



Action on multiple fronts, illegal poisoning and wind farm planning, is required to reverse the decline of the Egyptian vulture in southern Spain



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ABSTRACT

Large body-sized avian scavengers, including the Egyptian vulture (*Neophron percnopterus*), are globally threatened due to human-related mortality so guidelines quantifying the efficacy of different management approaches are urgently needed. We used 14 years of territory and individual-based data on a small and geographically isolated Spanish population to estimate survival, recruitment and breeding success. We then forecasted their population viability under current vital rates and under management scenarios that mitigated the main sources of non-natural mortality at breeding grounds (fatalities from wind farms and illegal poisoning). Mean breeding success was 0.68 (SD = 0.17) under current conditions. Annual probabilities of survival were 0.72 (SE = 0.06) for fledglings and 2 yr old non-breeders, 0.73 (SE = 0.04) for non-breeders older than 2 yrs old and 0.93 (SE = 0.04) for breeders. Probabilities of recruitment were 0 for birds aged 1–4, 0.10 (SE = 0.06) for birds aged 5 and 0.19 (SE = 0.09) for older birds. Population viability analyses estimated an annual decline of 3–4% of the breeding population under current conditions. Our results indicate that only by combining different management actions in the breeding area, especially by removing the most important causes of human-related mortality (poisoning and collisions on wind farms), will the population grow and persist in the long term. Reinforcement with captive breeding may also have positive effects but only in combination with the reduction in causes of non-natural mortality. These results, although obtained for a focal species, may be applicable to other endangered populations of long-lived avian scavengers inhabiting southern Europe.

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1. Introduction

Forecasting the fate of threatened populations and designing adequate conservation measures is one of the greatest challenges for scientists and conservation managers (Morris and Doak, 2002). Population viability analysis (PVA) is a key tool to model population dynamics, estimate extinction probabilities and evaluate the adequacy of different management strategies for

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maximizing population persistence (Caswell, 2001; Morris and Doak, 2002). To project realistic future population numbers and make credible conservation diagnoses of threatened species, PVA requires robust data on population size and/or demographic parameters (Morris and Doak, 2002). Age- and stage-dependent patterns of survival and reproduction determine the shape of the reproductive value function (McNamara and Houston, 1996), which ultimately drives population growth rates (Caswell, 2001; Morris and Doak, 2002).

The estimation of age- and stage-dependent demographic parameters in long-lived species requires individual long-term monitoring programs (Grande et al., 2009; Hernández-Matías et al., 2013; Sanz-Aguilar et al., 2009). This is the case for long-lived territorial raptors, in which individual marking and monitoring of both territorial and non-territorial birds require extraordinary field

effort. Consequently, estimates of age-dependent vital rates within a species are typically available for only a limited number of populations and are used to apply PVA to different populations or closely related species (Carrete et al., 2009; Hernández-Matías et al., 2013; Martínez-Abraín et al., 2012). However, the results obtained from a single population cannot be taken as characteristic of the species or exported to other populations without caution (Sanz-Aguilar et al., 2009). Inter-population differences in demographic parameters, such as reproduction, survival or age-dependent recruitment, may exist even for very close populations (Sanz-Aguilar et al., 2009). Consequently, to robustly forecast population fates and evaluate conservation actions, an improvement in the current knowledge of inter-population variability in demographic parameters of endangered species is urgently needed (Hernández-Matías et al., 2013).

Due to their rapid decline worldwide and the ecosystem services they provide, scavenger vultures are considered priority species for conservation (Directive 2009/147/EC of the European Union on the Conservation of Wild Birds). As with other raptor species, vultures are threatened by multiple human factors including persecution (poisoning), habitat destruction, changes in sanitary policies and agricultural practices and fatalities due to infrastructures (Ogada et al., 2012). Reintroduction or reinforcement programs based on demographic data and PVA analyses have been carried out for several species (e.g., white-tailed eagles *Haliaeetus albicilla* Green et al., 1996; California Condors *Gymnogyps californianus* Meretsky et al., 2000; or Griffon vultures *Gyps fulvus* Sarrazin and Legendre, 2000). However, the introduction of individuals should be implemented only after environmental causes of decline or potential threats have been dealt with (Ewen et al., 2012; Pérez et al., 2012).

The Egyptian vulture (*Neophron percnopterus*) is a globally endangered long-lived scavenger that has experienced a severe population decline throughout its range (BirdLife International, 2007). The Spanish population which comprises ca. 80% of European population and has declined by 25% in the last two decades (Donazar, 2004) due to high non-natural mortality rates (Iñigo et al., 2008). Thus, conservation actions are urgently needed. The main causes of non-natural mortality (i.e., poisoning, electrocution, collision and direct-persecution) have been identified (Hernández and Margalida, 2009; Grande et al., 2009; Cortés-Avizanda et al., 2009) and in some cases roughly quantified (i.e., wind farm mortality, Carrete et al., 2009). Poisoning and wind farm mortality mainly affect territorial breeders (Carrete et al., 2009; Hernández and Margalida, 2009). This is especially relevant for a long-lived species in which population growth rates are expected to be highly sensitive to changes in adult survival (Sæther and Bakke, 2000). On the other hand, a European studbook for the Egyptian vulture and the European Endangered Species Program (EEP) for this species is being developed in order to reinforce and/or reintroduce populations from captive breeding programs (<http://www.zoopraha.cz/en/animals/we-help-them-to-survive/projects/7687-egyptian-vulture-conservation-in-the-balkans>; see also BirdLife International, 2007; <http://www.capovaccaio.it>).

This study focuses on the most southern European population of Egyptian vultures (Andalusia, Spain), where numbers of Egyptian vultures have dropped precipitously during the last few decades to the current <25 pairs isolated from other populations (Carrete et al., 2009). Although the dynamics of the species in terms of the number of breeding territories occupied are well known (Carrete et al., 2007; Donazar, 2004), detailed estimates of survival parameters are only available for the Ebro population in Northern Spain (Grande et al., 2009) and there are no age-dependent estimates of recruitment. These deficiencies lead to important uncertainty in population viability analyses (Tauler et al., 2015),

which directly affect the design of management actions for the conservation of the species on a broad scale.

Our specific objectives were to: (1) assess the viability of the southern Spanish population of Egyptian vultures through the estimation of local demographic parameters (survival, recruitment and breeding success); (2) evaluate the potential existence of inter-population variability in demographic parameters for the species by comparing the estimated vital rates with available estimates (Grande et al., 2009); and (3) forecast population viability by considering different management approaches, particularly the mitigation of human-induced mortality associated with wind farms and poisoning and the release of different numbers of fledglings to reinforce the population.

2. Methods

2.1. Species and study area

The Egyptian vulture is a highly opportunistic species, foraging on small wild prey and on carcasses of small and medium-sized animals (Donazar, 1993). Non-breeders typically aggregate around predictable food resources (e.g., landfills or vulture restaurants, so-called “muladares”) during the breeding season (Donazar et al., 1996; López-López et al., 2013). Individuals acquire adult plumage and are able to reproduce at five years of age (Carrete et al., 2009). They tend to recruit into territories near their natal areas and, once established, adult breeders are extremely philopatric to their breeding territories (Donazar, 1993; Carrete et al., 2007). Continental Western European populations of Egyptian vultures are migratory, with birds crossing the Sahara and spending the wintering season (and sometimes their first year of life) in the sub-Saharan Sahel region (Carrete et al., 2013; López-López et al., 2014).

The study was conducted from 2000 to 2013 in the Cádiz and Málaga regions of Andalusia (Southern Spain) (Fig. 1). Egyptian vultures are distributed around hills and mountain piedmonts. Four to six supplementary feeding stations have been available in the study area, which would indicate that food resources are not a limiting factor (Benítez et al., 2001; Margalida et al., 2012). During the study period, 175 Egyptian vultures were captured and individually marked with both darvic and aluminum rings: 159 fledglings were captured in their nests and 4 individuals aged 1 yr-old, 4 aged 2 yrs-old, 3 aged 3 yrs-old, 1 aged 4 yrs-old and 4 breeding adults (unknown age) were captured using cannon nets. Age was determined on the basis of plumage characteristics (Cramp and Simmons, 1977). Resightings of marked individuals during the breeding season ($n = 100$) and recoveries of dead birds ($n = 3$) were recorded until 2013.

Thirty-three breeding territories were found in the study area from 2000 to 2013. From 2000 to 2004, 20 to 32 territories were annually prospected, but from 2005 onwards monitoring efforts were intensified and all known territories (including active and abandoned territories) and all those cliffs *a priori* identified to be adequate to hold a breeding pair, were prospected every year. Territories were prospected every two weeks (typically spending 1 to 2 h per visit) during the breeding season and data on territory occupancy and breeding success (i.e., number of chicks fledged by territory and year) was collected. When adult absences were detected, nest sites were carefully inspected to detect potential dead birds inside nests. The territories adjacent to nest sites, foraging areas and nearby wind farms were then covered looking for carcasses (Carrete et al., 2009). Causes of death were determined by necropsy and pathology procedures (Hernández and Margalida, 2009).

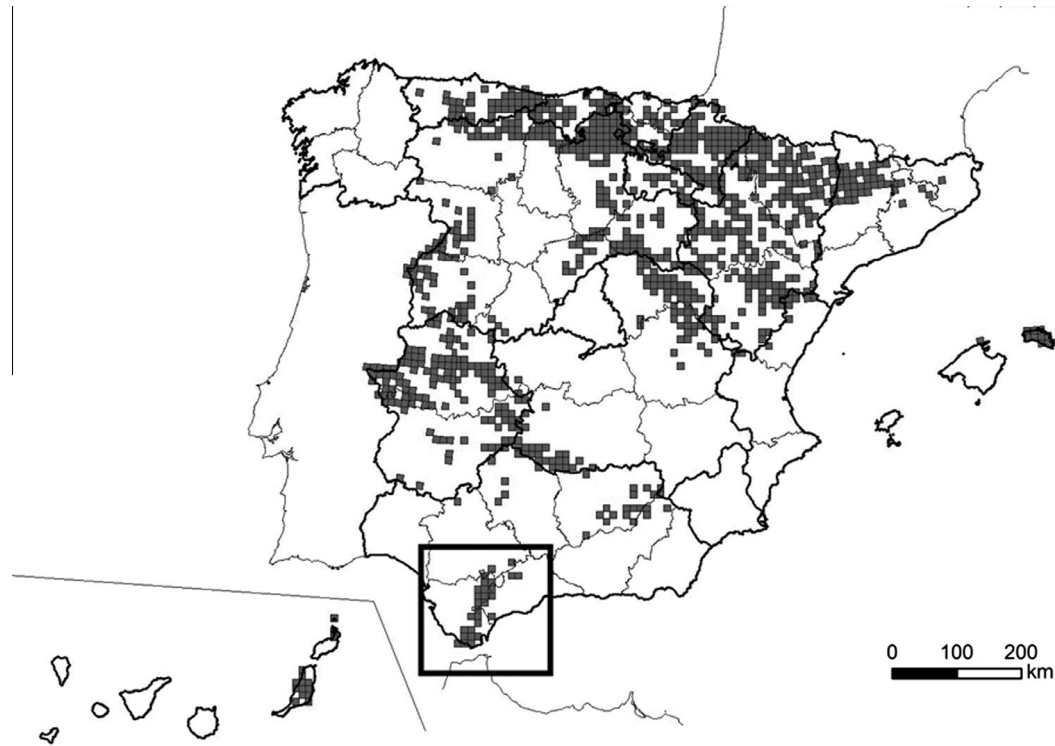


Fig. 1. Egyptian vulture breeding distribution in Spain (grey dots) and study area (black square). Figure modified from Donázar (2004) with the permission of SEO/Birdlife.

2.2. Estimation of demographic parameters

Breeding success of Egyptian vultures in southern Spain was previously determined by Margalida et al. (2012) so we used the same procedure for our estimates (i.e., number of chicks fledged divided by the number of monitored pairs) but extending the dataset to all known breeding territories and years.

Survival, resighting, recovery and recruitment probabilities were simultaneously estimated by means of multievent capture–recapture models (Pradel, 2005). Capture–recapture analysis began with the assessment of the goodness-of-fit (GOF) of the Arnason–Schwarz multisite model to the data using program U-CARE 2.3.2 (Choquet et al., 2009a).

The multievent framework distinguishes what can be observed in the field (the events coded in the encounter histories) from the underlying biological states of the individuals, which must be inferred (Pradel, 2005). Here, the events were ‘0’ (bird not observed on a particular occasion), ‘1’ (vulture captured as a chick), ‘2’ (vulture captured or resighted as a non-breeder), ‘3’ (vulture captured or resighted breeding) and ‘4’ (vulture recovered recently dead). The model included 5 underlying biological states: 3 states for live individuals, coded F (fledgling), NB (non-breeder), and B (breeder); and 2 states for dead individuals, coded RD (recently dead) and D (long dead). The multievent model (see details in Appendix A) estimated the initial state probabilities (the annual proportions of individuals belonging to the states F, NB, and B), the probabilities of transition between the states (survival and recruitment) and the probabilities of the events (resighting and recovery). These parameters were estimated simultaneously by maximum likelihood using program E-SURGE 1.6.3 (Choquet et al., 2009b).

Given the limited amount of data, and based on previous knowledge of the species biology (Grande et al., 2009), our starting model considered the following parameter constraints: (1)

survival may vary between fledglings, young non-breeders (2–5 yrs-old), old non-breeders (older than 5 yrs-old) and breeders; (2) recruitment begins at 5 years old; (3) the resighting of first year birds and the recovery of dead corpses are highly improbable so they were considered constant over time; and (4) resighting probabilities depend on field effort (i.e., time), and a combination of breeding status and age: for non-breeders, this changes with age (from 2 to 4 yrs-old), and is also different-predictably lower-than that of breeders given their territorial habits. We then considered simpler models taking into account alternative age/breeding status structures for the parameters of interest (see below). For resighting parameters, we considered models in which resighting probabilities differed among: non-breeders of 2 yrs, non-breeders older than 2 yrs and breeders; and non-breeders older than 1 yr and breeders. For recruitment parameters we considered models in which recruitment differed for birds 5 yrs and older; or was equal from 5 yrs onwards. Finally, we considered models in which survival differed among fledglings, non-breeders older than 2 yrs and breeders; differed among non-breeders younger and older than 3 yrs and breeders; differed between non-breeders and breeders; and was equal for all birds. Model selection was based on Akaike’s Information Criterion adjusted for the effective sample size, AICc (Burnham and Anderson, 2002). Models within 2 points of AICc were considered equivalent. To avoid overparameterized models, during model selection we first selected the best age class structure for resighting, second for recruitment and then for survival. When models differed in <2 points of AICc, their structure of the parameters was used to model the remaining parameters. For each model j , we calculated the Akaike weight, AIC w_j , as an index of its relative plausibility (Burnham and Anderson, 2002). Estimates were obtained by model averaging from the full model selection in which each model contributed to the final estimate according to its AIC w_j (Burnham and Anderson, 2002).

2.3. Population viability analyses

We calculated the observed mean population growth rate λ_{obs} in terms of number of occupied territories from 2005 to 2013 (when all territories were prospected) as the geometric mean of annual λ (Morris and Doak, 2002). Using the observed annual values of breeding population size (N_t), we calculated the count-based stochastic population growth (λ_s) and its confidence interval by means of a linear regression procedure (see details in Morris and Doak (2002) and R code in Sanz-Aguilar et al. (2014)).

Age and stage structured deterministic and stochastic matrix population models were built to forecast deterministic (λ) and stochastic population growth rates (λ_s) and calculate extinction probabilities for the studied population (Caswell, 2001; Morris and Doak, 2002) using the package POPBIO in software R (Stubben and Milligan, 2007; Team, 2005). Only the female population was modeled and the life cycle was based on different age/stage classes showing differences in survival or recruitment as estimated by capture–recapture analyses (Fig. 2.). Fecundity was defined as the number of females produced by a breeding female (=breeding success * sex ratio). We assumed that sex ratio at birth was 0.5. We calculated the deterministic population growth rate λ , the sensitivity (the change in λ associated with a change in a demographic parameter), the elasticity (the proportional sensitivity) and the generation time (the asymptotic increase in mean generation number per year) (Caswell, 2001) (Appendix B). The initial population size for each age class and breeding stage used in the stochastic simulations was estimated by combining the stable age distribution obtained by the deterministic matrix population model (Appendix B) and the observed number of breeding pairs at the beginning of the study period. The variance of survival and recruitment estimated from capture–recapture and breeding success estimated by territory monitoring was incorporated into the model by randomly selecting parameter values from a beta-distribution for survival and a lognormal distribution for fecundity (Fieberg and Ellner, 2001; Morris and Doak, 2002). Demographic stochasticity was also included in the population projection; the Poisson distribution was used for fecundity and the binomial distribution for survival. We ran 10,000 stochastic population model simulations over 10, 20, 30, 40, 50 and 100-year periods. Mean stochastic population rates over trajectories λ_s , extinction probabilities, time to extinction over extinct trajectories and the breeding population size at the end of the time period considered over non-extinct trajectories were calculated (Caswell, 2001; Morris and Doak, 2002) (Appendix C).

2.4. Management scenarios

Carrete et al. (2009), through an intensive survey (once a week) of wind farms and vulture territories, estimated a mean annual

wind farm mortality of 0.008 (SD = 0.03) for non-breeder and 0.015 (SD = 0.016) for breeder Egyptian vultures in the study area. We calculated the minimum annual poison-related mortality of breeders (from 2002 to 2013) as the ratio between the number of recoveries of poisoned Egyptian vultures in the study area (adult birds marked and unmarked) and the number of breeders.

We simulated different management scenarios using the breeding population observed at the end of the study (i.e., year 2013) as a starting point to infer future population dynamics. We followed the same analytical procedure discussed above. We simulated the mitigation of the 50%, 75% and 100% minimum breeder and non-breeder mortality caused by wind farms and the 50%, 75% and 100% minimum breeder mortality caused by illegal poisoning by adding mean mortality values to mean survival probabilities. We also simulated an annual supplementary incorporation of 4–20 fledglings in the population (considering a balanced sex ratio). Finally, we simulated scenarios in which different conservation actions were combined: 50% and 100% mitigation of mortality and annual incorporation of 4 and 8 additional fledglings in the population (which is a feasible range).

3. Results

3.1. Demographic parameters

Mean breeding success during the study period was 0.68 (SD = 0.17). Annual breeding success declined from the beginning of the study period and stabilized in the later years (Fig. D.1, Appendix D), as previously reported by Margalida et al. (2012).

The overall goodness-of-fit test of the Arnason-Schwarz multi-state model was not statistically significant ($\chi^2 = 9.37$, d.f. = 18, $p = 0.95$). When modeling resighting probabilities (Models 1–3, Table D.1, Appendix D), two models had similar AICc values ($\Delta\text{AICc} < 2$, Models 2–3, Table D.1, Appendix D). Model 2 included differences in resighting probabilities for non-breeders aged 1 ($\text{NB}_{(1)}$) non-breeders aged 2 ($\text{NB}_{(2)}$), non-breeders older than 2 yr-old ($\text{NB}_{(\geq 3)}$), and breeders (B), varying in parallel over time among all birds aged ≥ 2 . Model 3 also included differences in resighting probabilities for non-breeders aged 3 ($\text{NB}_{(3)}$). Models considering constant recruitment probabilities after age 6 or age 5 were very close in terms of AICc ($\Delta\text{AICc} < 2$, Models 4–7, Table D.1, Appendix D), and both were better than the models in which recruitment varied among birds of 5, 6 and ≥ 7 yrs of age (Models 2–3, Table D.1, Appendix D). The best models in terms of AICc ($\Delta\text{AICc} < 2$) were those including different survival probabilities for breeders and non-breeders (Models 13–15, Table D.1, Appendix D). Models considering temporal variation in survival did not show any support ($\Delta\text{AICc} > 20$, results not shown).

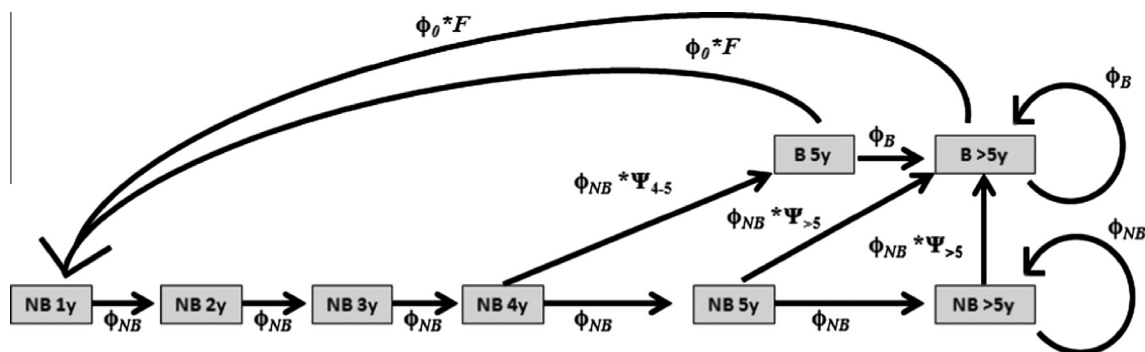


Fig. 2. Life-cycle of Egyptian vulture in the studied population. Notation: NB = Non-breeder, B = breeder; 1y, 2y, 3y, 4y, 5y, >5y = age classes from age 1 to older than 5 years old; ϕ_0 = fledgling survival; ϕ_{NB} = non-breeder survival; ϕ_B = breeder survival; Ψ_{4-5} = recruitment at age 5; $\Psi_{>5}$ = recruitment at ages older than 5; F = breeding success*sex ratio.

Resighting probabilities were very low for first-year individuals (0.01, SE = 0.01), increasing with age for older birds and reaching the highest value for breeders (Fig. D.2, Appendix D). Recovery probabilities were 0.03 (SE = 0.01). Model averaged estimates of recruitment were 0 for birds aged 1–4, 0.10 (SE = 0.06) for birds aged 5 and 0.19 (SE = 0.09) for older birds. Model averaged estimates of survival were 0.72 (SE = 0.06) for fledglings, 0.72 (SE = 0.05) for non-breeders of 2 yrs of age, 0.73 (SE = 0.04) for non-breeders older than 2 yrs of age and 0.93 (SE = 0.04) for breeders.

Minimum poison-related mortality estimates based on recoveries of 8 unmarked and 2 marked breeding birds between 2002 and 2013 varied between 0 and 0.075, with a mean annual breeder mortality of 0.019 (SD = 0.02).

3.2. Population viability

The proportion of occupied territories declined since the beginning of the study period (Fig. 3), showing a negative population growth rate $\lambda_{\text{obs}2005-2013} = 0.948$ (i.e., a mean annual decline of 5.2%, $n = 33$). The count-based stochastic population growth rate was 0.948 (CI: 0.898–1.001).

The estimated population growth rate λ by means of a deterministic Leslie matrix model based on the life cycle (Fig. 2) and demographic parameters estimated for the species in the study area was $\lambda = 0.965$ (95%CI: 0.80–1.13), indicating a mean annual expected decline in the breeding population of approximately 3–4%. The stable age distribution indicated that the population should be primarily composed of breeders older than 5 years (53%, Table D.2, Appendix D), which are also the individuals with the highest reproductive value (0.278, Table D.2, Appendix D). Accordingly, breeder survival showed the highest elasticity and sensitivity (0.79 and 0.82, respectively; Table D.3, Appendix D), followed by non-breeder survival (0.15 and 0.19, respectively; Table D.3, Appendix D). Estimated generation time was 34 years.

Stochastic population models estimated extinction probabilities of zero for the next 20 years (Table 1). The estimated extinction probabilities under the current demographic scenario within 50 yrs were low (7% of trajectories become extinct at 50 years), but greatly increased in the long term (69% at 100 years) (Table 1). Substantial reductions in population size were projected, even for the short term (Table 1). Mean female breeding population size estimated over a time period of 10 years was higher (19 breeders, Table 1) than the population size observed (17 breeders, year 2013, Fig. 3). However, confidence intervals (95% CI: 15–23) included the observed population size at the end of the study.

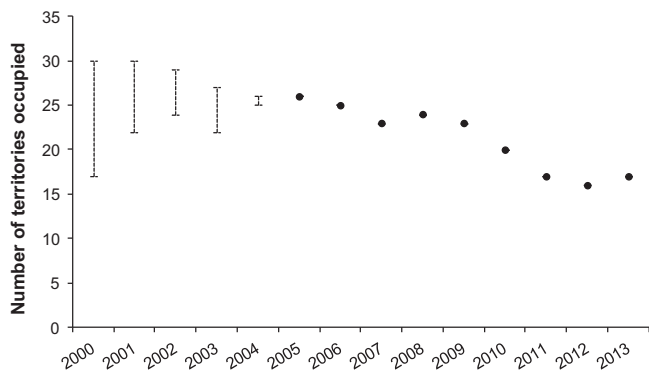


Fig. 3. Annual number of occupied Egyptian vulture territories in Andalusia (Spain). Bars indicate the minimum certain number plus the non-prospected territories. Points indicate certain number of territories occupied among the 33 known breeding territories of the species in the study area.

Table 1

Results of stochastic population modeling of Egyptian vultures in Andalusia. Breeding numbers in 2005 (26 breeders) were considered as a starting point.

Time period	Ext	T_Ext	Pop size B (CI)	λ_s
10 years	0		19 (15–23)	0.962
20 years	0		13 (9–17)	0.963
30 years	0.002	28	9 (5–13)	0.960
40 years	0.017	36	7 (3–11)	0.961
50 years	0.068	43	5 (1–10)	0.962
100 years	0.692	73	3 (1–7)	0.994

Notation: Ext = probabilities of extinction; T_Ext = mean time to extinction over extinct trajectories; Pop size B = mean female breeding population size over non-extinct trajectories (CI = 95% confidence interval); λ_s = stochastic population growth rate.

By considering the current number of females ($n = 17$ in 2013, Fig. 3) as a starting point for simulations, greater reductions in numbers are expected (Fig. 4, Fig. E.1 Appendix E).

3.3. Management scenarios

Management scenarios that partially or totally suppressed mortality from wind farms or illegal poisoning resulted in a more optimistic but still negative trend for the breeding population in the next 50 years (Fig. 4A, Figs. E.2–E.7, Appendix E). The incorporation of supplementary fledglings in the population will not mitigate the expected short-term population decline (10 years), but would help to stabilize (with 4 to 12 fledglings released annually, Fig. 4B, Figs. E.8–E.10 Appendix E) or increase breeding population size in the long-term (with >16 fledglings released annually, Fig. 4B, Figs. E.11 and E.12, Appendix E). Scenarios in which management actions were combined predicted that the population may persist in the long-term with: total mitigation of one cause of mortality and annual incorporation of 8 supplementary fledglings (Fig. 4C, Figs. E.14 and E.17, Appendix E); total mitigation of both causes of mortality (Fig. 4C, Fig. E.21, Appendix E); or with 50% mitigation of both causes of mortality and annual incorporation of 8 supplementary fledglings (Fig. 4C, Fig. E.26, Appendix E). The population may grow if both causes of mortality were totally mitigated and >4 additional fledglings entered the population annually (Fig. 4C, Figs. E.23 and E.24, Appendix E). Extinction probabilities greatly decreased when management actions were considered (Table E.1, Appendix E).

4. Discussion

4.1. Local demographic parameters

Our survival estimates showed that only 20.2% and 14.7% of fledglings would survive to 5 and 6 years of age, respectively, which is very similar to the values estimated for the Ebro population in northern Spain: 19.5% and 14.6% up to 5 and 6 years old, respectively (Grande et al., 2009). Costs of migration in long-lived species are higher for young and inexperienced individuals (Klaassen et al., 2014; Sanz-Aguilar et al., 2012; Sergio et al., 2014). In addition, Egyptian vultures from different populations share wintering areas in Africa (Carrete et al., 2013; López-López et al., 2014) and Grande et al. (2009) found that 30% of the temporal variation in survival was determined by environmental conditions in wintering grounds. If the survival of young birds is mainly affected by migration and wintering conditions, as has been showed for other trans-Saharan migrants such as White Storks *Ciconia ciconia* (Schaub et al., 2005) and Lesser Kestrels *Falco naumanni* (Mihoub et al., 2010), this may explain why the survival of non-breeding Egyptian vultures in northern and southern Spain was nearly the same.

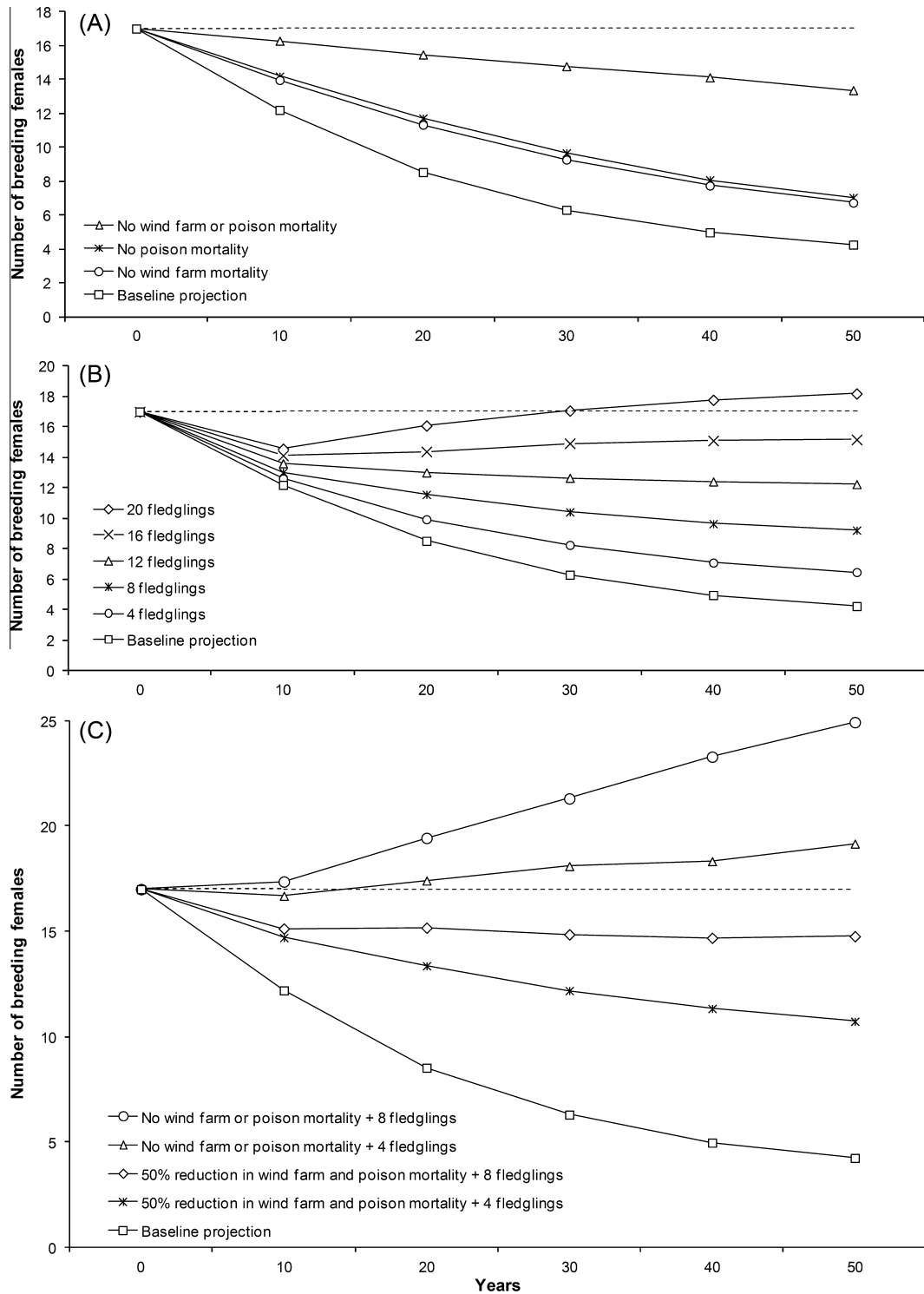


Fig. 4. Projections of expected mean breeding population size of Egyptian vultures for the next 50 years under current demographic parameters (baseline projection) and different scenarios of management actions: (A) reduction of mortality rates; (B) incorporation of yearly additional fledglings in the population; (C) and combined actions. Dashed line indicates the value of the initial breeding number in 2013 (17).

Our estimate of breeder survival was, however, much higher (0.93, SE = 0.04) than that estimated in the Ebro population (0.83, SE = 0.04, Grande et al., 2009). It is worth noting that our estimate of breeder survival is based on the capture–recapture histories of a small number of individuals ($n = 9$), so this estimate may not be representative of the entire southern Egyptian vulture population.

Nevertheless, given that the population model based on estimated demographic parameters matched well with the observed dynamics, this may be a realistic or slightly overestimated value. By considering different values of breeder survival, the same number of breeders present at the end of the study was projected by the population model when breeder survival was 0.91 (results not

shown). This suggests that local factors at breeding territories could greatly influence adult mortality in this species (Carrete et al., 2007, 2009; Hernández and Margalida, 2009; Tauler et al., 2015).

We also provide the first estimates of the age-dependent recruitment curve for the species. As may be expected in a long-lived species with deferred breeding (Sanz-Aguilar et al., 2009), our estimates showed a progressive recruitment from age 5 (in which only 10% of live individuals become breeders) onwards. In fact, birds with adult plumage (≥ 5 yrs old) are usually seen in non-breeding communal roosts (*pers. obs.*). Previous population models performed for the species considered a full recruitment at age 5, which, as we show here, is an overestimation of breeding probabilities (Carrete et al., 2009; Tauler et al., 2015). Given that the studied population is in decline, no negative density-dependent access to reproduction would be expected, and the pattern of recruitment may differ from that expected in a stable or growing population (Ferrer et al., 2004). Consequently, we would like to point out the importance of caution when extrapolating estimates to other local populations (Sanz-Aguilar et al., 2009, 2014).

4.2. Population prospects and potential efficacy of management actions

Poisoning is a widely recognized mortality factor threatening scavenger populations probably since the 19th century, and is responsible for the eradication of some species throughout most of their former European distribution ranges (Bijleveld, 1974; Martínez-Abraín et al., 2009). On the contrary, wind farm fatalities are an emerging risk for raptor species (Carrete et al., 2009; Bellebaum et al., 2013; Martínez-Abraín et al., 2012; Schaub, 2012). Wind farm fatalities have a less recognized impact although it is expected that its importance will grow steeply due to the predictable development of “green energies” (Pullen and Sawyer, 2011). Our results show that under current mortality rates associated with both threats the studied population will decline to extinction in a matter of a few decades (Table 1). This is a typical scenario for long-lived animals highly sensitive to changes in adult survival (Sæther and Bakke, 2000). Our estimates of mortality by poisoning, and to a lesser extent by wind farms, are probably underestimated (Carrete et al., 2009; Hernández and Margalida, 2009), so by eliminating these human-induced mortality factors population prospects should be more optimistic than those predicted here. In any case, our projections indicate that only by combining management actions on different fronts will the population persist. Moreover, by mitigating mortality of breeders, breeding success may increase directly but also indirectly via the acquisition of breeding experience (Carrete et al., 2006; Margalida et al., 2012) with additional benefits for population persistence (Green et al., 1996).

The likelihood of persistence of the studied population may increase by immigration of individuals from outer breeding areas (Schaub et al., 2010; Tauler et al., 2015). Unfortunately, this possibility is not very realistic and it was not taken into account. Natal dispersal distances in the species are typically short (median natal dispersal = 20 km, Grande et al., 2009) and the studied population is relatively isolated from its closest neighbors (Fig. 1), so we believe that a rescue effect by immigration is highly improbable. Conservation projects typically release juveniles to reintroduce or reinforce endangered populations (Green et al., 1996; Meretsky et al., 2000; Sarrazin and Legendre, 2000). In our case, scenarios including the release of fledglings into the Andalusian population show that the predicted short-term decline (for the next 10 years) will continue, and the population will only be recovered in the long-term by high numbers of released fledglings (>16 by year), which is a highly unrealistic conservation measure. In addition,

the release of individuals to the wild is admissible only if causes of decline or extinction (here human-related mortality) have been previously eradicated or at least mitigated (Ewen et al., 2012; Pérez et al., 2012).

Combating illegal poisoning is a major challenge for vulture conservation (Hernández and Margalida, 2009; Oro et al., 2008; Ogada, 2014) but requires long-term efforts and funding (Whitfield et al., 2003). On the contrary, wind farm mortality could be rapidly reduced by applying local measures (e.g., eliminate dangerous turbines and stop turbines during the breeding season) because accidents are typically distributed at a few windmills and farms (Carrete et al., 2012; Martínez-Abraín et al., 2012). The strategies to prevent this source of mortality should first address the spatial planning by means of avoiding breeding areas, foraging areas and potential areas for population expansion (e.g., abandoned territories), and migration routes. In contrast to poisoning, wind farm fatalities may be negligible in the African wintering grounds where there are only two wind farms in Mauritania (http://www.thewindpower.net/windfarms_africa_en.php) outside of the core area of wintering Egyptian vultures (Carrete et al., 2013). However, other mortality factors, such as electrocution, might be a major source of mortality in certain areas in the Sahel (Angelov et al., 2012).

Obviously, other conservation measures may also be implemented. Supplementary feeding, a common conservation measure for threatened scavengers (Cortés-Avizanda et al., 2012; Duriez et al., 2012; Moreno-Opo et al., 2015) may enhance juvenile survival and breeding success (Oro et al., 2008). Feeding stations in the study area have an apparent positive effect by attracting and increasing site fidelity of immature birds (Benítez et al., 2009), which in turn may increase the probability of territory persistence (Carrete et al., 2007). However, its negative effects at the community level (e.g., increased competition with larger species) are not negligible (Donázar et al., 2009; Cortés-Avizanda et al., 2012). In addition, human disturbance at breeding sites (although not quantified) may be a potential problem for some territories in the study area (Benítez et al., 2001). Measures aimed at avoiding the presence of humans in the vicinity of breeding sites that may result in breeding success increases are thus highly recommended (Zuberogoitia et al., 2008). However, as Egyptian vultures are long-lived species with deferred breeding, potential improvements in breeding success may not reverse the current population decline. In fact, only scenarios with >16 additional chicks released predicted a growth in population. This would represent a highly improbable mean breeding success for the species (more than 1.5 chicks per breeding pair).

The substantial short-term decline and high long-term probabilities of extinction projected for the studied population highlights the urgent necessity of conservation actions. Moreover, this may be a common scenario for other breeding areas of Egyptian vultures (Liberatori and Penteriani, 2000; Veleviski et al., 2015) and other large body-sized avian scavengers throughout the Old World (Ogada et al., 2012). Unfortunately, new alarming threats continue to appear (e.g., recently approved toxics for veterinary use, Margalida et al., 2014). Reintroductions and reinforcements are socially attractive but also expensive and with doubtful efficacy (Pérez et al., 2012). We believe that before these conservation actions become totally unavoidable to maintain viable populations, administrations should focus their conservation efforts on those human-related factors responsible for current population declines.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.03.029>.

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