moreover established from a small sample size (only 10 birds; Bustamante, 1998). We examined 16 pairwise combinations of decreases of adult and pre-adult survival (0%, 1%, 2% and 3%) from the values reported in Table 1 in separate simulations using the fecundity rates of the Corsican population and ceiling density dependence. We also used an age-based deterministic model to estimate annual adult and juvenile mortality rates as well as fecundity rate that would allow a population to remain stable (i.e., $\lambda = 1$) by compensatory changes in those parameters (see Meretsky et al., 2000 for a similar approach).

Using the demographic rates reported in Table 1, we examined the sensitivity of to changes in the average value of the carrying capacity (0, +10, +20 units from $K = 40$) and its temporal variability (by setting its standard deviation to 0, 5 and 10) in nine separate combinations.

2.4. Conservation scenarios for the Corsican bearded vulture

We considered four realistic conservation scenarios that could be implemented: (i) the increase of the carrying capacity by supplemental feeding, (ii) the increase of fecundity due to selective food provisioning, (iii) the release of juveniles into Corsica, and (iv) the establishment of a population network within the Mediterranean. The overall aim of these conservation scenarios is to reduce the extinction risk of the Corsican bearded vulture population by either increasing its currently low fecundity (through supplemental feeding) or by increasing its population size (through the introduction or dispersal of juveniles into Corsica). The demographic rates of the basic model (Table 1) were used when evaluating the effects of each conservation strategy on the extinction risk of the Corsican bearded vulture population.

3. Results

3.1. Sensitivity analysis

Our results show that a slight decrease in survival rates affected only slightly the average abundances (Fig. 1(a)), but had a more marked effect on extinction

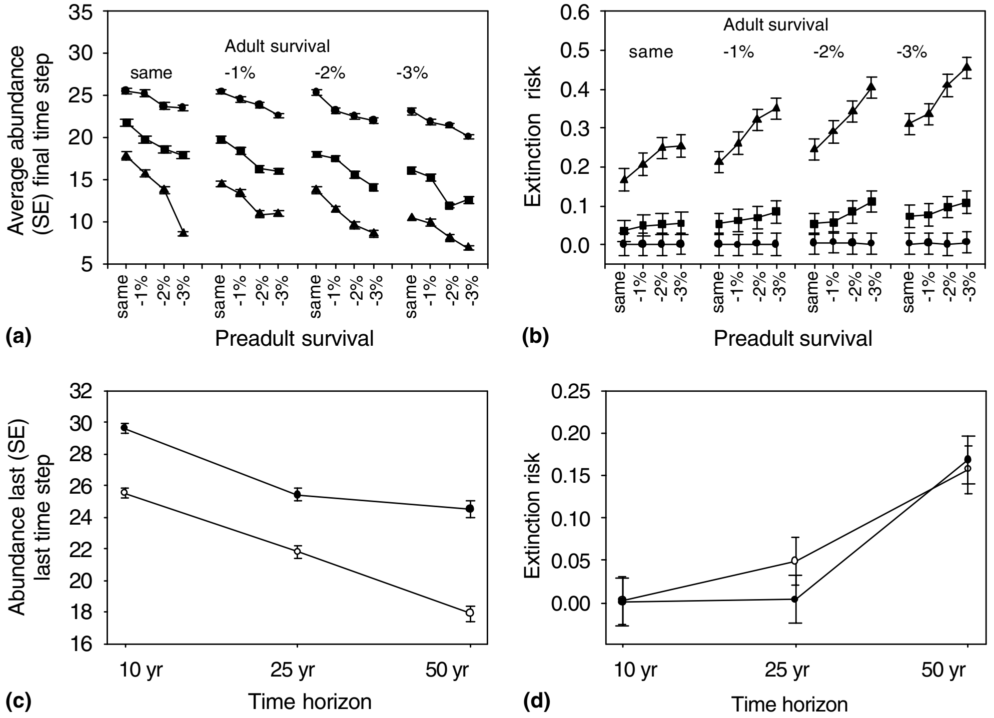

Fig. 1. Sensitivity of the basic model to the average survival rates and to the type of density dependence on the average final population abundance and the extinction risk for different time horizons (10 years, circles; 25 years squares; and 50 years, triangles). Panels A and B: combinations average adult and juvenile survival rates. Values of survival of the basic model are indicated as "same" in the legends. Panels C and D: type of density dependence ($K = 40$ for both models and $R_{\max} = 1.0165$ for the contest model; see main text for further details). Extinction risk is the probability that the population becomes extinct at any year during the simulations. The results for every combination of changes in adult and juvenile survival rates and of the type of density dependence for each time horizon were obtained using separate simulations. Bars in panels A and C are standard errors of the final population abundance, and in panels B and D are Kolmogorov–Smirnov 95% confidence intervals of the extinction risk.

risk, especially at 50 years (Fig. 1(b)). It also appeared that a decrease of adult survival rates had less effect than a similar decrease in preadult survival rate. Given the strong effect of survival rates on simulation results, we additionally modelled the compensatory changes in annual fecundity rate necessary to sustain decreases of both adult and juvenile survival rates while assuring population replacement, i.e. with the long-term population growth rate set to one (Fig. 2). We found that a decrease of up to 10% in both adult and juvenile survival rates (respectively set at 94% and 93% in the basic model) could be compensated by increases in fecundity from 0.18 (basic model) to 0.80 fledglings per year, still a realistic value as it has been measured in both sides of the Pyrenees (Heredia and Heredia, 1991; Terrasse, 1991) before density-dependent factors reduced fecundity rates to ca. 0.5 (Margalida et al., 2003). Decreases or increases of 25% of K-value strongly affected the mean abundance of the population, and also the extinction probability (although to a much lesser extent: Fig. 1(c) and (d)). The reverse results were observed with regard to variation in K, which mostly affected extinction probabilities, at least at 50 years (Fig. 1(d)).

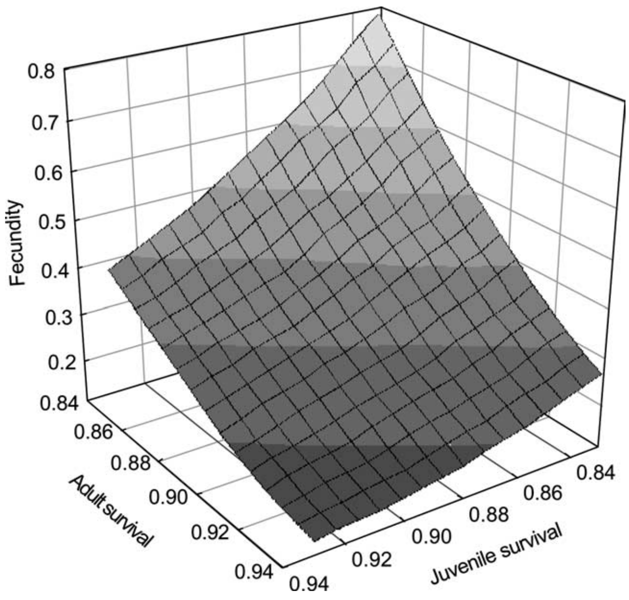

Fig. 2. Combinations of survival (adult and juvenile) and fecundity rates that yield a finite annual growth rate of one, as obtained by eigenanalysis of the basic model (Table 1) without considering neither density dependence nor temporal variation in survival and fecundity rates.

Similarly, the type of density dependence (ceiling versus contest) only had a slight effect on mean abun-

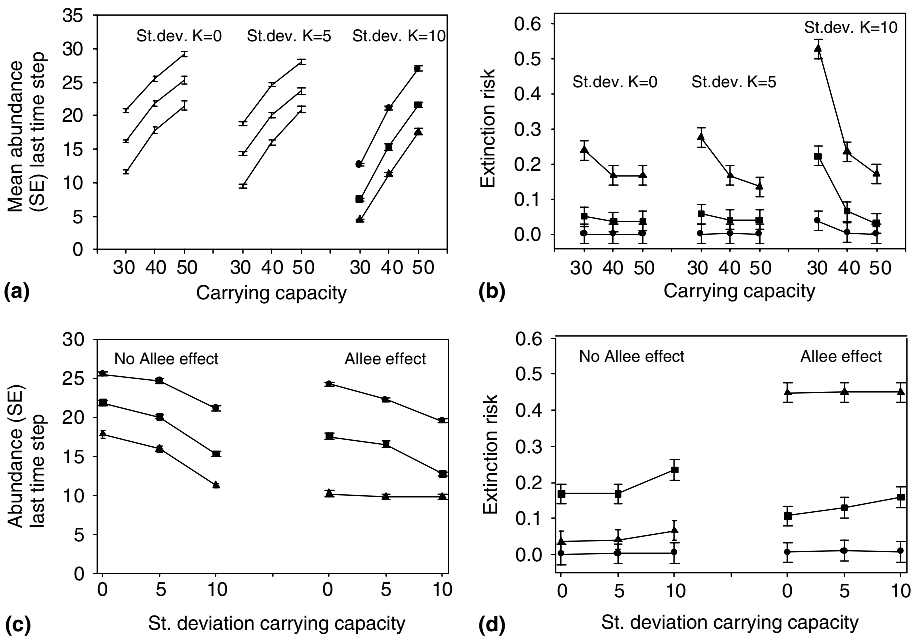

Fig. 3. Sensitivity of the basic model to the average and the temporal variation of the carrying capacity on the extinction risk (Panels A and B) and on the average final population abundance (Panels C and D) and for different time horizons (symbols and bars as in Fig. 1). The results for every combination of changes in adult and juvenile survival rates and of the variability in K for each time horizon were obtained using separate simulations.

dances, but not on extinction probabilities (Fig. 3(a) and (b)). For the simulations that follow, we set $K = 40$ and to be constant over time and density dependence to be of ceiling type, conditions that would render conservative predictions for the Corsican bearded vulture population.

3.2. Effect of initial population size and extinction risk

We first considered the effect of demographic stochasticity at 10, 25 and 50 years. While no extinction occurred in the models without demographic stochasticity at any time horizon, the inclusion of this feature yielded extinction rates of 0.1%, 3.6% and 16.8% at 10, 25 and 50 years, respectively. This rather important difference between the two models is not surprising, since an initial population size of 25 individuals is well within the range of population sizes for which demographic stochasticity is known to increase the extinction rate (e.g. Burgman et al., 1993). To check whether this explanation could hold for the present situation, we tested whether an increase in the initial population size would result in a decrease of the extinction risk. However, since K was set at 40 in the basic model, we had to increase K as we increased initial population size in separate simulations. We did it by maintaining the ratio (0.625) of 25 individuals (initial population size) to $K = 40$ for all trials. As expected, extinction risk at 50 years decreased with increasing initial population size (Fig. 4), and from this curve, we conclude that if managers would like to achieve a risk of extinction close to zero (e.g., below 5%), the population size should be around 50 individuals (i.e., with a K of ca. 80). This is actually close to the theoretical population size at which demographic stochasticity can be considered negligible, a result that was found already when ignoring this parameter in the model. Below we test and compare four potential scenarios with regard to this specific goal and compare them according to their effect in decreasing the baseline extinction risk as predicted by the basic model.

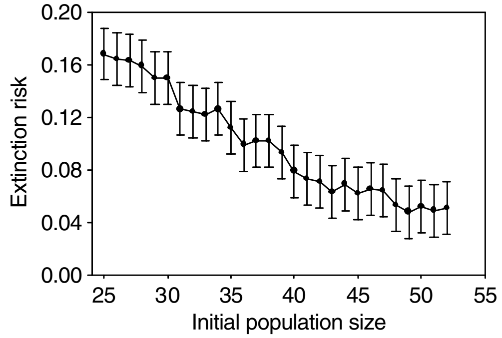

Fig. 4. Changes in the extinction risk with increasing initial population size. Each value was obtained using the same demographic parameters of the basic model by increasing the initial abundance and adjusting the carrying capacity as to keep a constant ratio (0.625) for separate simulation.

3.3. Contrasting alternative conservation strategies for the bearded vulture in Corsica

Scenario 1: increasing carrying capacity

We simulated several scenarios with K ranging from 30 to 80 individuals, and leaving all other parameters from the basic model unchanged. Two strategies for increasing K were tested: increasing the amount of resources "naturally" (i.e., either domestic or wild ungulates), which was simulated in the models with a positive trend in K (incremented by one bearded vulture individual per year), or increasing the food resources by supplemental feeding. We used increments of ca. one ton of carcasses per year that would correspond to the food requirements of three individuals, assuming that one-half of these additional resources is consumed by bearded vultures. Thus, K increased in this case by increments of three individuals per year. In both cases, the increase in K was stopped before reaching a value of $K = 80$ (i.e., the value for 50 individuals in the population).

Surprisingly, in neither situation did the increase in K have a noticeable effect on extinction risk (Fig. 5(a) and (b)) even at 50 years. The decrease (from 16% extinction risk, as in the basic model), was at best by 5% (i.e. extinction risk still being 11%), even for direct increase to $K = 77$ through artificial feeding from the first year (meaning ca. 12 tons of carcasses provided per year). No detectable effect was found for a natural increase of K, even at 5 units per year (corresponding to an increase rate in ungulate populations at about 12.5% per year). Overall, this again probably resulted from the strong effect of demographic stochasticity affecting the population at the initial stages of the simulations.

Scenario 2: increasing fecundity through selective feeding

It may be conceivable, without trying to increase carrying capacity at the global level of Corsica (i.e., in this model, K remains at 40), to provide additional food directly usable by breeding pairs during incubation, or early stages of chick rearing that seem to be critical for the breeding success in the Pyrenees (A. Margalida, pers. comm.; Margalida et al., 2003). This conservation strategy would result in a slight increase of fecundity, although it may be technically difficult to implement (see Section 4). We modelled this possibility using values of fecundity ranging from 0.14 up to 0.30 fledglings per pair and per year. Conversely to acting directly on K, this strategy had clear effects on both extinction probabilities (at 25 and 50 years), with a fecundity of 0.3 fledglings per pair decreasing extinction risk at 50 years to a low of ca. 5% (Fig. 5(d)).

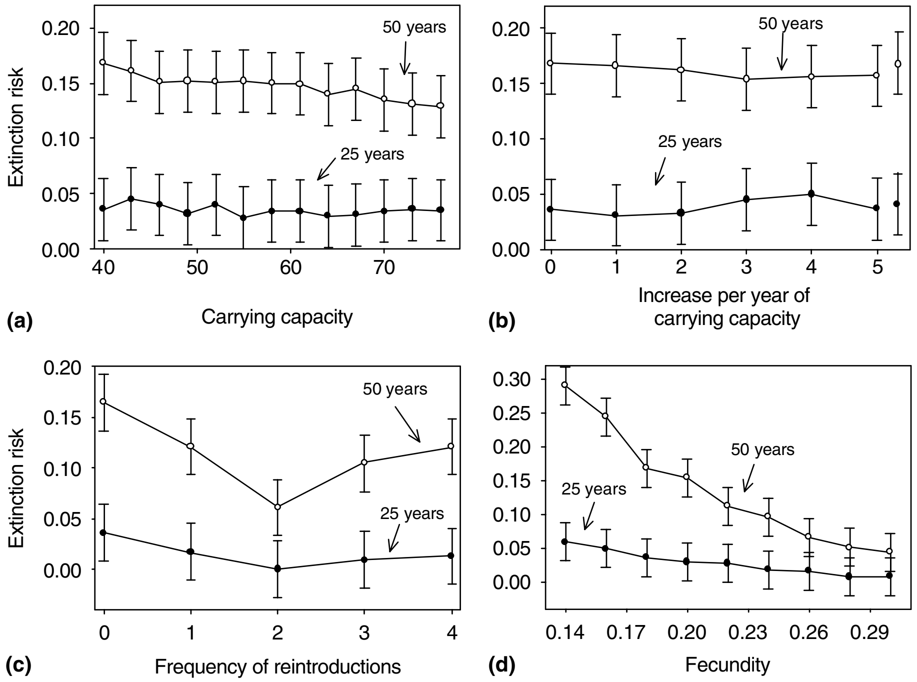

Fig. 5. Effect of different conservation actions on the predicted extinction risk for 25 (open circles) and 50 years (filled circles) using the demographic rates of the basic model. Panel A: Immediate increase of the carrying capacity from baseline value $K = 40$; three units of carrying capacity approximately correspond to one ton of supplementary food. Panel B: Progressive increase in the carrying capacity of 1, 2, 3, 4, 5 units per year up to a $K_{\max} = 77$ which was kept until the end of the simulations. The symbols to the right of the graph are the increase in the carrying capacity of 1.48 units of K per year during 25 years, and of 0.74 units of K per year during 50 years. Panel C: Frequency of release of one-year old birds into Corsica. A total of 12 animals were reintroduced in the first 12 years of the simulation at different frequencies per year. Panel D: Increase in the average fecundity due to additional feeding at the nest during the fledgling period. The results for every combination of changes in parameter values for each time horizon were obtained in separate simulations.

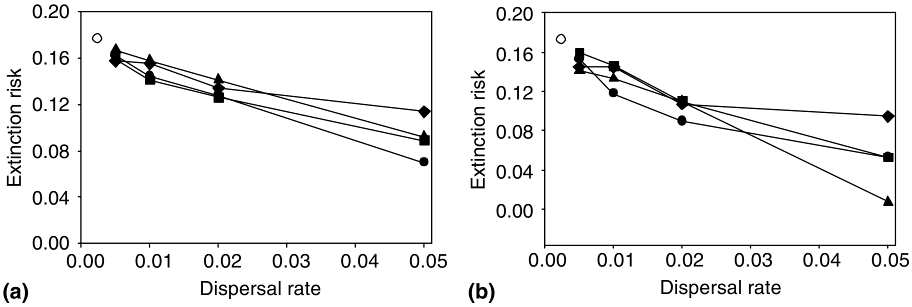

Fig. 6. Extinction risk of the Corsican population of bearded vulture assuming the dispersal of juveniles from one (Panel A) and two (Panel B) nearby hypothetical populations for different values of the migration rates and environmental correlation between the populations (circles: 0.125; squares: 0.25; triangle: 0.5 and diamond: 0.75). The predicted extinction risks of Corsican population for each time horizon are shown at the left of each series for comparison. We used the demographic rates, the carrying capacity and the initial age structure of the basic model and assumed that migration was symmetric between each pair of populations. The results for each combination were obtained in separate simulation.

Scenario 3: increasing population size through supplementation from captive stock

Another possibility could be to supplement the bearded vulture population of Corsica. We modelled release of fledglings rather than adults because up to now, releases in bearded vulture have only been performed with fledglings. We simulated only very small values of supplementation (12 fledglings at total, over the 12 first years of the simulation), and tested different scenarios: one fledgling per year every year (12 releases), two fledglings every two years (six releases), three fledglings every 3 years (four releases) and four fledglings every 4 years (three releases). The best strategy appeared to be six releases of two birds (Fig. 5(c)), and this nearly achieved the goal of reducing extinction probability over 50 years to a low of 5%.

Scenario 4: increasing population size through the existence of a metapopulation

We assessed the potential effect of establishing a network of populations of the bearded vulture in areas near Corsica that were either formerly inhabited by the species (Sardinia; Schenk, 1976) or that are currently being repopulated after a successful reintroduction programme (southern French–Italian Alps; Arlettaz, 1996). While there is hardly any information on dispersal rates between extant bearded vulture populations, the recent progressive scattering of the reintroduced population in the Alps (Frey and Zink, 2000) and the spatial expansion of other reintroduced vulture populations over large areas (Sarrazin and Legendre, 2000), would suggest the possibility of modest dispersal rates for the species once local populations are established. We modelled the effect of metapopulation behaviour in systems of two and three bearded vulture populations on the extinction risk faced by the extant Corsican population. In our simulations, each population had the same demographic rates and initial age structure as the extant Corsican population. We varied the values of the two main parameters determining the extent to which dispersal events alter local population dynamics: dispersal rates and environmental correlations between pairs of populations (Burgman et al., 1993). Dispersal rates, expressed as the proportion of fledglings dispersing between populations, varied from 0.005, 0.01, 0.02, to 0.05 (the last value corresponds to a rate of one fledgling in 20 that disperse to each population per year). Environmental correlation, expressing the similarity of fluctuation of environmental conditions of two populations, ranged from 0.125, 0.25, 0.5, to 0.75. We thus formed 16 combinations of these parameter values that were separately simulated for 25 and 50 years. The results (Fig. 6) show that the even modest dispersal rates between populations (at the current abundance and age distribution of the Corsican population, a rate of 0.05 in a three populations system corresponds to the natal dispersal of one juvenile every six years) having relatively similar environmental fluctuations could decrease the extinction risk of the Corsican bearded vulture population over 50 years from ca. 16% to less than 5% especially in the system of three interconnected populations.

4. Discussion

4.1. Validity of the model and sensitivity analysis

Although population viability analyses (PVA) can rarely identify the actual causes for population declines, they allow one to explore the relative importance that different factors (including factors having a systematic impact on a species' demography) have on the extinction risk (Reed et al., 2002; Beissinger and McCullough, 2002). However, despite their increasing use for making management and conservation assessments and for determining priorities for threatened and endangered species (e.g. Beissinger and McCullough, 2002; Morris and Doak, 2002), demographic PVA models should be viewed with caution as they require a large amount of age-specific demographic data rarely available for endangered species. Our results showed that the bearded vulture in Corsica has a relatively high extinction risk (16.5% during the next 50 years) mostly due to the effects of demographic stochasticity arising from its small, although relatively constant, population size (see Bennett and Owens, 1997 for general discussion). Moreover, the bearded vulture Corsican population is currently restrained to its current size (although it could potentially increase at a growth rate of 1.6% per year) because it seems to be close to its carrying capacity (25 against 40 individuals). However, these results must be interpreted with caution given that several key parameters were missing either for the bearded vulture as a whole, or for the Corsican population. As with any model, a detailed assessment of parameter estimates as well as a careful sensitivity analysis must be conducted before reaching definite conclusions about model predictions.

A Ceiling model of density dependence was chosen, as it is likely to better reflect the type of regulation existing in Corsican bearded vulture population, compared to the contest model. Bearded vultures are probably able to increase their hunting effort to compensate for the decreases in resource abundance (as other raptors: Newton, 1998), but their hunting success is ultimately dependent on prey death rate, which is unrelated to bearded vulture searching effort (because they do not kill their prey). Thus, the population may slowly approach its carrying capacity while still growing at maximum rate, which is best depicted in the ceiling model in which the values of the demographic rates do not decline monotonically as population size increases to the carrying capacity.

Reliability of estimates of survival rates is low as they are based on small number of birds that have been followed and resighted in the Spanish Pyrenees. For instance our results showed that, within the range of values and demographic rates considered, pre-adult survival was the demographic parameter whose variation had the largest influence on the predicted extinction risk. This result may seem counterintuitive since adult survival is the demographic rate that mostly determines the deterministic, asymptotic growth rate of long-lived species (e.g. Bennett and Owens, 2002). As the average survival rates of adults and preadults were similar, we suggest that the higher sensitivity of the extinction risk to changes in preadult than to adult survival is because the temporal variability of the latter is roughly twice that of the former (Table 1). Interestingly, preadult survival is also the demographic parameter suggested to have had the largest impact on the bearded vulture increase in the Pyrenees, where increases in adult recruitment over the last 15 years have been linked to increases of preadult survival, despite of the concurrent decline in breeding success (Antor, 1999; Margalida et al., 2003; Razin and Bretagnolle, 2003).

It is also possible that the low observed breeding success of the Corsican bearded vulture could be due to inbreeding depression related to the small size of this population (review in Hedrick and Kalinowski, 2000), although the levels of genetic variability of this population remain to be assessed. There is currently no reason to believe that adult mortality due to poaching might be an important threat for the Corsican bearded vulture, since only two cases of illegal killing have been reported over the last 15 years.

4.2. Future of the Corsican population of the bearded vulture

Given that demographic stochasticity appears to be one of the main threats to the Corsican population of bearded vulture, conservation strategies should aim at increasing the population or metapopulation size to, or above, roughly 50 adults. We investigated four different scenarios, of which the release of two juveniles every other year for 12 years and the increase of fecundity (for instance through selective food provisioning) may reduce by more than one-half the current extinction risk of Corsican bearded vulture population. Although these two conservation strategies may have the greatest impact on extinction risk, they do not necessarily represent the most realistic strategies from the viewpoint of implementation. The rationale, feasibility and model implementation of each conservation scenario is discussed below.

Food supplementing is currently the main conservation strategy used for bearded vulture across Europe, in Spain, France (Pyrenees and Corsica) and Greece (e.g. Heredia and Razin, 1999; Xirouchakis et al., 2001). These food supplementing programmes in the French and Spanish Pyrenees have led to increases in the adult recruitment through, apparently, the increase in preadult survival rather than productivity of pairs (Antor, 1999; Garcia et al., 1996). It is worth noting that direct evidence of this causal link is missing (though probable), since wild ungulate populations in these areas have also increased at the same time (Razin and Bretagnolle, 2003). Nevertheless, contrary to our expectations, even substantial increases in the carrying capacity through large supplemental feeding produced very modest decreases in the extinction risk, thus calling into question the efficacy of one of the main pan-European conservation strategies for this species. We suggest that the reason why the similarly large food supplementation in Corsica (currently 2.5 tons of carcasses per year) has not had the positive effect observed in the Pyrenees is because the Corsican population is much closer to its carrying capacity than those of the French and Spanish Pyrenees. The carrying capacity is largely determined by number of ungulate carcasses whose availability can be estimated with very reasonable accuracy in Corsica.

While estimates of carrying capacity at the French and Spanish Pyrenees are unavailable, they are bound to be much larger than the current bearded Vulture population abundance, which would allow further increases of the bearded vulture populations in these areas.

The second scenario involves artificial feeding at a selective breeding stage that would help to increase fecundity from its current average value of 0.18 to ca. 0.30 fledglings per pair per year. Selective food provisioning at the nest has been already done in other raptor species, either as an experiment or as a conservation measure (e.g. hen harrier *Circus cyaneus*, Redpath et al., 2002). Selective feeding (with flesh and skin rather than bones) at early chick rearing stage is currently undertaken in some areas in Spain, but we still lack a quantitative evaluation of the effect of this type of feeding on the breeding success of bearded vulture. It appears that most breeding failures in Corsica occurs at the incubation stage, while the remaining failures occur at late chick rearing stage, thus suggesting that selective feeding should perhaps take place at other breeding stage than early chick rearing.

The third scenario, reinforcement of the Corsican population by releasing fledglings, depends on the availability of these birds from captive breeding programs that are extremely costly and take a long time for long-lived birds. However, similar strategies have been used successfully for other vulture species, such as the griffon vulture in central France (Bonnet et al., 1990), the California condor (Snyder and Snyder, 2000) and of course the bearded vulture. In the case of the bearded vulture, this strategy would be easy to start, given the presence of breeding centres in Austria, France, Germany, Spain and Switzerland (Frey, 2000). However, no birds from Corsica are currently held in captivity. Three questions would thus have to be answered: which birds, how many, and how long. Recent studies (Negro and Torres, 1999; Gautschi, 2001) show the existence of genetic differences between birds from Asia (that have been used for reintroduction programs in the Alps) and those from the Caucasus, Greece and Western Europe. No studies have yet evaluated Corsican birds, but a comparative study among European populations has shown that the two extinct populations from Sardinia and Alps (before reintroduction) had an important gene flow (Gautschi, 2001), suggesting that Corsican bearded vultures should have belonged to the same lineage. Thus, the captive breeding stock currently used in the Alps could probably be used for reintroductions in Corsica (though see Gautschi, 2001 for a discussion on outbreeding depression on reintroduced bearded vultures in the Alps, suggesting that this issue should be considered before carrying out any reintroductions in Corsica). Second, our results suggested that even very low numbers of releases would reduce extinction risk. Similar released number of juveniles have been used in the reintroduction of this species in the French Alps, where between 2 and 5 fledglings were released annually between 1987 and 2000 (Frey, 2000). In our approach however, we assumed that all juveniles introduced become part of the breeding population (and there is no dispersal), which is probably unrealistic, and thus a slightly higher number of juveniles should be released to account for potential difficulties of integration of these released individuals into the breeding population. Lastly, if started, the reintroduction strategy should be continued until the breeding population size in Corsica reaches 50 birds.

The last conservation strategy consisted in re-establishing a population network within the Mediterranean. While this could be a very efficient strategy, its efficacy depends on the spatial extent and the magnitude of dispersal among populations that is currently unknown. Running a simulation of the current Corsican population with the demographic rates of the basic model for a much longer time window (500 years), the population size must exceed 750 individuals in order to achieve an extinction risk lower than 5%. This figure of 750 individuals is clearly unrealistic given the size of mountain areas in Corsica and thus suggests that exchanges with other neighbour populations must have occurred over historical time. Anecdotal evidence further suggests that bearded vulture actually travel large distances: there are at least two birds from northern Corsica observed flying north over the sea (Thibault, 1983), and another Corsican bird was photographed in north-west Sardinia in 1996. We are therefore confident that Corsican bearded vulture population could be connected to distant populations: the best strategy appeared to consist of a network of three, rather than the tow currently existing populations (Corsica, and the Alps), thus advocating for a reintroduction program in Sardinia.

4.3. Conservation of small and insular populations of long-lived raptors

Populations of large raptors, especially when they reach very small sizes are particularly sensitive to reductions in demographic rates, notably survival rates. However, contrary to California condor (Meretsky et al., 2000), we found that bearded vulture would be able to cope with rather high mortality rates. A 10% increase of mortality rate could be compensated by increase in fecundity reaching ca. 0.8 fledglings per pair, a value which is high but that has been observed for several years in the populations of the Spanish and French Pyrenees.

Apart from these demographic issues, we further suggest that insularity is also a key factor. During mid and late Pleistocene, the main Mediterranean islands (Balearics, Corsica, Crete, Malta and Sardinia) sheltered large raptor species (eagles *Aquila* spp., *Haliaeetus albicilla*, vultures *Gyps* spp., *Aegypius monachus*, *Gypaetus barbatus*, eagle-owl *Bubo insularis*: see Alcover et al., 1999; Louchart, 2002). Their presence was associated with medium-sized and small wild endemic ungulates and lagomorphs (Alcover et al., 1999; Robert and Vigne, 2002). Some of these species had large breeding ranges over the Palearctic, being distributed on islands as well as mainland (e.g. *Gyps melitensis*, *Gypaetus barbatus*), and their persistence on islands could have involved metapopulation functioning. However, other species (e.g. *Aquila* sp. nov. and several subspecies of *A. chrysaetos*; Alcover et al., 1999; Louchart, 2002) that were strictly endemic to those islands had specialised morphology, suggesting that they were adapted to a narrow trophic niche. Rapid extinction of the insular mammal fauna during the Holocene following human colonisation (Vigne, 1992; Vigne et al., 1997) led to the extinction of the endemic large raptor species. Conversely to those specialised taxa, more ubiquitous large raptor species that were distributed over the Palearctic were able to survive at least until the mid-twentieth century on the Mediterranean islands, thanks to the raising of goats, sheep and cattle following human colonisation, and to their dispersal abilities.

Our results suggested that the metapopulation (including reinforcement) and the supplemental feeding conservation strategies would have the highest impact. Supplemental feeding, as we have seen, may not work in Corsica. Furthermore, compared to the reinforcement strategy, the metapopulation strategy has two critical advantages: first, it mimics the likely population structure that existed over historical time and second once the metapopulation is established, there would be no further need for any conservation action.

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