

Assessing the effects of different management scenarios on the conservation of small island vulture populations

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Summary

Although the population of Griffon Vulture *Gyps fulvus* is significantly increasing in Europe, in Italy the species is still on the Red List as 'Critically Endangered', with the last natural population persisting on the island of Sardinia. Several episodes of poisoning hampered the success of conservation actions implemented in the years 1987–1995. In 2005 there were estimated to be only 31–32 territorial pairs, with the population occupying the territories of Alghero and Bosa. We used a long-term dataset of reproductive records from the Sardinian Griffon Vulture populations to run a population viability analysis (PVA) to evaluate the extinction risk using the Vortex simulation software. The model estimated the probability of extinction over the next five generations (estimated generation time: 11 years, simulation time used: 55 years) as 96.4% for the Alghero population, and near-zero for the Bosa population. We used sensitivity analyses to understand how uncertainty about parameter values affect model outcomes. Population projections were evaluated under different management scenarios tackling the main threats (poisoning and human disturbance) and implementing conservation actions (supplementary feeding and restocking). Our results showed that population size is a critical factor in affecting the projections of population dynamics of Griffon Vultures. Sensitivity analyses highlighted the importance of poisoning events to population persistence and showed that juvenile and adult mortality rates had a secondary impact on population viability. The only conservation measure effective in significantly increasing stochastic growth rates in the Alghero population, whose initial population was set at five individuals, was the complete removal of poisoning events. When targeting the Bosa population (initial population size 94 individuals), supplementary feeding, mitigation of the risk of poisoning episodes, restocking, and mitigation of human disturbance in the reproductive sites significantly

increased stochastic growth rate. A cost-effectiveness analysis should be performed to prioritise interventions.

Keywords: population viability analysis, Griffon Vulture, feeding stations, restocking, human disturbance

Introduction

Population declines and species extinctions may have devastating ecological consequences by disrupting key ecosystem processes such as decomposition, pollination and seed dispersal (Şekercioğlu et al. 2004, Buechley and Şekercioğlu 2016). Avian scavengers are part of the detrital food web of ecosystems and they provide the important ecological service of recycling carrion biomass, thereby contributing to waste removal, disease regulation, and nutrient cycling (DeVault et al. 2003, Moleón et al. 2014). Replacing some of these services has not only conservation costs but also unnecessary environmental and economic costs associated with carcass transport and processing (Morales-Reyes et al. 2015). Unfortunately, vultures are experiencing dramatic population declines worldwide, to the extent that they are now among the most threatened animal taxa (Ogada et al. 2012, Safford et al. 2019, Santangeli et al. 2019).

The Griffon Vulture *Gyps fulvus* is a typical scavenger, feeding exclusively on carcasses of medium- and large-sized animals (Campbell 2015). One of the main limiting factors for vulture conservation in Europe is the availability of safe food, due to changes in its geographic occurrence, quality and unavailability as a result of changes in European sanitary policies (Donazar et al. 2009, Margalida and Colomer 2012) and repeated poisoning events (Margalida and Mateo 2019). Other threats include collision and electrocution on energy infrastructure, which is affecting the species especially in countries with an abundant population (Botha et al. 2017). Unintentional poisoning caused by veterinary drugs has caused severe declines in *Gyps* vulture species across Asia. In Europe one case of suspected poisoning of a Griffon Vulture caused by flunixin, a non-steroidal anti-inflammatory drug, was recorded in 2012 in Spain (Zorrilla et al. 2015). In that country, which holds > 95% of the European breeding population of the Eurasian Griffon Vulture, using a simulation model of a vulture population, the expected rate of decline of the Spanish population of Eurasian Griffon Vultures caused by these deaths is 0.9–7.7% per year (Green et al. 2016). Habitat degradation and human disturbance are considered additional, but more localised, threats (Botha et al. 2017). To counter these threats, there are several official ongoing conservation programmes in different European countries with campaigns to minimise poisoning and provide safe food at feeding stations constituting the main activities. As a result, the population in Europe is significantly increasing, and it is estimated at 32,400–34,400 pairs, with Spain alone accounting for an estimated 25,000 pairs (BirdLifeInternational 2018). Its range has also expanded thanks to reintroduction projects in France, the Italian peninsula and the Balkans (Deinet et al. 2013).

However, in Italy the Griffon Vulture is still included on the Red List as ‘Critically Endangered’ (Rondinini et al. 2013), with the last natural population persisting on the island of Sardinia. Distributed over the whole island up to the late 1940s with an estimated population of 800–1,200 individuals (Aresu and Schenk 2006), the population of Griffon Vultures in Sardinia dropped very rapidly after the second half of 20th century, mainly due to the use of poisoned baits. In central-eastern Sardinia the Griffon Vulture was present up to the 1980s, after which the population survived only in the north-western part of the island (Schenk et al. 2008). By 2005 the number of territorial pairs was estimated at only 31–32, and the population was distributed in the territories of Alghero and Bosa (Aresu and Schenk 2006). Moreover, the other large vulture species present on the island Black Vulture *Aegypius monachus*, Bearded Vulture *Gypaetus barbatus* had become extinct by the second half of the last century. The long-term conservation of the Sardinian

population of Griffon Vultures is therefore pivotal not only to preserve its role in the ecosystem but also to allow the development of a wider conservation plan to restore the vulture guild on the island.

The Sardinian population of Griffon Vultures has been closely monitored since 1986, and a relatively large dataset on breeding records (30 years, 861 records) is available. The population was managed by restocking and supplementary feeding between 1987 and 1995. However, poisoning episodes in 1997, 1998 and 2006 hampered the conservation actions implemented.

The aim of the present study is to estimate the probability of persistence of Griffon Vultures in Sardinia and to explore the effects of possible management actions aimed at ensuring their conservation. We conducted population viability analysis (PVA) using Vortex simulation software (Lacy and Pollak 2014), which is one of the most commonly used tools for PVAs. The program uses vital rate estimates (survival, reproduction, dispersal), along with population characteristics (e.g. initial population size, age distribution, carrying capacity, and harvest or restocking), to simulate population dynamics over time by creating a representation of each individual in the population, and following their fate through a time series of stochastic demographic and environmental events (Lacy 1993 and 2000). Sensitivity of population trajectories to key demographic parameters and population projections under different management scenarios tackling the main threats to the persistence of this species (poisoning and human disturbance) and implementing concrete conservation actions (activation of feeding sites and restocking) are presented.

Methods

Baseline model inputs

Demographic parameters were introduced into Vortex simulation software (Version 10.2.6; Lacy and Pollak 2017) in order to build a PVA. We developed a baseline model using demographic input parameters from a variety of sources, including original data, previously published information and discussions with experts on the species (Table 1). The parameters used in the baseline method are those of unmanaged populations. We parameterized the baseline model as a two-population projection (Alghero and Bosa population, with different reproductive rates and located at a distance of 40 km from each other) with 1,000 iterations to provide reliable estimates of risk. We scaled extinction risks to generations (O'Grady *et al.* 2008, Reed and McCoy 2014) and extended the time frame to five generations (55 years). Estimated generation time was approximately 11 years as calculated in Vortex using the Euler equation (Lacy *et al.* 2017). We defined extinction as occurring when only one sex remained. Because little is known about the effects or impacts of inbreeding depression on Griffon Vultures, and because in 1987–1995 restocked individuals ($n = 60$) from Spain and France were released in Sardinia, we developed models without including inbreeding depression. Estimates for age at first reproduction, lifespan and brood size were set as fixed variables in our PVA, whereas stochasticity was built into models through environmental variation in the proportion of females breeding successfully in a year and age-specific annual survival (Table 1). The potential effects of harvesting and genetic management were not included in the simulations.

Dispersal

As a two-population projection, we had to define in our scenario the dispersal rates among populations. Over the years, dispersal of immature vultures from the Alghero area to Bosa has been observed by ornithologists, while no record exists of the dispersal of individuals from the Bosa area to Alghero. We thus assumed that 15% of vultures aged 1–3 years disperse from Alghero to Bosa and that both sexes disperse. We also assumed that the survival of dispersers did not differ from non-dispersers, given the low distance between the two populations.

Table 1. Vortex parameter inputs for the baseline Griffon Vulture population model. EV: environmental variation.

| Parameter | Value | Source |
|--|---|--|
| Species description | | Assumed |
| Inbreeding Depression | No | |
| EV Correlation of Reproduction and Survival? | Yes | |
| Dispersal among population | | Assumed |
| Dispersing classes | Age range: Youngest 1 yr, Oldest 3 yr - Dispersing sexes: males and females | |
| Survival of dispersers | 71.6% | |
| % of individuals that disperse | Bosa: 0%; Alghero 15% | |
| Reproductive System | | Campbell, 2015, García-Ripollés and López-López, 2011, Pavoković and Sušić, 2006 |
| Reproductive System | Long-term monogamy | |
| Age of 1st Offspring Females | 5 | |
| Age of 1st Offspring Males | 5 | |
| Maximum lifespan | 20 | |
| Max Age of Reproduction | 20 | |
| Max # Broods/Year | 1 | |
| Max # Progeny/Brood | 1 | |
| Sex Ratio at birth in % Males | 50 | |
| Reproductive Rates | | Original data |
| Breeding propensity | Alghero: 81.8; Bosa: 72 | |
| EV (SD) in breeding propensity | Alghero: 33.7; Bosa: 8.13 | |
| Distribution of Broods each Year (reproductive success) | 0- Alghero 18, Bosa 31; 1-Alghero 82, Bosa 69 | |
| Mortality rates (equal values for male and females and for the two populations) | | García-Ripollés and López-López, 2011 |
| from 0 to 1 (SD) | 14.2 (3.9) | |
| from 1 to 2 (SD) | 14.2 (3.9) | |
| from 2 to 3 (SD) | 14.2 (3.9) | |
| from 3 to 4 (SD) | 3.3 (3.7) | |
| from 4 to 5 (SD) | 3.3 (3.7) | |
| Annual mortality after age 5 (SD) | 3.3 (3.7) | |
| Catastrophes | | Original data |
| One type | Poisoning | |
| Frequency (Alghero and Bosa populations) | 10% | |
| Severity: reproduction | Alghero: 0.592; Bosa: 0.787 | |
| Severity: survival | Alghero: 0.625; Bosa: 0.796 | |
| Mate Monopolization | | |
| % Males in Breeding Pool | 100% | |
| Initial Population Size | | |
| Stable Age Distribution? | Yes | Assumed |
| Initial Population Size | Alghero: 5; Bosa: 94 | 2014 estimates - LIFE14/NAT/IT/00484 project, personal communication |
| Age ratios (% of population) | Stable age distribution | García-Ripollés and López-López, 2011, Pavoković and Sušić, 2006 |
| Carrying Capacity (K) | Alghero: 100; Bosa: 500 | Aresu and Schenk, 2006 |

Reproductive system

Griffon Vultures are long-term monogamous, and individuals of both sexes can breed at five years old. They lay one egg per clutch. Maximum age of reproduction is estimated at 20 years (Pavoković and Sušić 2006, García-Ripollés and López-López 2011). Griffon Vultures are sexually monomorphic, and the sex ratio cannot be estimated from field observations. Therefore, we assumed an equal sex ratio for the population, and that the sex ratio at birth was equal.

Reproductive rates

Reproductive rates used in the model were obtained by calculating the mean and SD of breeding propensity (number of breeding pairs/territorial pairs) and reproductive success (number of fledglings/breeding pairs) from field data recorded from 2004 to 2014 in the Alghero and Bosa populations (Table 1). This was a subset of a larger dataset of reproductive records collected from 1986 to 2014.

Field work in each breeding season was carried out between December and August to observe the entire breeding period of the species (courtship flights, building nest, deposition, brooding, hatching, breeding of the chicks and the first flight of juveniles). Observations were carried out from vantage points or by rubber dinghy at 300–600 m from the breeding sites with binoculars (8x42, 10x50) and scopes (20–60 x 80). Each colony was visited 6–10 times during each year. Parameters recorded during the breeding period were:

1. Number of territorial pairs: pairs observed in mating behaviour (display flights, nest repair, mating);
2. Number of breeding pairs: pairs incubating the egg;
3. Number of fledglings.

Number of territorial pairs, breeding pairs and fledglings counted from 1986 to 2014 are presented in Figure S1 in the online supplementary material. Reproductive records in Sardinia from 1986 to 2014 are summarised in Table S1.

Mortality rates

Age-specific mortality rates were taken from the literature (Le Gouar *et al.* 2008, García-Ripollés and López-López 2011) (Table 1). Due to the absence of site-specific mortality rates available in the literature, they were considered the same for all populations without sex differences (García-Ripollés and López-López 2011).

Catastrophes

From 1986 to 2014, three main poisoning events occurred in the Sardinian populations of Griffon Vultures (1997, 1998 and 2006). The episodes resulted in a loss of a significant number of individuals (approximately 40–60), contributing to the critical demographic status of Sardinia's Griffon Vultures. As a result, in our baseline model we included poisoning as a local catastrophic event that can occur in Sardinia. The frequency was set at 10% (3 episodes in 30 years). The effect of catastrophic events on survival and/or reproduction was modelled including a severity factor ranging from 0 to 1 (Lacy *et al.* 2017). The severity factor with respect to reproduction was modelled at 0.592 and 0.787 for the Alghero and Bosa populations, respectively. This means that, in the period of the catastrophe, reproductive rates decreased by 40.8% and 21.3% in the Alghero and Bosa populations, respectively. Survival severity factor was set at 0.625 and 0.796 for the Alghero and Bosa populations, which means that survival rates decreased by 37.5% and 20.4% in the Alghero and Bosa populations, respectively. For example, in a poisoning event in the Alghero population, survival rates of birds aged 0 to 3 years were changed from 85.8% (considering that mortality rates were set at 14.2 for both sexes and populations) to 53.6% [$85.8 - (85.8 * 0.375)$]. For birds aged more than 3 yrs, survival rates were changed from 97.3% to 60.8%. For reproduction we considered for each population the mean decrease in productivity from the year before the

catastrophe to the year in which it occurred. For survival, we calculated for each population the decrease in territorial pairs from the year before the catastrophe to the year in which the catastrophe occurred, after subtracting the annual mortality rate of 0.033. We applied this value for the whole population, on the assumption that poisoning would have the same possibility of occurring in all age classes.

Initial population size and age structure

To verify if the baseline model inputs gave realistic projections, we used as a starting point the population size in 1986 (15 and 47 individuals, for the Alghero and Bosa population, respectively) (Aresu and Schenk 2006) and a simulation time of 28 years (from 1986 to 2014). Figure S2 shows how our projections matched the most recent observation data of 2014. Thereafter, we updated the initial population size to 2014 estimates (five and 94 individuals, for the Alghero and Bosa population, respectively; project LIFE/14/NAT/IT/000484, pers. comm.) to develop our baseline scenario (Table 1). Precise age-class distribution for each species and each population was not available. Therefore, following the recommendation of Lacy *et al.* (2017) initial population size was modelled in both cases as a stable age distribution.

Carrying capacity (K)

VORTEX implements carrying capacity as a probabilistic truncation across all age classes when K is exceeded. If the population size exceeds K at the end of a particular time cycle, additional mortality is imposed across all age classes in order to reduce the population back to this upper limit (Lacy *et al.* 2017). Based on historical data on Griffon Vulture population size and distribution in Sardinia (Aresu and Schenk 2006), we set K as 100 in the Alghero population and as 500 in that of Bosa.

Sensitivity analysis

We performed sensitivity analysis to understand how uncertainty about parameter values affect model outcomes. We followed the perturbation approach which involves systematically changing a single parameter to see how much a parameter value can be changed until a population either declines to extinction or persists throughout the study period (if it is going extinct under baseline conditions). We varied each key parameter by $\pm 5\%$, $\pm 15\%$, $\pm 25\%$, and $\pm 50\%$, while holding all other parameters to baseline values. The parameters examined were juvenile (< 3 yrs) and adult mortality rates, breeding propensity, reproductive success, frequency and severity of poisoning. Each scenario was run for 1,000 iterations and 55 years.

Management scenarios

Different scenarios were simulated to assess how the implementation of different management strategies and changes in environmental conditions affect the probability of extinction of the two Sardinian populations of Griffon Vultures. Probability of extinction (PE) was calculated as the proportion of the 1,000 iterations in which the population went extinct. Scenarios were based on reasonable options of population management, following (Soutullo *et al.* 2008). To this end, we used similar figures for simulations as those provided by (Pavoković and Sušić (2006) and (García-Ripollés and López-López (2011) in a PVA of Griffon Vultures.

Each alternative scenario was modelled with three intensity levels (low, medium and high) of the magnitude of change in the demographic variables in relation to the baseline model (García-Ripollés and López-López 2011). Demographic parameters were modified as described below and detailed in Table 2, with all other parameters of the baseline scenario kept unchanged. We modelled effects of:

Table 2. Simulated scenarios used in PVA of the Griffon Vulture in Sardinia (Italy). Empty cells mean that demographic parameters were not changed from the baseline.

| | Mortality | | Breeding propensity | Reproductive success | Catastrophic events | | | | Supplementation |
|------------------------------|-----------------|-------------------|---------------------|----------------------|---------------------|-----------|------------------------|--------------------|--------------------|
| | From 0 to 3 yrs | From \geq 3 yrs | | | Occurrence | Frequency | Severity: reproduction | Severity: survival | Number of vultures |
| Supplementary feeding low | -10% | / | / | / | / | / | / | / | NO |
| Supplementary feeding medium | -15% | / | / | / | / | / | / | / | NO |
| Supplementary feeding high | -20% | / | / | / | / | / | / | / | NO |
| Poisoning medium | / | / | / | / | YES | + 5% | / | / | NO |
| Poisoning low | / | / | / | / | YES | + 5% | - 0.1 | - 0.1 | NO |
| Poisoning absent | / | / | / | / | NO | NO | NO | NO | NO |
| Supplementation actual | / | / | / | / | / | / | / | / | 123 |
| Supplementation medium | / | / | / | / | / | / | / | / | 252 |
| Supplementation high | / | / | / | / | / | / | / | / | 384 |
| Human disturbance high | / | / | - 10% | - 10% | / | / | / | / | NO |
| Human disturbance medium | / | / | / | + 10% | / | / | / | / | NO |
| Human disturbance low | / | / | + 10% | +10% | / | / | / | / | NO |

1. Supplementary feeding: it is expected to decrease mortality in juveniles and immature birds (Oro *et al.* 2008). This effect was modelled by decreasing mortality rates from 0 to 3 years of age by three intensity levels (-10%, -15%, -20%; Table 2);
2. Changes in the occurrence and severity of catastrophic events such as poisoning: this effect was modelled by decreasing the frequency of poisoning (from 10% to 5%, poisoning medium), by decreasing its frequency and severity (5% frequency, severity in survival and reproduction decreased by 0.1; poisoning low) and by completing removing its occurrence (poisoning absent);
3. Restocking: previous conservation efforts in Sardinia included a restocking programme carried out in the Bosa area (Montiferru/Oriстано) with the release of 60 Griffon Vultures from Spain and France over the years 1987–1995. With the implementation of the project LIFE Under Griffon Wings (LIFE14/NAT/IT/000484), a second restocking programme is being implemented with the release of 63 more vultures from Spain and from reproduction in captive breeding programmes (ARTIS Zoo, Amsterdam, The Netherlands) over the years 2018–2019. We thus simulated the effects of supplementation modelling three scenarios: supplementing the above-mentioned number of Griffon Vultures (supplementation actual), supplementing six and 12 juveniles every five years for 30 years to the Alghero and Bosa populations, respectively (medium supplementation); supplementing 12 and 20 juveniles every five years for 30 years to the Alghero and Bosa populations, respectively (high supplementation). Age classes of restocked vultures are detailed in Table S2.
4. Human disturbance in the reproductive sites: breeding success may be adversely affected by disturbance, as described in Spain (Arroyo *et al.* 1990). In Sardinia, disturbance near nesting sites caused by hunters, photographers and hikers led to a decrease in the reproductive success of the colony (Aresu and Schenk 2006). Therefore, an increase in human disturbance was modelled by decreasing breeding propensity and reproductive success by 10% (human disturbance high), while its mitigation was modelled by increasing reproductive success by 10% (human disturbance medium), and by increasing both reproductive success and breeding propensity by 10% (human disturbance low; Table 2).

Stochastic growth rates (stoch-r) of alternative management scenarios were compared with the baseline demographic scenario by means of the Friedman test (Hollander and Wolfe 1999). This test is the non-parametric alternative to the one-way repeated measures analysis of variance ANOVA and is recommended because it makes no assumptions about the distribution of the data (e.g. normality and equality of variance). Statistical comparisons were performed in Minitab 17 Statistical Software (2010; State College, PA: Minitab, Inc.; www.minitab.com).

Results

Baseline model

Stochastic results for the baseline scenario are shown in Table 3. Population growth rates are negative for Alghero population (-0.0209). The model estimated the probability of extinction as 96.4% (0 SE), the mean time to first extinction being 14.8 years (0.37 SE, 11.6 SD), corresponding to ≈ 1 generation. As for the Bosa population, population growth rates were positive (0.0139). The model estimated the probability of extinction as 0.5% (0 SE), the mean time to first extinction being 43.2 years (4.45 SE, 9.96 SD), corresponding to ≈ 4 generations. The mean final population size of the extant Bosa population 244.24 (4.85 SE; 153.06 SD).

Sensitivity analyses

Sensitivity analysis showed that probability of extinction did not vary significantly for all simulated values of percent of juvenile and adult mortality in the Alghero and Bosa population (Figure 1). Growth rates of the Alghero population showed a regressive trend with an increase

Table 3. Stochastic results for under different scenarios simulated (440 years, 1,000 runs) in a PVA in Sardinia (Italy) for the Griffon Vulture. Stoch-r: stochastic growth rates; PE: proportion of the 1000 iterations in which the population went extinct; N-extant: mean population size, only for those remaining extant; N-all: mean population size, across all populations extant or extinct; Mean TE: of iterations that suffer extinctions, mean time to first population extinction.

| Scenario | Population | stoch-r | SD(r) | PE | N-extant | SD(N-ext) | N-all | SD(N-all) | MeanTE |
|------------------------------|------------|---------|--------|-------|----------|-----------|--------|-----------|--------|
| Baseline | Alghero | -0.0209 | 0.2433 | 0.964 | 7.53 | 11.01 | 0.31 | 2.5 | 14.8 |
| | Bosa | 0.0139 | 0.1298 | 0.005 | 244.24 | 153.06 | 243.03 | 153.64 | 43.2 |
| Supplementary feeding Low | Alghero | -0.0193 | 0.2384 | 0.96 | 11.08 | 11.35 | 0.48 | 3.13 | 14.8 |
| | Bosa | 0.0188 | 0.1297 | 0.001 | 281.83 | 156.84 | 281.54 | 157.01 | 40 |
| Supplementary feeding medium | Alghero | -0.0179 | 0.2369 | 0.961 | 10.69 | 10.96 | 0.47 | 2.99 | 15.5 |
| | Bosa | 0.0212 | 0.1294 | 0.002 | 301.4 | 153.75 | 300.8 | 154.18 | 41 |
| Supplementary feeding High | Alghero | -0.0183 | 0.2412 | 0.951 | 13.08 | 15.49 | 0.69 | 4.42 | 15.3 |
| | Bosa | 0.0228 | 0.1294 | 0.002 | 316.03 | 152.6 | 315.4 | 153.09 | 42 |
| Poisoning medium | Alghero | -0.008 | 0.2171 | 0.869 | 15 | 13.76 | 2.06 | 7.08 | 18.4 |
| | Bosa | 0.0352 | 0.0966 | 0 | 422.77 | 107.54 | 422.77 | 107.54 | 0 |
| Poisoning low | Alghero | -0.0076 | 0.2077 | 0.846 | 13.69 | 13.64 | 2.2 | 7.26 | 19.2 |
| | Bosa | 0.0419 | 0.0706 | 0 | 474.36 | 53.34 | 474.36 | 53.34 | 0 |
| Poisoning absent | Alghero | 0.0065 | 0.1784 | 0.643 | 20.62 | 16.8 | 7.48 | 14.03 | 21.3 |
| | Bosa | 0.0537 | 0.045 | 0 | 498.65 | 7.26 | 498.65 | 7.26 | 0 |
| Supplementation actual | Alghero | 0.0057 | 0.3117 | 0.425 | 23.57 | 23.91 | 13.79 | 21.41 | 27.5 |
| | Bosa | 0.0296 | 0.1318 | 0 | 359.55 | 127.37 | 359.55 | 127.37 | 0 |
| Supplementation medium | Alghero | 0.0214 | 0.3352 | 0.094 | 28.55 | 24.91 | 25.98 | 25.02 | 39.6 |
| | Bosa | 0.0342 | 0.1398 | 0 | 383.7 | 116.92 | 383.7 | 116.92 | 0 |
| Supplementation high | Alghero | 0.0374 | 0.3759 | 0.024 | 42.43 | 28.28 | 41.46 | 28.62 | 50.4 |
| | Bosa | 0.0398 | 0.1454 | 0 | 399.48 | 108.33 | 399.48 | 108.33 | 0 |
| Human disturbance low | Alghero | -0.0134 | 0.24 | 0.918 | 12.28 | 11.03 | 1.05 | 4.61 | 15.9 |
| | Bosa | 0.033 | 0.13 | 0 | 377.5 | 134.22 | 377.52 | 134.22 | 0 |
| Human disturbance medium | Alghero | -0.0156 | 0.24 | 0.935 | 12.98 | 13.93 | 0.89 | 4.76 | 15.9 |
| | Bosa | 0.0241 | 0.13 | 0.001 | 323.6 | 154.03 | 323.26 | 154.29 | 52 |
| Human disturbance high | Alghero | -0.0312 | 0.24 | 0.993 | 6.29 | 3.99 | 0.06 | 0.62 | 13.4 |
| | Bosa | -0.0051 | 0.13 | 0.017 | 112 | 102.25 | 110.13 | 102.39 | 43.1 |

in mortality rates, but they did not turn positive even at -50% mortality of adults or juveniles. In the Bosa population, perturbation of juvenile and adult mortality showed a transition point from positive to negative growth rates at +25% and +50% mortality, respectively. Variation in breeding

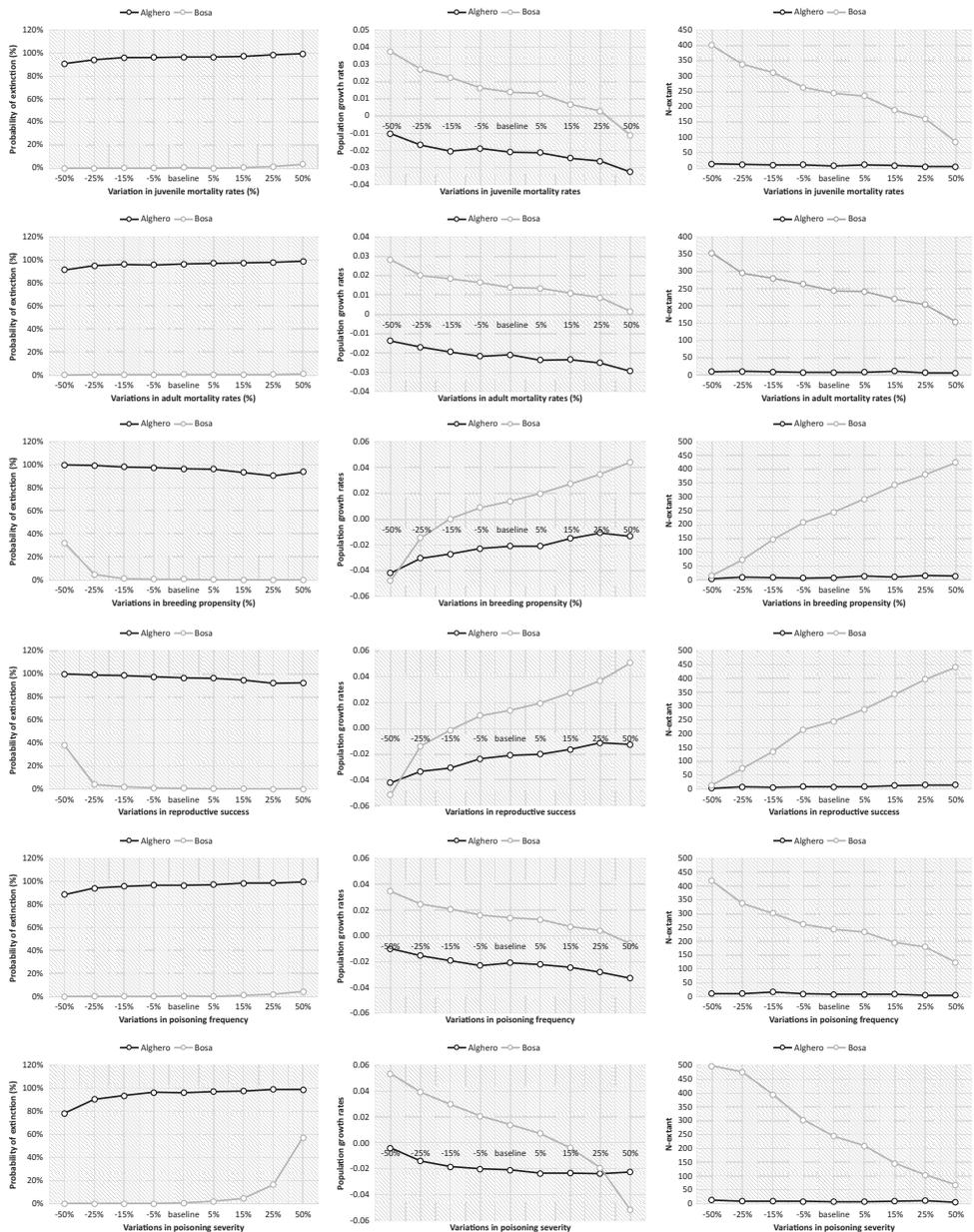


Figure 1. Sensitivity analysis of key demographic parameters (juvenile and adult mortality rates, breeding propensity, reproductive success, poisoning frequency and severity) on probability of extinction, population growth rates and mean size of the extant population (N-extant) for the Alghero and Bosa populations of Griffon Vultures. Points represent tested parameter values.

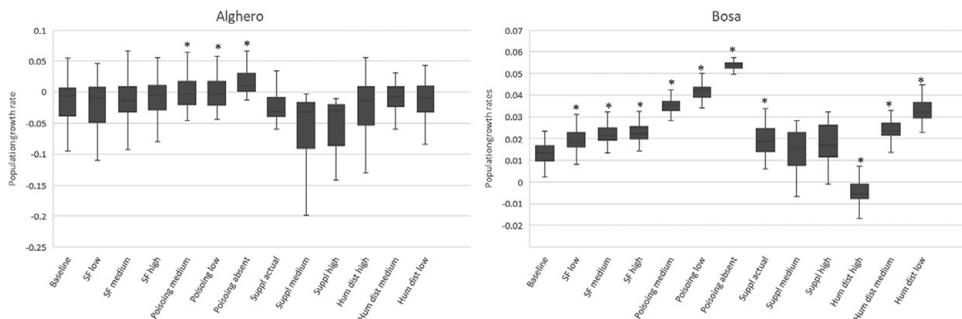


Figure 2. Comparative stochastic population growth rates under different scenarios simulated (55 years, 1,000 runs) in a PVA in Sardinia for the Griffon Vulture. SF supplementary feeding, Suppl: Supplementation, Hum dist: Human disturbance.

* Asterisk indicates significant differences from the baseline: Friedman ANOVA $P < 0.0001$.

propensity and reproductive success did not change significantly the trajectories of the Alghero population (Figure 1). On the other hand, growth rates of the Bosa population turned negative when reproductive parameters decreased by $> 15\%$. Hence, the population transitioned rapidly from low to high probability of extinction when breeding propensity and reproductive success decreased by more than 25% . Variation in the frequency of poisoning episodes did not change significantly the probability of extinction of the two populations (Figure 1). Growth rates turned negative in the Bosa population when the frequency of poisoning episodes increased by $+50\%$. Probability of extinction of the Alghero population decreased from 96.4% to 78.5% when the severity of poisoning episodes, in terms of reduction in reproductive parameters and survival, decreased by 50% . The Bosa population transitioned rapidly from low to high probability of extinction when the severity of poisoning episodes increased by $> 15\%$. Above this value also growth rates turned negative (Figure 1).

Management scenarios

Comparative stochastic population growth rates under the different simulated scenarios are shown in Figure 2. Overall population projections under the simulated management scenarios are shown in Figure S3.

Supplementary feeding

The projections obtained for the Bosa population indicated that lowering juvenile and immature mortality by supplementary feeding increased population growth rates significantly at all levels modelled (Figure 2; Friedman ANOVA $P < 0.0001$). On the other hand, the measure could not reverse population trends and failed to change population growth rates (Friedman ANOVA $P > 0.05$) for the Alghero population (Figure 2).

Catastrophic events (poisoning)

In both the Alghero and Bosa populations, the mitigation of poisoning events caused a significant increase in population growth rates at all the intensity levels modelled (Friedman ANOVA $P < 0.0001$; Figure 2). In the Bosa population, the reduction in poisoning frequency and severity (poisoning low) and its complete removal (poisoning absent) allowed the population to reach the carrying capacity (Table 3). In the Alghero population, the reduction in poisoning episode frequency (poisoning medium) and severity (poisoning low) was not enough to make population growth rates positive. However, it could lower the probability of extinction and increase the mean

final population size of the extant population (Table 3). When the occurrence of this catastrophe was completely removed (poisoning absent), population growth rates turned positive in the Alghero population and the probability of extinction dropped from the baseline 96.4% to 64.3% (Table 3).

Supplementation

This measure produced a significant increase in growth rates of the Bosa population only in the scenario “supplementation actual” (Figure 2; Friedman ANOVA $P < 0.0001$). In the other two intensity levels tested, the increase in population growth rates was not statistically significant. As for the Alghero population, the increase in population growth rates was not statistically significant (Figure 2). However, at all level tested this measure reduced the probability of extinction and increased the mean final population size of the extant population (Table 3).

Human disturbance

In the Bosa population, the effect of human disturbance showed that population trends are significantly affected by changes in reproductive rates at all the levels modelled (Friedman ANOVA $P < 0.0001$; Figure 2). When reproductive rates decreased as a result of human disturbance (human disturbance high), population growth rates turned negative (Friedman ANOVA $P < 0.0001$) and the mean final population size of the extant population was reduced (Table 3). By contrast, this measure was not effective in changing the growth rate of the Alghero population.

Discussion

According to the baseline model, our predictions of future population trends match the observational data, thus providing a measure of reliability of the modelling approach used in this study. Our sensitivity analyses showed that the uncertainty on mortality rates should not have impacted significantly on population projections. Griffon Vulture populations in Sardinia have not grown in the last 30 years. Reproductive parameters of the Sardinian populations are lower compared to those of other island (Xirouchakis 2010) and mainland populations (López-López *et al.* 2004, Demerdzhiev *et al.* 2014). Together with the very small population size, the relative high incidence of poisoning incidents and the lack of immigration, this places the Alghero population of Griffon Vultures at high risk of extinction in the short-term. On the other hand, the Bosa population, thanks to a larger population size, showed near-zero probability of extinction in the next 55 years (≈ 5 generations). However, its growth rates are significantly lower than those shown in other Griffon Vulture PVA analyses (Pavoković and Sušić 2006, García-Ripollés and López-López 2011). The existence of a flow of individuals between the two populations could provide a more optimistic scenario for the Alghero population. However, while dispersal of immature vultures from the Alghero area to Bosa has been observed by ornithologists, no record exists on the dispersal of individuals from the Bosa area to that of Alghero. Management actions should increase the attractiveness of the Alghero area for vultures and this highlight the importance of addressing the conservation of the species from a global perspective (Ortega *et al.* 2009, Margalida *et al.* 2018).

PVAs have been criticised due to the high number of parameters required to build a model with an acceptable degree of realism, and hence the high degree of uncertainty that is usually associated with their results (Coulson *et al.* 2001). However, PVAs rarely have the goal of providing accurate estimates of population status and trend; more often they are instrumental in supporting managers and policymakers in the decision process for the conservation of endangered populations in a context of uncertainty (Reed *et al.* 2002). Consequently, this study provides baseline estimates of the relative sensitivity of populations projections to changes in key demographic parameters.

Our results highlighted that the Alghero and Bosa populations showed a different sensitivity to the perturbation of the key parameters tested, thus suggesting that population size is a critical factor in affecting the projections of population dynamics of Griffon Vultures. This is a species with a low intrinsic growth rate because of its small clutch size. Compared with high-fecundity

populations, low-fecundity populations recover slowly from a severe reduction in density and thus spend more time at small sizes (Bennett and Ian 1997). Therefore low-fecundity species are more likely to become extinct after a catastrophic or stochastic event (Lande 1987, Bennett and Owens 1997). Observational data presented in this study show that the number of territorial pairs of the Alghero population was not restored after the poisoning event of the years 1997–1998. Sensitivity analyses showed that Alghero population trajectories were not significantly changed by variations in the key demographic parameters. Only by reducing the severity of poisoning episode by half could we observe a significant reduction in extinction probabilities. In line with this observation, the simulation of different management scenarios showed that the only measure effective in significantly increasing growth rates in the Alghero population was the mitigation of poisoning events, at all intensity levels simulated. The increase in population size by supplementation did not cause a statistically significant change in population growth rates, but it increased the mean final size of the extant population and it reduced the probability of extinction at all levels tested. The model calculated that the supplementation of the actual number of vultures supplemented in 2018 (project LIFE14/NAT/IT/000484) would reduce the probability of extinction from the baseline 96.4% to 42.5%. On the contrary, measures increasing survival rates, such as supplementary feeding, and reproductive rates, such as the mitigation of human disturbance, had no effect in changing population dynamics. These results suggest that demographic stochasticity is one of the main threats to the Sardinian population of Griffon Vultures. The same result was obtained when evaluating the extinction risk of the Bearded Vulture population in Corsica (a small, isolated breeding population of 8–10 pairs) (Bretagnolle *et al.* 2004).

However, the mitigation of catastrophic events and the implementation of supplementation programmes are not the easiest strategies to implement. Poisoning is regarded as the main threat to vulture conservation not only in southern Europe but also worldwide (Hernández and Margalida 2008, 2009, Margalida 2012, Margalida *et al.* 2019). The mitigation of this threat generally includes awareness campaigns, economic sanctions and legal punishment for poisoners when applicable. Banning the most frequently used poisons is another solution and a number of regulations have banned pesticides such as carbofuran, aldicarb or endrin in many parts of the world including the USA, Canada and the European Union, due to their negative impacts on non-target species (Martínez-Haro *et al.* 2008). However, banning does not completely guarantee that poisoning will stop because people illegally obtain these compounds or continue with this practice using alternatives (Martínez-Haro *et al.* 2008, Chiari *et al.* 2017). The use of poisons to kill animals seems to be strongly related to the lethality and availability of the formulations suggesting that the most toxic and available compounds are the most used (Martínez-Haro *et al.* 2008, Santangeli *et al.* 2016). Therefore, actions should also focus on ensuring the monitoring of manufacturing process and use by consumers of the highly toxic and available compounds (Plaza *et al.* 2019). Another strategy is the use of dogs to detect poisons. For instance, in Spain and Italy specialized dogs are trained to detect poisons in the field (Plaza *et al.* 2019). In Sardinia the anti-poison dog unit activated in 2016 with the project LIFE Under Griffon Wings (LIFE14/NAT/IT/000484) obtained the first ever judicial prosecution of a large-scale poisoning incident in the island. In general terms, however, the complete eradication of the threat is difficult to achieve without mitigating the causes of conflicts between humans and carnivores and scavengers (Badia-Boher *et al.* 2019). The conflict between vultures and livestock, raised by the presumed killing of livestock by Griffon Vultures, also increased the use of poisoning against this species, mainly in Spain and France (Margalida *et al.* 2014).

Implementing a restocking programme, on the other hand, is costly and depends upon the availability of funds and human resources. The restocking programmes implemented in Sardinia relied upon regional and EU funds.

When targeting a larger population, however, sensitivity analysis showed that perturbation of mortality rates of juvenile and adult birds, reproductive parameters, poisoning frequency and severity changed population trajectories. Sensitivity analysis highlighted that changes in juvenile mortality rates did not impact significantly on the probability of extinction of the population. In

line with these results, the simulated measures impacting on juvenile survival were the less effective in boosting population growth rates.

Supplementary feeding through the activation of feeding stations is a key part of vulture conservation in areas where sanitary constraints on carcass disposal largely limit vulture access to livestock carrion (Tella 2001, Donazar et al. 2009, Margalida et al. 2010), and their positive effect on vulture population viability is well known (Pavoković and Sušić 2006, Oro et al. 2008, García-Ripollés and López-López 2011). The main advantage of supplementary feeding is that it is easy to implement, and it has short-term effects on demographic parameters (Donazar et al. 2009). However, when feeding supplementation is managed as a limited number of heavy feeding stations, it poses several negative ecological effects (Cortés-Avizanda et al. 2016), such as density-dependent reduction of productivity (Carrete et al. 2006); buffering effects on dispersal strategies, making birds stay in the natal population as a consequence of conspecific attraction (Oro et al. 2008) or even effects on trophic cascades upon herbivores through facultative scavengers (Cortés-Avizanda et al. 2009). Heavy feeding stations can have negative effects also for non-target populations (Robb et al. 2008), bringing into question their potential benefits for community and population dynamics. Therefore, light and dispersed feeding stations should be prioritised (Deygout et al. 2009, Cortés-Avizanda et al. 2012, Moreno-Opo et al. 2015, Cortés-Avizanda et al. 2016). However, experimental work is needed to test the effectiveness of smaller, less predictable feeding stations to enhance juvenile and immature survival. In the present study, feeding supplementation increased the stochastic growth rate of the Bosa population at all intensity levels. However, sensitivity analyses showed that other measures were more effective in boosting population growth. Interestingly, a widespread management action was not as effective as expected in saving threatened populations from future negative trends. This result confirms previous findings in other vulture species (e.g. *Gypaetus barbatus*; Oro et al. 2008). The uncertainty of our estimates of mortality rates make it a priority for future field research on Griffon Vultures in Sardinia.

Population projections under scenarios of reduced frequency of poisoning forecast a positive outcome for the Bosa population, which reached the carrying capacity in two generations. Sensitivity analyses showed that an increase in the severity of poisoning episodes would lead to a significant increase in the extinction probabilities of the Bosa population. Several authors have highlighted the importance of mitigating this threat when developing PVAs in vultures (Oro et al. 2008, Monadjem et al. 2018, Murn and Botha 2018). However, the eradication of the illegal use of poison is neither easy nor time-efficient, and alternative measures acting synergistically in enhancing survival rates should be implemented to allow more time for tackling this threat (Oro et al. 2008).

Sensitivity analyses also showed that the Bosa population was highly sensitive to changes in reproductive parameters. Increasing reproductive rates by means of mitigating the threat of human disturbance in the reproductive sites predicted a positive outcome for the Bosa population at all intensity levels. The Griffon is a cliff-nesting vulture, which often nests in colonies that can comprise up to 100 pairs. Raptors are often sensitive to human activities around their nesting areas, which can cause nest abandonment and chick loss. Previous studies have highlighted the importance of human disturbance in the selection of a cliff as a nesting site (García-Ripollés et al. 2005, Gavashelishvili and McGrady 2006, Van Beest et al. 2008, Bamford et al. 2009). The conservation measure most often used by managers and conservationists to avoid disturbance is the establishment of spatial and temporal buffer zones around potentially sensitive areas (e.g. breeding sites), where disturbance activities are limited or prohibited (González et al. 2006, Margalida et al. 2011, Zuberogoitia et al. 2014). According to our projections, such measures should be applied to prevent a decrease in reproductive parameters of the Bosa colony.

In conclusion, the results of the present study confirmed that poisoning is a major threat for Griffon Vultures. The mitigation of this threat could increase population growth rates and decrease the extinction risk of the very small Alghero population. On the contrary, an increase in its severity

could hamper the short-term persistence of the larger Bosa population. Considering that poisoning is difficult to tackle and that mitigation measures usually pay in the medium-long term, in case of very small and threatened populations, a supplementation programme could help the population to persist in the short term. In the present study, larger population proved to be easier to manage since growth rates could be effectively increased by widespread and easy to implement conservation measures, such as mitigation of human disturbance in the reproductive sites. A cost-effectiveness analysis on the different management interventions should be performed as a follow up of this study to prioritize interventions.

Supplementary Materials

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0959270920000040>.

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