

When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps

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Summary

1. Reintroductions are commonly used for re-establishing self-sustainable populations in formerly inhabited areas. Reintroductions are expensive, and thus, it is worth performing a thorough demographic analysis of current and likely future population trajectories to guide strategic decisions on release policy.

2. Bearded vultures *Gypaetus barbatus* were exterminated from the Alps in the late 19th century, mainly due to human persecution. To re-establish them, captive-bred young have been released annually since 1986. Since the first successful breeding in the wild in 1997, the population has increased to 9 pairs in 2006. It is not known, however, for how long releases should be continued to obtain a self-sustaining, viable population.

3. We estimated age-specific survival probabilities with a mark–resighting model and quantified fecundity rates of released individuals. Using the resulting demographic estimates, we built a stochastic population model to estimate population growth rates, and explored the value of continuing to release birds for varying periods into the future.

4. Annual survival probabilities were high (first year of life, 0.88; later years, 0.96); average annual fecundity was 0.6 fledglings per breeding pair. Using the estimated survival probabilities, projected population growth rates would increase with additional years of releases. Yet, the population would grow, even if releases had stopped after 2006. Only if mortality increased by $\geq 50\%$ would the population start to decline.

5. *Synthesis and applications.* Our population dynamics model provides essential information to optimize decision-making within a major reintroduction programme. From a demographic viewpoint, releases of captive-raised bearded vultures can be ceased in the Alps. The resources freed could be redirected towards a close demographic surveillance of the free-ranging population, with periodic evaluation of its viability and the option to release birds if deemed necessary. Birds available from the captive stock could be used for reintroductions in other areas where the bearded vulture is extinct.

Key-words: Alps, conservation, fecundity, *Gypaetus barbatus*, population growth rate, parameter uncertainty, survival probability

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Introduction

Animal population reintroductions and translocations are likely to become a key tool in conservation biology in the 21st century (Sarrazin & Barbault 1996; Seddon, Armstrong & Maloney 2007). Reintroductions usually involve the intentional release of individuals from captive-reared stock into a species' historical range, or translocation of individuals from thriving populations into relict populations. Reintroductions make sense only when the principal cause of extinction has been eliminated (Griffith *et al.* 1989).

Although reintroductions and translocations are currently widely used to reinstall or restock populations, strategic decisions about release policy within such programmes are still too often based on empirical rules of thumb rather than on appropriate, quantitative scientific assessment. This is often associated with a lack of clearly defined quantitative goals and/or insufficient monitoring of the success or failure of the chosen management (Sarrazin & Barbault 1996; Seddon 1999; Armstrong & Seddon 2008). Several techniques developed by population biologists exist, which can assist in taking appropriate strategic decisions (Norris 2004). Often, released and translocated animals are individually marked, and therefore, vital rates can be estimated using capture–recapture models. Knowledge of these rates allows us to conduct population viability analyses which can provide decisive insights into management (Beissinger & Westphal 1998). Quantitative demographic analyses of reintroduced species are scarce (Sarrazin & Barbault 1996) and biased towards successful projects (Seddon, Armstrong & Maloney 2007). In order to orient future strategic decisions, we applied the demographic approach to the bearded vultures *Gypaetus barbatus* (Linnaeus) which have been reintroduced into the European Alps. This reintroduction programme is one of the largest and most publicized European reintroduction projects ever conducted.

The bearded vulture is a large (4.5–7.1 kg) scavenging raptor that mainly feeds on bones of medium-sized wild and domestic ungulates, and inhabits mountain ranges in Eurasia and Africa. It went extinct in the Alps between the late 19th and the early 20th century (Mingozzi & Estève 1997) mainly due to shooting and poisoning. In 1986, an international reintroduction programme, based on the release of birds born and reared in captivity was launched (Frey 1992). By 2005, 137 individuals had been released. The first successful reproduction of released birds in the wild took place in 1997, and by 2006, 9 breeding pairs were established across the range, with habitat preferences for limestone areas with abundant populations of ibex *Capra capra* L. and chamois *Rupicapra rupicapra* L. (Hirzel *et al.* 2004).

It has been proposed that releases in the Alps should be ceased as soon as the mean yearly number of wild-born fledglings equalled the average number of yearly released young ($n = 6.5$; Zink 2005a). A linear model of the number of wild-born fledglings against year predicted that this number would be greater than 6.5 by 2007. This strategy may be erroneous, as it focuses on productivity alone, a parameter whose relevance for population dynamics in a long-lived species is likely to be low

(Lebreton & Clobert 1991), and as it does not consider other relevant demographic parameters. Moreover, as the annual number of released individuals is used as the target, the management decision is not objective: the ultimate goal is the establishment of a naturally, self-sustaining population *in the wild*.

This study aims to estimate for how long further releases of young will be necessary for ensuring the long-term viability of the Alpine bearded vulture population. However, we focused on the establishment of a self-growing population (Armstrong & Seddon 2008) as a first step towards viability, without considering density dependence since we had no reliable estimate of the carrying capacity. We used a demographic model that incorporates all key demographic parameters estimated directly from data on the released individuals. We explicitly considered uncertainty in the parameter estimates for the population modelling to ensure careful management recommendations (Ellner & Fieberg 2003). Such a demographic assessment is also central for an optimal allocation of financial resources as every young has accumulated costs of up to €70 000 by the moment of its release (Frey 1998). Finally, we estimated the sensitivity of the population growth to changes in survival probabilities to explore the possible impact of an increased use of illegal poisoned baits. These may be used against the naturally expanding wolf *Canis lupus* L. population in the Alps (Valière *et al.* 2003), and might represent a serious threat to bearded vultures.

Methods

RELEASE OF YOUNG

Young bearded vultures reared in different zoos were released at an age of about 3 months (~3 weeks before fledging) in artificial eyeries at four sites well scattered across the entire Alpine range (Frey 1992). Starting in 1986, up to three birds were released per site annually, amounting to 137 birds released by 2005. The released birds were fed artificially until they were independent. All birds were marked individually prior to release with colour rings and with an individual pattern of bleached wing or tail feathers. The latter marks enable individual recognition until the termination of the first moult (until 2–3 years of age; Arlettaz 1996).

DATA COLLECTION

Throughout the Alps, professional ornithologists and hundreds of volunteer birdwatchers have monitored movements of the released birds since the beginning of the release programme. The birds were monitored before the start of wing and tail feather moult at 1–2 years of age, using the patterns of bleached feathers, and later by recording the individual colour ring codes. Moulting patterns, if discernable on pictures of birds in flight, were used when a good time series of photographic documentation was available for a given bird (Arlettaz 1996). In addition, recoveries of dead birds were recorded. Observations were transferred into a central data bank (International Bearded Vulture Monitoring, Vienna; Zink 2005b), where a reliability check was performed; specifically, double entries for a same bird in distant areas on the same day were eliminated, as they were indications of misidentifications. Such errors were scarce (< 5% of the observations). We restricted our analysis to observations relating to birds of certain identity.

The general survey demonstrated the dispersal potential of the species: many individuals moved several hundred kilometres from the release sites, and some individuals eventually settled far from these sites (Arlettaz 1996; Hirzel *et al.* 2004; Zink 2004). As a consequence, we consider the whole Alpine population as a single functional demographic unit in our analysis.

Monitoring of pair formation and reproductive success was conducted by trained biologists. The good spatial and temporal survey coverage as well as a high number of sightings of identified birds by independent observers within a given area suggests that the chance of failing to locate a territorial pair is low, and the chance of failing to detect a breeding pair is close to zero.

ESTIMATION OF SURVIVAL PROBABILITIES

From 1986 to 2005, 137 individuals were released, five died before they fledged and 132 individuals were included in our analyses. Naturally born individuals (33 up until 2006) were not considered, because they were not marked individually.

To estimate survival probabilities, we considered mark–resight data of the 132 individuals from 1986–2005, and dead recoveries up until May 2006 from the whole Alps. Only resightings ($n = 250$) from the months June–October in each year were included in order to meet the assumption of capture–recapture models that resightings shall be obtained within a short period of time. Additionally, 17 dead recoveries from throughout the year were considered.

We used a probabilistic multistate capture–recapture model (Nichols *et al.* 1992) to estimate annual survival probabilities jointly from the mark–resighting data and the dead recoveries. The model was constructed in such a way that an immediate resighting effect could be modelled (i.e. individuals that were seen in the preceding year had a higher probability to be seen in the current year than individuals that were not seen in the preceding year), which was detected by a goodness-of-fit test. We used U-CARE (Choquet *et al.* 2001) and E-SURGE (Choquet, Rouan & Pradel 2009) to analyse these data (see Supporting Information, Appendix S1).

MODEL SELECTION

Our aim was to obtain reliable survival estimates of released bearded vultures in order to perform a population viability analysis. We formulated different models and performed model selection based on the Akaike's Information Criterion adjusted for small sample size and overdispersion (QAICc, Burnham & Anderson 2002).

The life history of bearded vultures can be decomposed into four phases: juvenile, prospecting, establishment and territorial phases, respectively. The first year of life corresponds to the juvenile phase, when young become progressively independent from the adults. The next 2 years (2–3 years of age) can be considered as a dispersal phase, when immatures prospect and evaluate the landscape on a broad scale. Subadults at 4–5 years of age enter an establishment phase when they get more and more sedentary. Finally, in their sixth year of life, bearded vultures become fully territorial, adopting a definitive adult plumage; this is also when first breeding attempts may take place. Survival probabilities might differ between these phases. For instance, we expected lower survival in the juvenile and prospecting phases, compared to the establishment and territorial phases, because there are risks when birds enter an unfamiliar environment without the assistance of parents. Based on these life phases, we considered three different models for the age-specific changes in survival. The first model considers different survival probabilities for each phase

(denoted a4), the second assumes equal survival probabilities in the establishment and the territorial phases (a3), and the third assumes equal survival probabilities in the prospecting, establishment and territorial phases (a2). We also considered models in which survival probabilities varied across years. Only additive models (i.e. annual variations were the same in all age classes) were included due to their low number of parameters. Interactive models would have had very limited power to detect differential temporal variation for each age class given the small sample size.

Resighting probabilities were likely to depend on the age of the individuals because bleached feathers are lost during the first moult and because of the different behavioural patterns during the four phases described above. For example, during dispersal, birds may move to sites where fewer observers are active, which would decrease detection probability. We considered the same three age-class models as above for the resighting probabilities, as well as an additional model where the resighting probabilities did not depend on age. We always considered an immediate resighting effect, and also included models where the resighting probabilities had an additive time effect. If temporal variation in resighting had been present, it would have been induced by varying resighting effort, which would affect all individuals in a similar way.

We considered two age classes for the dead recovery probability. The probability of recovering dead birds might be higher in the first year than in later years because released birds usually remain close to the release sites, where the observation effort is much higher. We also included models without an age effect and models with additive time effects.

We conducted model selection in two steps because of the potentially large number of models. For the first modelling step, we considered 33 models (combination of 8 models for resighting with 4 models for dead recovery, plus a model close to that used to assess the goodness-of-fit). We identified the smallest set of models whose Akaike weights (w_i) sum to 0.95 (95% confidence set). In the second modelling step, we combined the structures of resighting and dead recovery included in the 95% confidence set with the six a priori defined models for survival. Finally, we calculated the model averaged mean for the parameters of interest based on the w_i .

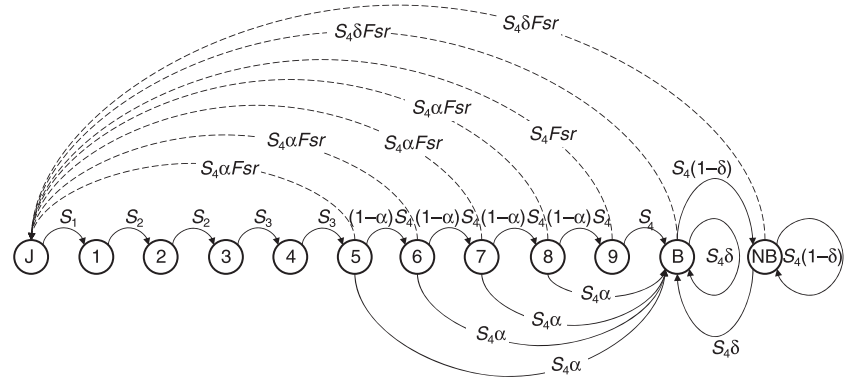
ESTIMATION OF FECUNDITY

Fecundity (F_t) was estimated as the production of fledglings in year t divided by the number of territories occupied by adult pairs in year t . A territory was considered as occupied from the year of first successful breeding onwards as long as an adult pair was present.

POPULATION MODELLING

Based on our life-history trait estimates, we constructed a post-breeding census, stage-classified projection model (Caswell 2001) with 12 stages. Six stages refer to the six age classes before maturity (J and 1–5; Fig. 1), four stages refer to mature individuals that have not yet reproduced (6–9), one stage refers to breeders (B) and one stage refers to mature non-breeders (NB). Survival probabilities were age-dependent as identified in the survival analysis. We assumed that reproduction starts at 6 years of age (Bustamante 1996; Brown 1997; Antor *et al.* 2007). Each year, half of the still inexperienced breeders (classes 6–9, Fig. 1) start to reproduce ($\alpha = 0.5$), and at 10 years of age all are assumed to have reproduced at least once. Always present in bearded vulture populations (Carrete *et al.* 2006), non-breeders were incorporated by assuming that a fraction of the potential

Fig. 1. Sketch of the life cycle of a bearded vulture population with post-breeding census as used for the present modelling. The nodes refer to the different stages with J, juveniles; 1–9, 1 to 9-year-old, inexperienced breeders; B, breeders; NB, non-breeders. The recruitment transitions are shown with broken lines, the survival transitions with solid lines. S_1 , first year survival; S_2 , annual survival from age 1 to 3; S_3 , annual survival from age 3 to 5; S_4 , annual adult survival; F , reproductive success; sr , sex ratio; α , probability that an as yet inexperienced mature individual starts to reproduce; δ , breeding probability. Note that only the female segment of the population is shown; the complete model includes males as well.



breeders skips reproduction each year. Furthermore, we assumed that fecundity of the reproducing individuals does not change with age. We explicitly modelled both sexes, since random deviations from an even sex ratio can affect population growth negatively in a small population (Legendre *et al.* 1999). The number of breeding pairs in a given year was assumed to be equal to the smallest number of reproducing individuals of either sex.

In order to incorporate demographic stochasticity, we modelled survival, fecundity, probability of starting reproduction, and breeding probability as binomial processes for each sex independently. The binomial process for fecundity was chosen because bearded vultures have at most one fledgling per year (Margalida *et al.* 2003). Mathematical details for the population model are provided in Supporting Information, Appendix S2.

Based on the estimated survival probabilities and on the number of released and wild born individuals, we calculated the number of individuals theoretically alive in each age class by 2006. The estimated number of experienced breeders amounted to 50 individuals (25 breeding pairs). However, we used the actually observed number of breeding pairs in year 2006 (9) and assumed that the remaining individuals will never reproduce. This leads to a very conservative scenario. Based on this initial stage-specific population size vector (7, 7, 6, 4, 5, 3, 2, 1, 0, 0, 9, 0) for each sex, we used simulation to model the population development. We modelled population growth over the next 25 years, since this is a time horizon relevant to management recommendations regarding future release policy. We estimated the population growth rate with a linear regression model of the logarithm of the annual number of breeding pairs against time (Caswell 2001). Ten thousand populations with these features were simulated to generate mean and 95% confidence intervals of the population growth rate. Simulations were performed in R (R Development Core Team 2004), and code is available in Supporting Information, Appendix S3.

To account for the uncertainty regarding the estimated survival probabilities in the population modelling, we generated for each iteration specific values from a beta distribution using the model averaged estimates of the mean and the variance of all age-specific survival probabilities. Uncertainty of fecundity was accounted for by creating for each iteration a binomial random variable using the total number of fledglings and the total number of breeding events as parameters. These generated parameter values were held constant across time for the given iteration.

Our main interest was to decide whether further releases of young are essential to ensure an optimal population development, and if so, for how long releases should continue. We therefore considered scenarios reflecting various durations of releases in the future. First,

we assumed that no further release took place after the releases in 2006. In the next cases, we assumed that 3 females and 3 males would be released each year for the next 5, 10 or 25 years. The uncertainty about some demographic parameters (fecundity, breeding probability) was accounted for in different scenarios. Our sample size was too small to test whether fecundity was constant or stochastic; consequently, we considered two options. In the constant case, we used the observed mean reproductive success (F) in the simulations. To model environmental stochasticity, we randomly chose a year-specific, observed fecundity (F_t). Because the fluctuations were very wide when the population size was low, we only considered annual fecundities from 1999 onwards. Further uncertainty surrounds the breeding probabilities (δ). We considered four scenarios ($\delta = 1, 0.8, 0.6$ or 0.4) to include a range from optimistic to pessimistic. The value of $\delta = 1$ is very optimistic and unlikely to be true, since floating non-breeders occur in many bearded vulture populations (Carrete *et al.* 2006). By contrast, the value of $\delta = 0.4$ is pessimistic in the long term, although it is similar to what is observed currently in the Alps. Based on observations in the Pyrenees, we regard $\delta = 0.8$ to be the most realistic value (Carrete *et al.* 2006). Thus, in total we considered 32 different scenarios (4 different duration of releases \times 4 different breeding probabilities \times 2 different fecundities).

Results

ESTIMATION OF SURVIVAL PROBABILITIES

Modelling of the resighting and dead recovery probabilities revealed that five top-ranked models yield a summed QAIC weight of > 0.95 (Supporting Information, Table S1). In these models, neither resighting nor dead recovery probabilities were time-dependent, but there was considerable uncertainty regarding the age structure in both parameters. We combined the resighting and dead recovery structure of these five models with the six different models of survival, obtaining 30 models in the final modelling step (Supporting Information, Table S2). Modelling uncertainty was considerable again, in particular regarding the age structure of the resighting and dead recovery probabilities. The four top-ranked models had constant survival probabilities across time and incorporated two age classes (first year vs. older individuals, QAIC weights summing up to 0.56), whilst lower-ranked models differentiated between three to four age classes.

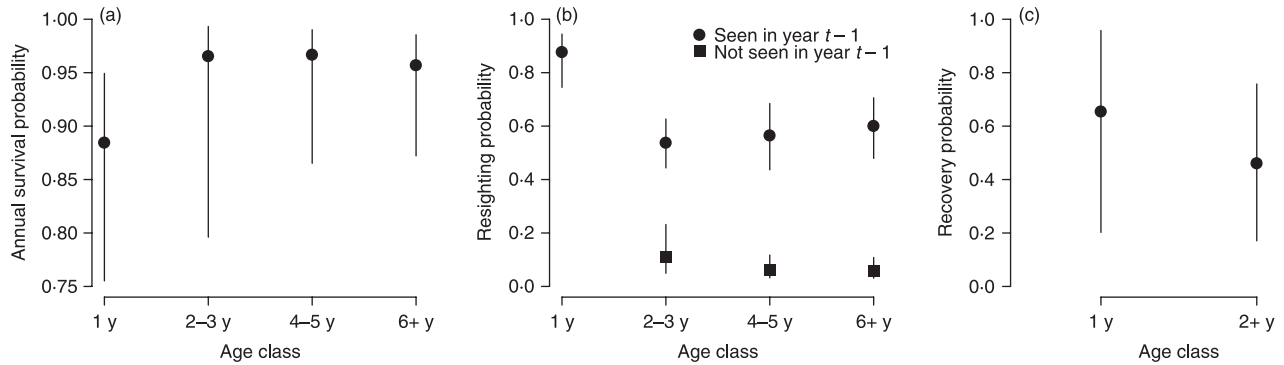


Fig. 2. Model-averaged probabilities of survival (a), resighting (b) and dead recovery (c) for bearded vultures in the Alps in relation to their age and previous resighting history. The over-dispersion coefficient was $\hat{\epsilon} = 1.224$. The vertical lines show the unconditional 95% confidence intervals.

The model averaged survival probabilities were lowest in the first year, as expected. Thereafter, however, they did not change much with increasing age (Fig. 2a). The 95% unconditional confidence intervals were relatively wide, reflecting uncertainty in the parameter estimates.

The model averaged resighting probabilities were highest in the year immediately following the release (Fig. 2b). If an individual was not seen in a year, the probability of recording it in the subsequent year, given that it survived, was very low. The dead recovery probabilities for young birds were higher than for older birds (Fig. 2c), but their confidence intervals were very large.

FECUNDITY AND POPULATION DEVELOPMENT

Bearded vultures reintroduced into the Alps from 1986 started to reproduce in the wild in 1996, totalling 55 breeding events with 33 fledglings by 2006. Average fecundity was thus 0.6, but there were considerable annual fluctuations (Fig. 3).

ASSESSMENT OF DIFFERENT RELEASE STRATEGIES

The projected average population growth rates over the next 25 years were > 1 , regardless of the duration of releases, the different options for fecundity and the different breeding probabilities (Fig. 4). They increased with increasing duration of releases. Mean population growth rates were higher when fecundity was constant than when affected by environmental stochasticity, but the difference was marginal. Increasing breeding probability affected population growth positively, but this effect declines the longer the releases continued. The confidence intervals of the population growth rate covered 1 only in the situation where releases stop immediately after 2006 and when the breeding probability is very low (0.4). Thus, a population decline cannot be ruled out completely under this pessimistic scenario, although it remains improbable.

The population growth rate strongly declined with increasing mortality (Fig. 5). Mortality needs to increase more than about 50% to render the mean population growth rate less than 1, indicating that such an increase can be supported even if no further individuals were released after 2006 and even if the breeding probability was low.

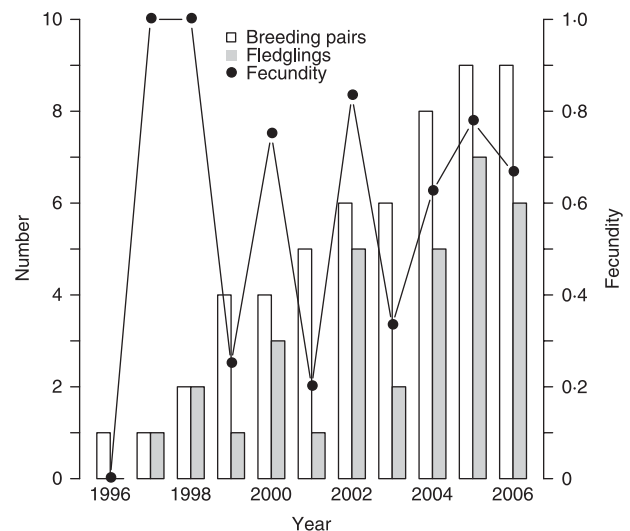


Fig. 3. Number of breeding pairs, total number of fledglings, and fecundity (number of fledglings per territorial breeding pair and year) of bearded vultures in the Alps from 1996 to 2006.

Discussion

This study represents the first attempt to estimate life-history traits of a free-ranging population of bearded vultures in natural conditions with reliable methods. This was possible because individuals were systematically marked from the beginning of the reintroduction and because we applied modern demographic estimation and analytical methods. Based on empirical estimates of vital rates, we could evaluate the growth rate of the Alpine bearded vulture population over the next 25 years under different durations of releases of captive-reared young while accounting for uncertainty in the estimates of the demographic parameters. Overall, our model suggests that the population will further increase even if releases cease after 2006, if breeding probability was low and if mortality increased slightly. We are confident that releasing young can cease without endangering the established population, as long as new factors of mortality such as poisoned baits does not increase mortality by more than 50%, fecundity remains the same on average and no catastrophic events occur.

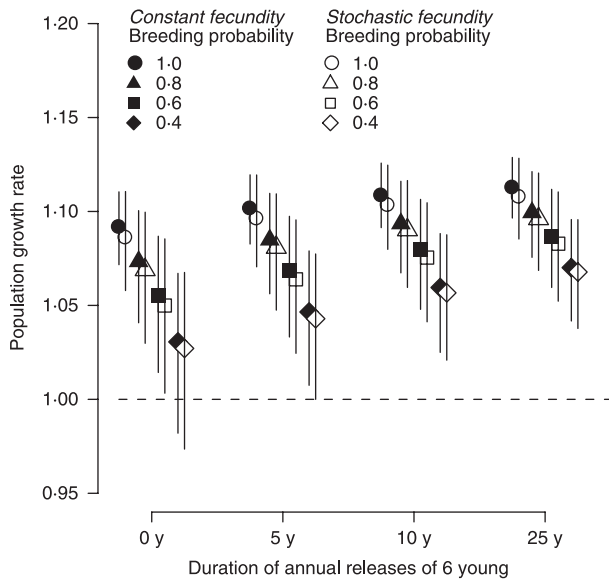


Fig. 4. Estimated population growth rates of Alpine bearded vultures averaged over 25 years in relation to different release strategies (no further releases after 2006, or releases of 3 males and 3 females each year for another 5, 10 and 25 years) and to different breeding probabilities, when fecundity is either constant or affected by environmental stochasticity. The vertical lines show the limits of the 95% confidence intervals.

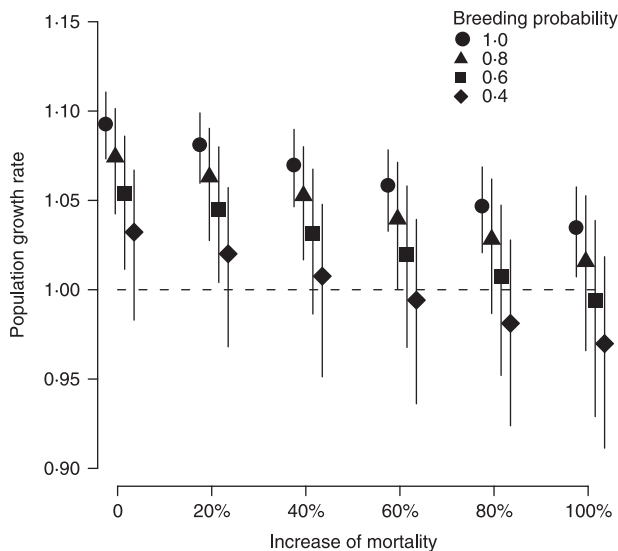


Fig. 5. Sensitivity of the population growth rate (averaged over 25 years) of Alpine bearded vultures to a linear increase of mortality rates across all age classes with variable breeding probabilities, when fecundity is constant and when no individuals were released. The starting values without increase of mortality (0 on the x-axis) refer to the average survival rates (Fig. 2). The vertical lines show the limits of the 95% confidence intervals.

Our population model is based on some simplifying assumptions, which may all impact on the modelling results. First, we did not consider environmental stochasticity for survival and age at first reproduction. If stochasticity occurs, the population growth rates would be lower (Tuljapurkar 1989)

and our conclusions too optimistic. However, given the survival probabilities that are close to 1 and the high sensitivity of population growth rate to survival, temporal variation of adult survival is expected to be small, and therefore, it is likely that any overestimation of the population growth rate is only slight. The sensitivity of the population growth rate to changes in the probability of starting to breed (α) is low, and therefore, variability needs to be strong in order to have any significant impact on population dynamics. Secondly, we assumed that adults that had not yet reproduced in the year 2006 would not reproduce in the future. If this assumption is wrong, which is very likely, then the population growth rate would in fact be higher than our conservative estimates. Taken together, we believe that the population growth rate estimates presented here are realistic.

Population growth is generally highly sensitive to changes in adult survival in long-lived species (Lebreton & Clobert 1991). Several studies have confirmed this to be the case for bearded vulture populations (Bustamante 1996; Bustamante 1998; Bretagnolle *et al.* 2004; this study) but previously, little was known about actual survival probabilities of free-ranging bearded vultures. Based on reliable methods, our estimates of survival recognize two age classes, where first year survival is slightly lower (0.88) than thereafter (0.96). A larger sample size and longer time series would be necessary to get more precise estimates, to detect finer age-structures and to assess the magnitude of temporal variation of survival probabilities. Moreover, data from naturally born individuals would be required to test if the release has costs in terms of survival, as observed in griffon vultures *Gyps fulvus* Hablitzl (Sarrazin & Legendre 2000; Le Gouar *et al.* 2008). Brown (1997) estimated survival of bearded vultures from South Africa using age ratio methods, which produces accurate estimates only under restrictive assumptions (Conn, Doherty & Nichols 2005). He obtained similar survival estimates for adults as the current study, but much lower estimates for young individuals during their first 4 years of life (~ 0.6). The only other information about species-specific survival probabilities comes from zoos, where bearded vultures appear to survive better than in the wild (year 1, 0.92; years 2–6, 0.99; year 6+, 0.97; Bustamante 1996).

Although we have estimated survival probabilities using a method which accounts for imperfect detection of both live and dead individuals, the precision of our estimates was relatively low. This mainly reflects the relatively small sample size (low number of individuals) and the heterogeneity of resighting probabilities among individuals. Although the monitoring was very intense, it was difficult to re-sight individuals once they had remained undetected for a year. Once they lost their conspicuous bleached wing feathers due to moulting, the resighting probability dropped dramatically because identification was then dependent on recording their colour rings or slight details in the moulting pattern, which is more difficult. Once birds became territorial, the probability of identification increased again because they mostly stayed within the same territory and observers invested a great deal of effort to identify territorial birds. Thus, resighting declined after the initial wing feather moult (second and third year of life,

i.e. prospecting phase) and increased during the establishment and territorial phases, which is well modelled with the trap-dependent resighting probabilities applied in this study.

As population dynamics are very sensitive to variation in survival and because little is yet known about the important demographic aspects (e.g. magnitude of temporal variation, sex-specific variation, survival of wild-born individuals), survival is a key parameter for future monitoring. The number of natural births will probably increase in the Alps in the near future, but so far naturally fledged birds have not been marked in order to avoid disturbances. This impedes any chance of monitoring survival of the reconstituting population. Genetic sampling (e.g. of feathers collected in the eyrie after fledging) seems to be a promising non-invasive method (Gautschi *et al.* 2000). If a mark-resighting-based monitoring programme, as the one developed here, is to be applied to genetic data, it must be ensured that repeated samples across years are collected from young and adult birds. In addition, sufficiently large sample sizes will be required, otherwise it will be difficult to detect small but relevant variations in survival probabilities. Furthermore, genetic tracking will presumably be expensive and its coverage will be less comprehensive than resightings of individually marked birds. In this respect, integrated population models, which combine demographic information from different sources may actually be useful to make the most efficient use of this diverse information (Schaub *et al.* 2007).

The average fecundity of 0.6 fledglings per breeding pair per year is a rough estimate due to the small size of the Alpine population. Yet, this value is within the range observed in other areas. In the Pyrenees, fecundity declined with increasing population density from about 0.8 to 0.4 within 25 years (Carrete, Donazar & Margalida 2006). Bearded vultures were more productive in South Africa (0.89, Brown 1997), but much less so in Corsica (France, 0.18, Bretagnolle *et al.* 2004) than in the Alps. As evidenced in other raptors (e.g. Krüger & Lindström 2001), fecundity in bearded vultures may decline with increasing density due to habitat heterogeneity (sub-optimal habitats colonized secondarily) and/or interference (Carrete, Donazar & Margalida 2006; Carrete *et al.* 2006). To date, there is no indication that fecundity is regulated by density in the Alps.

Based on our estimated survival probabilities and on the number of naturally born and released individuals, there should be 50 mature (at least 6 years old) individuals alive in 2006. Only 18 (9 breeding pairs, 36%) of these 50 adults were actual breeders that year, which in theory gives 32 additional mature individuals. Although non-breeding floaters are common in bearded vulture populations (Carrete *et al.* 2006), the comparative figure for the Alps seems to be very high. An important reason why so many mature individuals do not reproduce could be due to inverse density-dependent phenomena such as Allee effects (Derdedec & Courchamp 2007). First, the slightly biased sex ratio in the released individuals (43% males, 57% females, $n = 118$ sexed individuals), could lead to mating problems typical of small populations scattered over a huge area. Secondly, the local density of available

partners may still be too low in the Alps to allow mating choice and pairing to operate properly. For example, two of the released individuals only started to reproduce in their 13th and 17th year of life, respectively, which is an unusually old age for first reproduction in bearded vultures (Brown 1997; Antor *et al.* 2007). The observed annual population growth rate calculated from the number of breeding pairs between 1999 and 2006 was much higher (1.245) than the highest estimate drawn from our model (1.113). This difference cannot be explained by demographic mechanisms (e.g. immigration). The most likely reason is a sudden acceleration in the formation of new pairs and reproduction thereof, as the likelihood of new pair formations increases as a non-linear function of the number of mature birds within the population if an Allee effect occurs. We thus predict a decline in the proportion of non-breeding adults in the future, when this initial boosting mechanism will be over, with a progressive decrease of the observed population growth rate to values similar to those of our population modelling.

Although the Alpine bearded vulture population is presently increasing, with further releases judged superfluous, caution must be exercised with regard to any additional alteration of survival. Our model shows that the population would currently be capable of sustaining a 50% increase in mortality, even at very low breeding probabilities, which provides a buffer against potentially new emerging threats. Yet, in a population which consists of 50 individuals older than 6 years, an increase from 2 to 3 yearly fatalities would already lead to critical mortality levels. There is thus a real risk that the illegal practice of depositing poisonous baits against wolves currently recolonizing the Alps may obliterate the reintroduction effort. Tight monitoring of the poisoning situation is therefore essential to protect the bearded vulture population.

RECOMMENDATIONS FOR FUTURE MANAGEMENT

The model presented here shows that continued release of young bearded vultures into the Alps would enhance population growth rate, corroborating previous predictions (Bustamante 1998; Bretagnolle *et al.* 2004). However, the present analysis also demonstrates that the population has been self-sustainable since 2006. From a purely demographic viewpoint, we therefore recommend ending releases in the Alps and redirecting reintroduction efforts towards other areas where the species is now extinct (e.g. Sardinia, Balkans).

Demographic management in the Alps should now concentrate on close surveillance of the breeding pairs, with systematic collection of data on fecundity and survival probabilities of wild-born birds, which may differ from captive-reared birds. This requires systematic marking of young plus sampling of genetic material at the eyrie, practices avoided so far to minimize disturbance. In the future, analyses combining demographic and genetic information should be performed periodically. Further releases from captive populations should remain an option if the wild population declines in the future.

This study illustrates the relevance of detailed population modelling studies for orienting strategic decisions in large-scale reintroduction programmes. Even when the population size is still small, the acquired information may prove invaluable for directing conservation effort. Finally, reintroduction projects provide unique opportunities to gather data on the vital rates of free-ranging species which usually remain inaccessible for demographic investigations. Ironically, species that have become extinct in the wild, but have subsequently been rehabilitated in nature, may well be better understood than thousands of surviving species for which knowledge of their population dynamics would greatly assist conservation management.

Acknowledgements

We express our sincere thanks to the monitoring centres (Mercantour-, Ecrins, Vanoise-, Gran Paradiso-, Stelvio- and Hohe Tauern National Parks, Alpi Marittime Natural Park, ASTERS, Stiftung Pro Bartgeier, Réseau Gypaète Suisse Occidentale, Provincia Autonoma di Trento, Foundation for the Conservation of the Bearded Vulture) for allowing access to their data. We also thank hundreds of volunteers who regularly check bearded vultures across the Alps and report their observations. Marc Kéry, Lukas Jenni, Jean-Dominique Lebreton and two anonymous reviewers provided important comments on earlier drafts of the paper. Additional financial support was provided by the Stiftung Pro Bartgeier.

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Received 23 May 2008; accepted 14 October 2008
Handling Editor: Des Thompson

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details about the multistate-capture–recapture model

Appendix S2 Mathematical details about the bearded vulture population model

Appendix S3 R code for running the stochastic population model

Table S1. Modelling result for resighting and recovery probabilities

Table S2. Modelling result for survival probabilities

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