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Identifying key demographic parameters for the viability of a growing population of the endangered Egyptian Vulture *Neophron percnopterus*

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Summary

The Egyptian Vulture *Neophron percnopterus* is a threatened species throughout its world-wide range. The Iberian Peninsula holds 50% of its global population, which has declined by 25% over the last 20 years. Despite this negative global trend, an increase in the number of individuals over the last 25 years has been observed in Catalonia, where it has colonised areas in which it was previously unknown. In this study, we describe the demographic evolution of an increasing population of Egyptian Vultures in central and eastern Catalonia and we apply population models and maximum likelihood procedures to investigate both the main demographic processes driving the observed trends and the viability of the population. The number of pairs in this region increased from one to 22 in the period 1988–2012. The best-supported models suggest that adult survival in this population may be higher than in other Iberian populations and that furthermore, there is a continuous influx of immigrants. Based on the most likely scenarios, Population Viability Analysis predicts that the population will continue to increase. Sensitivity analysis indicates that the adult survival rate has the greatest influence on population dynamics so conservation efforts will be more effective if concentrated on improving this rate.

Introduction

Understanding the processes that shape population size and structure is one of the main objectives in ecology and is thus subject to extensive study (Begon *et al.* 1996, Levin *et al.* 2009). Population dynamics can be understood as the outcome of the addition (births and immigration) and loss (deaths and emigration) of individuals from a population. These demographic processes are regulated by both intrinsic and extrinsic factors: intrinsic factors consist of species' life-history traits such as age of first breeding, fertility, longevity and dispersal behaviour, whereas extrinsic factors are connected to environmental conditions such as food resources or weather, and are subject to marked variation over time and space (Levin *et al.* 2009). Currently, human activities have a severe impact on the environment (Loreau *et al.* 2001, Barnosky *et al.* 2012) and play an important part in the population declines and extinctions of species that are now occurring at unprecedented rates. Consequently, population theory plays a central role in modern conservation biology (Primack 2012). Population viability analysis (PVA) – the use of quantitative methods to predict the likely future status of a population – has

become a basic tool in current conservation research and practice (Morris and Doak 2002, Hernández-Matías et al. 2013). This type of analysis is based on a broad suite of population modelling and data-fitting methods of varying mathematical complexity whose aim is to estimate the expected values of the main descriptors of population dynamics that include the population growth rate and, particularly, the risk of extinction of a population over time (Beissinger and McCullough 2002).

In a global context in which many species are decreasing and/or are threatened, most PVA studies focus on analysing the causes of and possible solutions to human-induced population declines (Caughley 1994). Nevertheless, some species may in fact benefit from human activities (Duhem et al. 2003, Gangoso et al. 2012). The application of PVA methods to growing populations can provide useful quantitative information to understand demographic processes and to guide practitioners as it is commonly done for invasive species (Conroy and Senar 2009) and other threatened raptor species (Ortega et al. 2009). In this sense, tendencies in a species may vary from one population to another and, therefore, the study of populations with positive trends can provide very relevant information for conservation of declining populations. Usually, little demographic data are available for endangered species, but current statistical procedures may generate quantitative information useful to understand the demographic drivers of population dynamics and, consequently, provide evidence-based prescriptions to be applied by practitioners (Doak et al. 2005, Hernández-Matías et al. 2013).

The present work examines the recent expansion of the Egyptian Vulture population *Neophron percnopterus* in Catalonia (north-east Iberian Peninsula). To do so, we apply likelihood-based procedures on available field data in order to identify the demographic determinants of population dynamics and then we perform population viability analysis. The Egyptian Vulture ranges from the Indian subcontinent, Middle East, south-east of the former USSR to the Mediterranean Basin and the Sahel and eastern and southern Africa (Donazar 1993). This long-lived species lives in adult pairs that nest in caves situated on cliffs, defending the same territory year after year (Donazar 1993). Immature individuals are not territorial and usually form groups near predictable food sources such as landfills or supplementary feeding stations (Donazar 1993, Grande 2006). European populations of this species spend the winter in Africa (Sahel) and return to Europe to breed during spring and summer (Benítez et al. 2004).

The Egyptian Vulture is threatened worldwide and in recent decades its distribution has decreased significantly (Donazar 2004). At present, the conservation status of the Egyptian Vulture according to the IUCN Red List is 'Endangered'. Based on recent studies, the stronghold of this species' Palearctic population is in Spain (1,320–1,480 pairs) (Del Moral and Martí 2002, Donazar 2004). Even so, its Iberian population has declined by 25% over the last two decades (Donazar 2004), mainly due to poisoning and illegal persecution, but also as a result of the loss of traditional agricultural practices (Liberatori and Penteriani 2001, Donazar 2004) as well as electrocution and collision with power lines and wind farms in some areas of Spain (Donazar et al. 2002, Carrete et al. 2009).

In Catalonia this vulture declined in the 1960s and 1970s and became extinct in the most eastern part of its range (Muntaner et al. 1981, 1983). Nevertheless, in the late 1980s this tendency was reversed and some abandoned territories were recolonised (Estrada et al. 2005) and areas with no historical records were colonised. This is a paradigmatic case of a species in worldwide decline whose populations are decreasing at a local scale, except for part of its European range (north-east Catalonia), in which they are increasing and even expanding their distribution (García-Ripollès and López-López 2006, Mateo-Tomás et al. 2010).

The present study provides a demographic analysis of the colonisation by the Egyptian Vulture of an extensive area of Catalonia from 1988 onwards. The general aim of the study was to identify the demographical determinants of the observed population trend and to provide a useful guide for the conservation of this population and of other European populations currently in decline. The specific aims of this work are: (1) to describe the population dynamics from colonisation to the present day in the study area, (2) to estimate the vital rates in the study population, (3) to use

population models and likelihood-based methods to evaluate the contribution of immigration and adult survival to the observed past population growth rate, (4) to perform a PVA to predict the expected trend of the population and its risk of extinction, and (5) to identify conservation targets by analysing the sensitivity and elasticity of the population growth rate in relation to the main vital rates.

Materials and methods

Study area and data collection

The study area was located in central and eastern Catalonia (Figure 3) at altitudes in the range of 200–1,900 m asl throughout an area of cliffs running from the Prelittoral Mountains in the south to the pre-Pyrenean Mountains in the north. In between stretches a large lowland area covered mainly by farmland but with important extensions of forest and scrubland. The monitoring of this Egyptian Vulture population was carried out from 1988 to 2012. In 1988 only one breeding pair was known in the study area (Muntaner *et al.* 1983, Aymerich and Santandreu 1998). From this year up to 2012, regular cliff-nesting raptor censuses were performed in the area (Aymerich *et al.* 1991, Real and Mañosa 1997, Aymerich and Santandreu 1998, Baucells *et al.* 1998, Aymerich and Santandreu 2002, Guixé 2008, Hernández-Matías *et al.* 2013) and new colonising pairs located. All new occupied territories were monitored regularly in order to determine the level of occupancy and a subset of territorial pairs was monitored to obtain data on breeding success.

To determine the occupancy of territories, at least one visit was made with a spotting scope (20–60x) between March and mid-April. An area was considered unoccupied if no individuals were detected after four visits/days. At the end of the incubation period (42 days), nests were checked to detect the presence of nestlings. Seventy days after hatching, the nests were visited again to check the number of fledglings, which was used to estimate fledgling rates.

Life-history traits and life cycle

According to current knowledge of the life-history traits of this species, we defined a life cycle to be used in the population models described below. All simulations were based on this life cycle and only took females into account. The life cycle was based on a post-reproductive census of six age classes (Figure 1). After each breeding cycle, surviving females move into the next age class; only adult birds produce new individuals. In the results, the number of adult females was considered to be equal to the number of territorial pairs in the population.

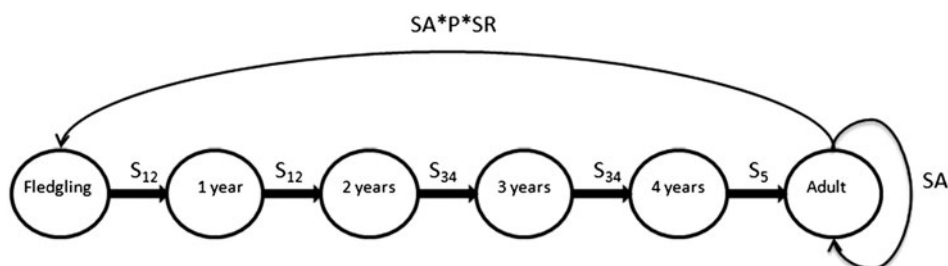


Figure 1. Diagram of the Egyptian Vulture life cycle. Nodes represent the different age classes considered in the model. S_{12} : yearly survival in first and second years of life, S_{34} : yearly survival in third and fourth years of life, S_5 : yearly survival in fifth year of life when the recruitment of individual occurs, SA : yearly survival of adult breeders, P : productivity and SR : sex ratio which was assumed at 1:1.

Estimation of demographic parameters

Based on the observed number of pairs, the population growth rate was estimated for the whole study period as $\lambda = (N_t / N_0)^{1/t}$, where N_0 is the initial population size, N_t the final population size and t the number of years between the start and the end of the study period. We also calculated the population growth rate during the period 1994–2012 given that this period was more appropriate for estimating the initial population size to be used in simulations. Productivity was calculated as the number of fledglings divided by the number of surveyed pairs. Other breeding parameters were calculated as breeding success (number of fledglings/number of laying pairs), fledgling rate (number of fledglings/number of pairs that have fledglings), percentage of laying pairs (number of laying pairs/number of territorial pairs), percentage of pairs with nestlings (number of pairs with nestlings/number of territorial pairs) and percentage of pairs with fledglings (number of pairs with fledglings/number of territorial pairs). Using the raw values of yearly productivity (and their associated sample variances), we applied White's method (White 2000) to obtain an estimate of productivity (corrected by the sampling variation associated with small sample sizes) and the temporal variance that we then used to simulate the environmental stochasticity of the models.

Survival estimations could not be made in the study population since ringing schemes have only been initiated in recent years. Additionally, methods based on age ratios (e.g. Hernández-Matías *et al.* 2011) were not applicable for this species since only territorial individuals in full adult plumage could be monitored with ease. Therefore, we employed in the models estimates available for this species obtained from a large-scale ringing scheme in 1990–2005 in the Ebro Valley, part of the species' largest population in the Iberian Peninsula (Grande *et al.* 2008). Survival rates of non-adults used in our models were: $S_{12} = 0.73$, $S_{34} = 0.78$, $S_5 = 0.60$. Adult survival was estimated using a subsample of territorial individuals and considering a model with the time effect (model 24 in Table 5 from Grande *et al.* 2008). Based on yearly estimates and the corresponding standard errors, we applied the method of White (2000) to estimate the temporal variance of this parameter.

Population models and the evaluation of the model assumptions

To carry out the simulations, the life cycle described above and shown in Figure 1 was portrayed in the model. To calculate how many individuals of each age class will survive and will pass on to the next age we applied Monte Carlo simulations, which allowed us to account for demographic stochasticity. To introduce demographic stochasticity on productivity we determined the probability of having zero, one or two fledglings for each productivity and then applied a multinomial distribution to calculate the number of fledglings for each year. Environmental stochasticity for adult survival and for productivity were incorporated into the model using their temporal variance estimates and simulated with, respectively, the 'beta' and 'stretched beta' distribution functions in package POPBIO (Stubben and Milligan 2007 based on the original code by Morris and Doak 2002).

Population models were initially used to assess the most likely factors explaining the observed population growth rate. To do so, we applied likelihood-based methods. We evaluated a set of models considering several sources of uncertainty regarding the degree of connection of the population with other populations (i.e. whether the population was closed or received immigrants) and the values of adult survival for the population. Evaluated models considered all possible combinations of assumed adult survival from 0.7 to 0.975 at intervals of 0.025, and immigration from 0 to 10 immigrants per year. The number of immigrants considered is the net number of adult females that arrive in the population assuming that both emigration and immigration occurs. Essentially, model choice relied on how likely the observed lambda is given each model's set of predictions. For each model the simulated lambda values resulting from 5,000 replicates were binned using fairly fine bins (0.05 bins). Then, the probability of the simulated lambdas being

within each bin was considered as a means of estimating the probability of seeing the observed lambda for the population, $P(\lambda)$. This probability was considered as a proxy of the likelihood of the observed lambda for each model. Models were chosen by comparing the $P(\lambda)$ for each considered model (Hilborn and Mangel 1997, Hernández-Matías *et al.* 2013). This analysis was restricted to the period 1994–2012 since before 1994 the population size was too small to be able to infer the initial population vector. By 1994 the territorial population consisted of three pairs and the initial population vector was approximated according to the stable distribution of ages obtained from the deterministic Leslie matrix model considering the life cycle and vital rates described above. The initial population vector considered was $n_0 = (1, 1, 1, 1, 1, 3)$, each vector element corresponding to the number of females in each given age class. Model scripts were developed in R code (scripts are provided in the online supplementary material).

PVA and the identification of conservation targets

We performed a PVA in which we considered four models. The first two corresponded to the two best-supported models in the previous analysis (scenarios 1 and 2 in the Results section). Additionally, we considered scenario 3 in which adult survival was assumed to be 0.891 (the most likely value provided by Grande *et al.* 2008) and the population was considered to be closed (0 immigrants per year). The last scenario (scenario 4) assumed the most likely adult survival estimated in the present study but considered a closed population. For each model, 5,000 replicates were simulated with a time horizon of 50 years. Population growth rate and extinction probability were calculated under each scenario (Morris and Doak 2002), whereby a population was considered to be extinct if the number of predicted breeding females was less than one. The probability of a fall by 50% in the number of pairs in 10 years was also calculated since this is one of the IUCN criteria used to classify a species as Endangered (IUCN 2012).

To identify the vital rates that had the strongest effect on the population growth rate we applied a simulation-based method in which the value of the vital rate of interest was increased by 25% and the values of λ recalculated (except for the number of immigrants, which was increased from one to two immigrants). To do so we considered the assumptions in scenario 1 in the Results section. Subsequently, we estimated the sensitivity and elasticity of λ to the main vital rates (S_{12} , S_{34} , S_5 , SA, P) and to the number of immigrants (N_{imm}).

Results

Population trends and estimation of demographic parameters

The population of the Egyptian Vulture in the study area grew from one to 22 pairs during the period 1988–2012 and expanded eastwards (Figure 2). The population growth rate observed this period was estimated at 1.137 (1.117 in 1994–2012). Productivity corrected by White's method was estimated at 1.168 (temporal variance = 0.404). Adult survival obtained with the same method was 0.891 and its temporal variance corrected was 0.003.

Other breeding parameters calculated were: breeding success 1.11 ± 0.60 , fledgling rate 1.17 ± 0.479 , percentage of laying pairs 83.54 ± 33.90 , percentage of pairs with nestlings 81.61 ± 32.47 , percentage of pairs with fledglings 78.45 ± 31.54 .

Evaluation of the model assumptions

Our estimates of likelihood showed a crest of maximum values tracing a (non-linear) diagonal from high values of survival and low values of immigration to low values of survival and up to five immigrants per year (Figure 3). Based on available information (Grande *et al.* 2008), values of adult survival below 0.85 would seem to be unlikely. Thus, we selected two scenarios as the best supported, one of which (scenario 1) assumed the entry of one immigrant per year and

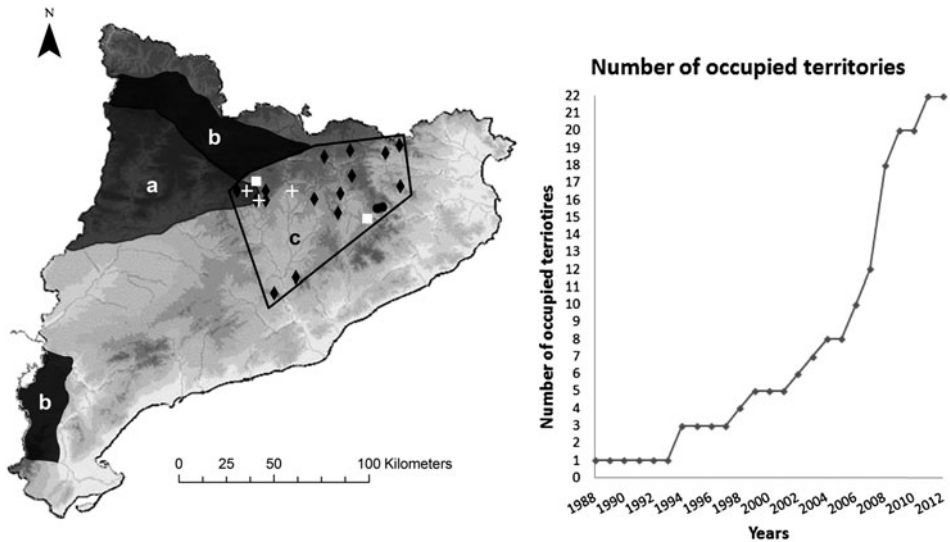


Figure 2. Left: Colonisation of Egyptian Vulture in Catalonia. (a) Represents the range of the species according to *Atlas dels Ocells nidificants de Catalunya* (Muntaner et al. 1983). (b) Represents the expansion of the species outside the study area, according to *Servei de Biodiversitat i protecció dels Animals, Generalitat de Catalunya* (2012). (c) Represents the study area. Symbols correspond to territorial pairs in the study area: white cross: 1988–1995, white square: 1996–2000, black circle: 2001–2005, black diamond: 2006–2012. Right: Number of occupied territories of Egyptian Vulture in the study area during the period 1988–2012.

adult survival of 0.950 (likelihood estimated at 0.947), while the other (scenario 2) assumed the entry of two immigrants per year and adult survival of 0.875 (likelihood estimated at 0.962) (see Figure 3).

Population Viability Analysis

Under scenario 1, the models predict that the population will continue to grow ($\lambda = 1.051$) and estimate an extinction probability of 0 in 50 years. Under scenario 2, the models predict a lower population growth rate ($\lambda = 1.022$) and an extinction probability also of 0. Under scenario 3, which assumes a closed population, the population growth rate was estimated at 0.994, implying that the population will remain at around 20 pairs, with an extinction probability of 0.011. Finally, under scenario 4, the population is predicted to increase with a growth rate of 1.039 and an extinction probability of 0 on a 50-year horizon (Figure 4). Under scenarios 1, 2 and 4, the probability of a 50% reduction in the number of pairs in 10 years was 0, but under scenario 3 was 0.049.

Sensitivity and elasticity of vital rates

Of all the parameters, adult survival had the greatest sensitivity (0.535) and elasticity (0.482); thus, relative increases in adult survival values would cause the greatest increase in the predicted population growth rate (Figure 5). The number of immigrants did not seem to have any important effect on the growth rate. This is because we used an increment of one immigrant (from one to two) to estimate the model's sensitivity and elasticity, thereby implying that the denominator of the expressions used to estimate these two metrics was much higher than for the other vital rates.

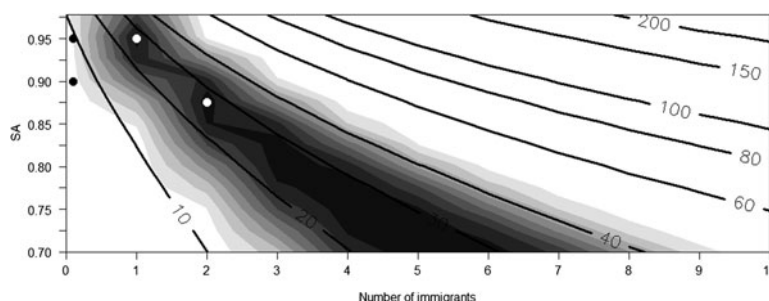


Figure 3. Likelihood estimate assuming different values of both adult survival (SA), from 0.7 to 0.975, and number of immigrants, from 0 to 10. Likelihood is represented by grey tones, from white (0) to dark grey (1). Black lines indicate the mean number of breeding pairs predicted under each scenario in 2012. White points indicate two most likely scenarios selected to perform the PVA (scenario 1 and 2). Black points indicate two closed population scenarios (3 and 4) selected to perform PVA.

As a result, the values of the metrics were much lower. However, the effect of immigration on the population growth rate was highly important, particularly between the scenarios of no immigration and of one immigrant (Figure 6).

Discussion

The Egyptian Vulture is an endangered species that has dramatically declined throughout its range (BirdLife International 2012), which includes the Iberian Peninsula, home to the bulk of the European population of this species. Despite this adverse scenario, a few local populations occupying small areas have recently grown (García-Ripollès and López-López 2006, Mateo-Tomás *et al.* 2010). We focused on one of these increasing populations in eastern Catalonia to investigate whether the observed trend could be explained simply by the establishment of individuals born in the study population or whether the arrival of immigrants was a necessary factor. To do so, we applied likelihood-based methods using a comprehensive demographic analysis. While population viability analysis is frequently applied to declining populations (Carrete *et al.* 2009), it is used much more rarely to study endangered species that are increasing in number (Ortega *et al.* 2009). We argue that identifying the demographic determinants of population increases may provide relevant information for guiding conservation managers and practitioners whose task it is to preserve populations of target species.

The results of our models strongly suggest that the increase observed in recent years in the Egyptian Vulture population in Catalonia was probably caused by a combination of higher adult survival than in other Iberian populations and the entry into the population of adults from outside the study area. Both adult survival and immigration play a key role in determining the dynamics of the population, as is to be expected for long-lived species (Real and Mañosa 1997, Saether and Bakker 2000). Our analyses were based on limited field data, a common issue when studying endangered species (Doak *et al.* 2005). Even so, the framework we applied based on likelihood methods was useful to tackle this constraint (Hernández-Matías *et al.* 2013).

Instead of adult survival or immigration, other demographic parameters could potentially affect the observed population trend. In the case of productivity, it was set at the values we estimated from the population and indeed, these values were higher than in other Spanish populations (C.R.P.R 1984, Donazar and Ceballos 1988, Fernández 1994, Donazar *et al.* 2002).

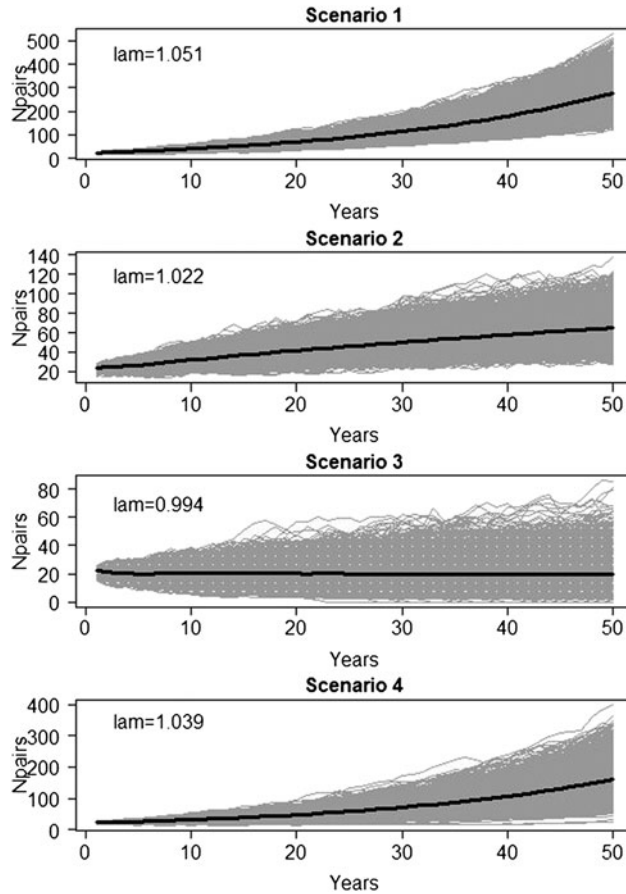


Figure 4. Projection of the population trend (in number of pairs) estimated for the next 50 years using models considered for PVA. All 5,000 replicates are represented in grey as well as the average trend represented by the black line.

Nonetheless, sensitivity and elasticity analyses indicate that, of all factors, adult survival has the strongest effect on the population growth rate and that non-adult survival and, specially, productivity are much less decisive, suggesting that the positive trend and the expansion of our population was not due simply to high levels of productivity. Regarding non-adult survival, we assumed in all models it was the same as described in the Ebro population. This assumption is reasonable if we consider that juvenile individuals from neighbouring populations share a similar life style; staying at the same wintering areas, aggregating in communal roosts and prospecting for potential breeding territories (Donázar 1993). Another assumption in our models was that all individuals recruit at five years old. Again, this seems reasonable if we bear in mind that Egyptian Vultures achieve maturity at this age (Donázar 1993) and that we studied a growing population and, therefore, no density-dependence is expected (Oro and Pradel 2000).

Unlike other areas of the Iberian Peninsula, where poisoning is the main cause of non-natural mortality in Egyptian Vultures (Hernández and Margalida 2009), the probable higher survival rates in the Catalan population could be due to the less widespread use of poison in Catalonia, especially in the study area. Support for this comes from the fact that during the period 1995–2010 only three Egyptian Vultures were found dead by poisoning in Catalonia, and all of them

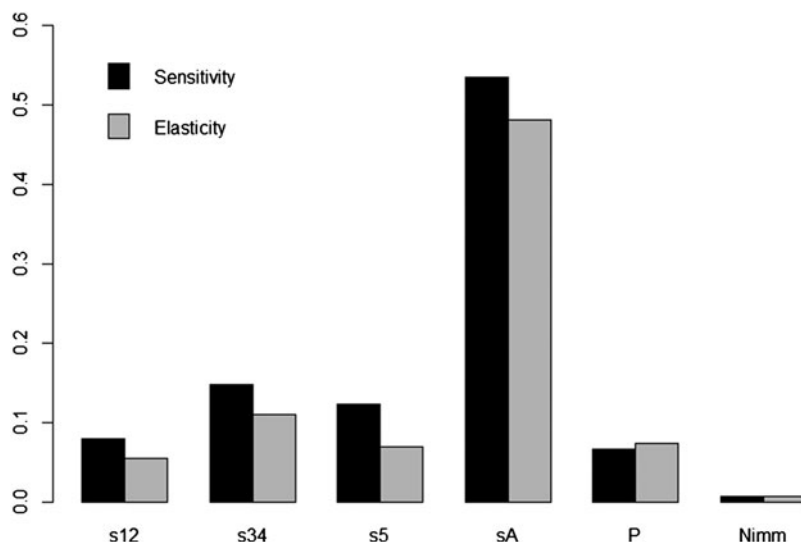


Figure 5. Sensitivity and elasticity of the population growth rate to main vital rates. S_{12} : yearly survival in the first two years of life, S_{34} : yearly survival in third and fourth years of life, S_5 : survival in fifth year of life, SA: survival of territorial individuals, P: productivity (number of fledglings per territorial pair), and Nimm: number of immigrants.

outside our study area (Hernandez 2006, Programa Antídoto unpubl. data). In other neighbouring areas such as Aragon, 47 individuals were found dead during the period 1996–2006 (Hernandez 2006) which highlights the different distribution and importance of poisoning events in the Iberian Peninsula. Electrocutation and collision with power lines and wind farms are also important causes of non-natural mortality of Egyptian Vulture in Spain (Donázar *et al.* 2002, Carrete *et al.* 2009), but available data coming from recovery centres report that this is not a major cause of death of the species in Catalonia since only one case of electrocutation has been reported up today (Servei de Biodiversitat, Generalitat de Catalunya *in litt.* 2013). On the basis of our results, management efforts in areas where the species' populations are decreasing should be directed to improving adult survival by eliminating the human related mortality that affects the species.

Our results also suggest that our study population is regularly receiving immigrating individuals from elsewhere. The Egyptian Vulture is a philopatric species with low natal dispersal distances (median natal dispersal 19.74 km, range = 0–150 km, $n = 26$; Grande *et al.* unpubl. data). Our study area is adjacent to a nucleus in north-west Catalonia (Lleida Pyrenees), which has increased - the number of pairs rose from 35 to 55 during the period 1983–2012 (Muntaner *et al.* 1983, Servei de Biodiversitat i Protecció dels Animals, Generalitat de Catalunya 2012). The reasons for the growth of this adjacent population are not well understood although it has been argued that Egyptian Vulture benefit from some feeding points provided for vultures (Margalida *et al.* 2010) but also the lower use of poison and consequently high adult survival could be taken in account. Therefore, we hypothesise that this neighbouring population nucleus is the most likely origin of the new pairs being established in our area. Supporting this idea, the colonisation pattern inside the study area shows that new territories were always near to an existing territory (less than 50 km), although long-distant natal dispersal events are also possible in this species (0–150 km) (Grande *et al.* unpubl. data).

It is known that new sanitary policies that reduced the availability of carcass resources affected some species of vultures via reduction of their vital rates and/or dispersal of individuals

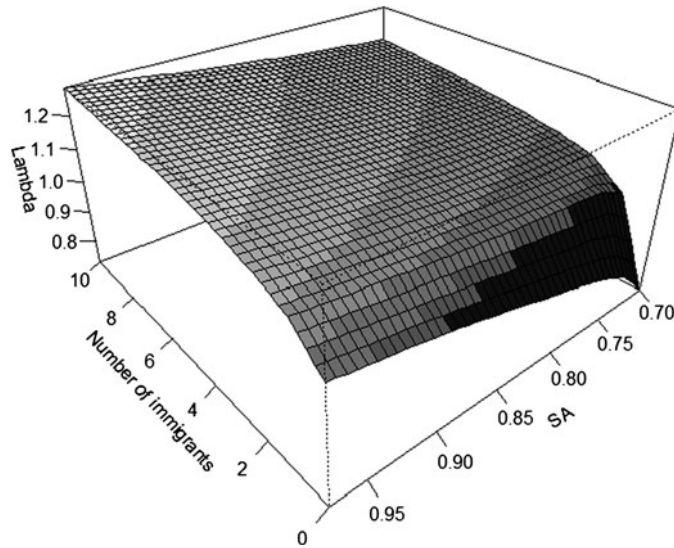


Figure 6. Contribution of immigration and adult survival to the population growth rate, assuming different values of both adult survival (SA), from 0.7 to 0.975, and number of immigrants, from 0 to 10. Values of lambda lower than 1 are represented in black, while values greater than one are represented in a grey scale, darker tones corresponding to lower values of lambda.

(Donázar *et al.* 2010, Margalida *et al.* 2010, 2014). In the case of Egyptian Vultures these policies seem not to be related to the increase in our population for two reasons; the neighbouring population of north-west Catalonia affected by the same regulations increased in the meantime and the breeding success seemed not to be affected by the possible consequent food shortages (Garcia and Margalida 2009) that is in concordance with the trends predicted by Margalida and Colomer (2012). So probably the specific lifestyle of this species (Donázar *et al.* 2010) can benefit from new environmental and human factors (landfill, extensive grazing) that occurred during the last few decades in our area favouring their colonisation and increase (Kiff 2000).

Assuming the most supported scenarios (1 and 2), both of which assume net immigration of adults, our PVA predicts continued population increase at a lower rate than that observed in the study period. However, even in the event that immigration stopped (scenario 4) the population would grow if adult survival is high. In contrast, in scenario 3 where adult survival is assumed to be equal to that estimated in the Ebro population, the population would stop growing although apparently it would remain stable. Even though the role of immigrants is commonly overlooked in population viability assessments, there is increasing evidence to suggest that immigration is a key determinant in population growth rates (Ward 2005, Schaub *et al.* 2013). It is also worth mentioning that all our predictions were made under the assumption that ecological conditions will not change. However, if declining trends in most of the species' range continue, fewer potential immigrants will be available to support the Catalan population, so it is important that future research aims to determine the ecological drivers of the vital rates of this population (e.g. Bakker *et al.* 2009). Conservation actions will thus have to take this question into account (Hernández-Matías *et al.* 2013).

Our results highlight that, despite major uncertainties, likelihood-based population analysis may provide relevant knowledge of the factors that regulate target populations. In the future, by reducing uncertainty, predictions can be refined so that advice for conservation managers can become more accurate. For example, it is essential to estimate survival, immigration and

recruitment rates, to continue the long-term ringing scheme initiated in 2012 in this area and then to apply *ad hoc* statistical methods. Furthermore, the study of the ecological and/or behavioural factors driving the settlement of new territories must also be studied. It is known that conspecific attraction (Reed and Dobson 1993, Grande 2006) and environmental features, either for nesting or foraging, also play a relevant role in colonisation processes (Webb *et al.* 2011). In our study area, most breeding pairs are located near landfills and farms, or in areas where extensive livestock farming is practised, and all these features are relevant sources of food for this species (Margalida *et al.* 2007, Gangoso *et al.* 2012, unpublished data). Therefore, it is crucial for the future effective management of this species to investigate the demographic relationships of the different local populations, the environmental determinants of its demographic characteristics and whether intensive human activities may have helped drive the increase in the studied Egyptian Vulture population.

Supplementary Material

The supplementary materials for this article can be found at journals.cambridge.org/bci

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