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ORIGINAL ARTICLE

Integrating effects of supplementary feeding, poisoning, pollutant ingestion and wind farms of two vulture species in Spain using a population viability analysis

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Abstract Population viability analyses (PVAs) are a useful technique in risk-assessment studies aimed at determining which demographic parameters are most influential in population persistence. Here, we incorporate demographic and environmental stochasticity in the construction of individual-based models integrating the effects of different scenarios in a PVA of the Eurasian Griffon Vulture (*Gyps fulvus*) and the endangered Egyptian Vulture (*Neophron percnopterus*) in Spain. Scenarios were based on reasonable options of population management, including effects of supplementary feeding (decreasing mortality and increasing fecundity), extensive wind farm development (increasing mortality), and catastrophic events such as poisoning (decreasing fecundity and survival) or pollutant ingestion (decreasing fecundity but no effect on survival). Our results show that those measures affecting survival show higher negative effects on population growth rate than those affecting fecundity. The outcomes were different and highly depend on the initial conditions and the species considered, with stronger negative effects on Egyptian Vulture populations. For both species, under similar conditions, the effects of massive poisoning, even occurring at low time frequency, had stronger negative consequences in population trends than the pollutant accumulation, or other actions affecting survival, such as installation of wind farms. Measures aimed at improving survival and fecundity such as supplementary feeding at vulture restaurants give rise to positive population trends. The establishment of management actions aimed at improving the birds' survival and increasing breeding success will probably boost the scavengers' populations into an upward trend, which is particularly important in the case of the endangered Egyptian Vulture.

Keywords Elasticity analysis · *Gyps fulvus* · *Neophron percnopterus* · PVA · Vortex software

Zusammenfassung Population Viability Analysis (PVA) ist eine nützliche Methode in Risikobewertungsstudien, die darauf abzielt, zu ermitteln, welche demographischen Parameter für das Fortbestehen von Populationen am einflussreichsten sind. Hier berücksichtigen wir demographische Stochastizität und Umweltstochastizität bei der Konstruktion individuenbasierter Modelle, welche die Effekte verschiedener Szenarien in eine PVA für den Gänsegeier (*Gyps fulvus*) und den stark gefährdeten Schmutzgeier (*Neophron percnopterus*) in Spanien integrieren. Die Szenarien beruhen auf angemessenen Optionen von Populationsmanagement, welche die Effekte von Zufüttern (erniedrigt die Mortalität und erhöht die Fruchtbarkeit), großflächigem Bau von Windenergieparks (erhöht die Mortalität) und katastrophalen Ereignissen wie Vergiftung (erniedrigt die Fruchtbarkeit und das

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Überleben) oder Schadstoffaufnahme (erniedrigt die Fruchtbarkeit, aber hat keinen Effekt auf das Überleben) einschließen. Unsere Ergebnisse zeigen, dass diejenigen Maße, die das Überleben beeinflussen, stärkere negative Effekte auf die Wachstumsrate der Population haben als die, welche die Fruchtbarkeit beeinflussen. Die Folgen waren unterschiedlich und hängen stark von den anfänglichen Bedingungen und der betrachteten Art ab, wobei die negativen Effekte auf die Schmutzgeierpopulationen stärker waren. Für beide Arten hatten unter ähnlichen Bedingungen die Effekte schwerer Vergiftung stärkere negative Folgen für die Populationsentwicklung als die Anreicherung von Schadstoffen oder andere Maßnahmen, die das Überleben betrafen, wie die Errichtung von Windenergieparks, und das obwohl Vergiftungen selten auftraten. Maßnahmen, die darauf abzielen, das Überleben und die Fruchtbarkeit zu verbessern, wie das Zufüttern in „Geierrestaurants", führen zu positiven Populationsentwicklungen. Die Etablierung von Managementmaßnahmen, die anstreben, das Überleben und den Bruterfolg der Vögel zu verbessern, wird die positive Populationsentwicklung dieser Aasfresser wahrscheinlich fördern, was besonders im Falle des stark gefährdeten Schmutzgeiers wichtig ist.

Introduction

Population viability analyses (PVAs) are a useful technique in risk assessment studies aimed at determining which demographic parameters are most influential in population persistence (Beissinger and McCullough 2002). One of the advantages of current PVAs is that they are able to incorporate spatial structure, environmental and demographic stochasticity into population models (Lacy 1993, 2000). PVAs are used to estimate the likelihood of a population's extinction, and are particularly useful to compare alternative management options by means of sensitivity analyses (Akçakaya and Sjögren-Gulve 2000; Naujokaitis-Lewis et al. 2008). One of the most used tools for PVA is the Vortex simulation software (Lacy 1993, 2000; Miller and Lacy 2005; e.g. Nilsson 2003; Soutullo et al. 2008; Duca et al. 2009; Ferrer et al. 2009; Carrete et al. 2009), which models population dynamics on an individual basis as discrete, sequential events (e.g. births, deaths, catastrophes, etc.) that occur according to defined probabilities (see software description in Miller and Lacy 2005).

To date, Spain holds more than 95% of the European population of the Eurasian Griffon Vulture (*Gyps fulvus*) and approximately 40–50% of the Egyptian Vulture (*Neophron percnopterus*), and still maintains one of the healthiest populations of scavengers' guild all over Europe (Ferguson-Lees and Christie 2001). However, population trends and the degree of threat are different between the two species. Whereas the Eurasian Griffon Vulture has an estimated population of 25,541 breeding pairs in Spain and is globally and regionally catalogued as "Least Concern" (BirdLife International 2004; Del Moral 2009a), the Egyptian Vulture has 1,452–1,556 breeding pairs according to the last national census conducted in 2008 (Del Moral 2009b), and is globally and regionally catalogued as "Endangered" (BirdLife International 2008). The Eurasian Griffon Vulture has experienced an overall increase in its Spanish stronghold, where it has increased substantially between the first censuses in the late 1970s and the present (Del Moral and Martí 2001; Del Moral 2009a). By contrast, the Egyptian Vulture declined substantially between 1970 and 1990, and has experienced only a slight increase in the last 20 years (Del Moral 2009b).

One of the traditional management practices concerning vultures is the so-called "*muladares*", also known as "vulture restaurants" or "supplementary feeding stations", traditional feeding places where farmers dump organic remains of dead cattle. Vulture restaurants are broadly distributed all over inner Spain, mainly close to traditional livestock areas, and are commonly located in remote regions. For many years, farmers have been taking a financial advantage from vultures which feed on cattle remains, by avoiding unnecessary expenditure in moving these remains to remote dumping sites. With the increase of intensive cattle raising in factory farms during the second half of the twentieth century, the availability of huge quantities of carrion dumped in vulture restaurants notably increased. Consequently, a parallel increase of Griffon Vulture populations occurred all over Spain (Parra and Tellaría 2004). However, since the outbreak of the neurodegenerative disease in cattle, Bovine Spongiform Encephalopathy (BSE) and its new variant in humans, Creutzfeldt-Jakob disease (vCJD or nvCJD), mandatory regulations of the European Union have led to the closure of existing vulture restaurants in order to avoid the likely risk of transmission (Regulation EC No. 1774/2002 of the European Parliament). As a consequence of this food shortage during the past 5 years, the populations of scavengers seem to have been affected, with juvenile survival and breeding success being reduced (Camiña and Montelío 2006; review in Donázar et al. 2009). This has been especially apparent for the species that benefited most from the vulture restaurants, such as the Griffon Vulture, which has experienced some local declines and a reduction in breeding performance (García-Ripollés and López-López, unpublished data). Nevertheless, the effect on other scavenger species like the Egyptian Vulture still remains unknown. The demographic influence of supplementary feeding is still the subject of scientific debate (Sánchez-Zapata et al. 2008; Margalida et al. 2010).

Other threats have been reported to affect avian scavengers' populations such as the accumulation of veterinary drugs and antibiotic residues (Oaks et al. 2004; Green et al. 2004, 2006; Lemus et al. 2008, 2009), uncontrolled and indiscriminate use of poisoning (Gangoso et al. 2009; Hernández and Margalida 2009), and, recently, the broad development of wind farms, which is rapidly occurring all over the Iberian Peninsula (De Lucas et al. 2007; Tellería 2009a, b, c; Carrete et al. 2009). At the beginning of the twenty-first century, Spain is the second highest wind energy-producing country in Europe and the third in the world (World Wind Energy Association, http://www.wwindea.org).

In the light of the current situation of extensive changes of human activities, including new energy-producing sources, livestock management and increased human pressure, it becomes necessary to integrate the effects of all these factors in a PVA. To this end, we here incorporate demographic and environmental stochasticity into the construction of individual-based models, integrating the effects of supplementary feeding, poisoning, pollutant ingestion and wind farms in a PVA of two vulture species in Spain. In addition, we perform a comprehensive sensitivity analysis in order to explore the effects of possible management actions aimed at maintaining stable populations of both species and to assess the risk of extinction in the medium and long term.

Methods

Study area and data collection

Two separated PVAs were developed, one for the Eurasian Griffon Vulture and another for the Egyptian Vulture, in continental Spain. Data on vulture populations were taken from the Spanish National Censuses carried out by field ornithologists all over the country and coordinated by the Spanish Ornithological Society (Arroyo et al. 1990; Perea et al. 1990; Del Moral and Martí 2001, 2002; Del Moral 2009a, b) (more information on surveys available at http://www.seo.org/).

To model demographic trends of Spanish populations of Griffon and Egyptian Vultures, five different subpopulations were modelled. Data were partitioned following the same classification of the 2nd Eurasian Griffon Vulture National Census (Arroyo et al. 1990), on the basis of five main regions named Iberico Massif, Baetic Massif, Pyrenees, Cantabric mountain range and Central Massif (Fig. 1). These five regions encompassed almost the whole Iberian populations of both species, and they were considered as representative of the different local trends experienced by the Spanish populations in the last decades. We used as starting point the initial population size in 1989 for the Eurasian Griffon Vulture (Arroyo et al. 1990) and the period 1987–1988 for the Egyptian Vulture (Perea et al. 1990).

Model parameter input

Demographic parameters were introduced into the Vortex simulation software (version 9.93; http://www.vortex9.org) in order to build a PVA for each species (Lacy 1993, 2000). Basic parameters were taken from the literature to create the baseline model which was compared to different alternative simulated scenarios (see below) (Table 1). Vortex simulates a population by stepping through a series of events that describe the typical life cycle of sexual organisms: selection of partner, reproduction, mortality, growth, emigration and immigration. Iteratively, the program creates an image of every individual and follows its fate throughout its life. It uses pseudorandom numbers which will determine whether the bird reproduces or not, whether it lives or dies, emigrates or not, etc., for every iteration (Miller and Lacy 2005). As a consequence, it produces different results with the exact input parameters, incorporating the influence of stochastic fluctuations in the population fate. Vortex calculates a stochastic population growth rate (*stoc-r*) as the ratio of the population size in the current year to the previous year for each scenario (Miller and Lacy 2005). Mean population growth rate is calculated across iterations and output (Lacy 2000). In our case, 500 runs were simulated for each scenario, as recommended by Harris et al. (1987). Two temporal terms were projected following Pavokovic and Susic (2006), one consisting of 25 years time period (medium term), and one of 50 years (long term). The period of 25 years allowed the implementation and testing of a preserving strategy for the species, whereas 50 years would allow the determination of the species persistence in a reasonable amount of time (Pavokovic and Susic 2006). Deterministic growth rate (*det-r*) was automatically generated by Vortex (Lacy 1993, 2000) by means of classical analysis of the projection matrix for the initial population (Caswell 2001). Data about dispersal rates for both species were still scarce, and hence populations were modelled as isolated, even though it is likely that some birds could disperse among populations. In fact, Egyptian Vultures are highly phylopatric according to observations of tagged birds, ringing recovery data (Grande 2006) and recent GPS satellite telemetry information (García-Ripollés et al. 2010). Data on the spatial structure of Eurasian Griffon Vultures were also insufficient although juvenile and subadult birds could behave as dispersers and information about recruitment of this species was still scarce. Precise age-class distribution for each species and each population were not available. Therefore,

Fig. 1 Study area showing Spanish provinces (administrative units). The provinces included in each of the five populations (in *bold*) analysed in the PVA are shown in *grey*

following Miller and Lacy's (2005) recommendation, initial population size was modelled as a stable age distribution. A similar assumption was made by Pavokovic and Susic (2006) in a PVA of Griffon Vultures. Extinction was assumed to occur when only one sex remained in the population (Miller and Lacy 2005). The reproductive system was modelled as long-term monogamy for both species (Ferguson-Lees and Christie 2001) and reproductive rates were taken from the literature (Arroyo et al. 1990; Del Moral and Martí 2002) varying among different populations (Table 1). Density-dependent effects on reproduction have been previously reported for raptors (e.g. Newton 1998; Ferrer et al. 2006) and, particularly, for vultures (e.g. Fernández et al. 1998; Carrete et al. 2006). Vortex models density dependence with an equation that specifies the proportion of adult females that reproduce $P(\mathrm{N})$ as a function of the total population size (Miller and Lacy 2005). This equation is: $P(N) = (P(0)-((P(0)-P(K))*((N/K)\hat{}B)))*(N/(A + N))$; where $P(0)$ is the percentage of adult females breeding at low density; $P(K)$ is the percentage of adult females breeding at carrying capacity; N is the initial population size; K is the carrying capacity; B is the steepness parameter, which determines the shape of the curve relating the percentage of adult females breeding to population size; and A is the Allee parameter, which accounts for the decrease in the proportion of females breeding at low densities. In our case, $P(0)$ were set as the productivity values obtained from the literature (Arroyo et al. 1990; Del Moral and Martí 2002). Following Miller and Lacy's (2005) rationale, $P(K)$ and B were derived from a regression analysis of data on the breeding rate of each population over total population size. In our case, $P(K)$ corresponded to a 20% reduction of $P(0)$, and fitted B was an exponential decay at rate 4. N was obtained from the literature (Arroyo et al. 1990; Perea et al. 1990), and K was calculated as the population size in 2008, the last available censuses (Del Moral 2009a, b), multiplied by 1.15 and rounded up to the closest 100. We used this figure since the population size in 2008 for both species was the largest size so far reached. No Allee effect was considered ($A = 0$), given that it has not been reported in the literature. Age-specific mortality rates were taken from the literature (Sarrazin et al. 1994; Sarrazin and Legendre 2000; Le Gouar et al. 2008; Grande et al. 2009; 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. The potential effects of inbreeding depression, harvesting, supplementation, and genetic management were not included in the simulations.

Sensitivity analysis

Four different scenarios were simulated in order to assess how changes in environmental conditions would affect population trends. Changes in population growth rates of stochastic simulations (*stoc-r*) were compared among different scenarios over time frames of 25 and 50 years. Probability of extinction (*PE*) was calculated as the proportion of the 500 iterations in which the population went extinct. The main interest of sensitivity analyses is to compare what management strategies are more efficient from a conservation point of view (Naujokaitis-Lewis et al. 2008), and not to predict how many pairs the study area can

Table 1 Summary of input parameters used in the baseline scenario for the PVA of the Eurasian Griffon Vulture (*Gyps fulvus*) and the Egyptian Vulture (*Neophron percnopterus*) in Spain

Parameter	Eurasian Griffon Vulture	Egyptian Vulture	Source*
Reproductive system	Long-term monogamy		a
Age of first offspring (males and females)	4	6	b, h
Maximum age of reproduction	20	15	b, h
Maximum number of broods per year	1	1	a
Sex ratio at birth	1 1	1 1	b
Density dependent reproduction	Yes	Yes	j
% Breeding at low density, *P*(0)	*I*: 64.00; *B*: 71.00; *P*: 63.00; *C*: 80.00; *Ce*: 69.00	*I*: 96.82; *B*: 80.00; *P*: 65.08; *C*: 68.42; *Ce*: 91.51	c, d
% Breeding at carrying capacity, *P*(*K*)	*I*: 51.20; *B*: 56.80; *P*: 50.40; *C*: 64.00; *Ce*: 55.20	*I*: 77.46; *B*: 64.00; *P*: 52.06; *C*: 54.74; *Ce*: 73.21	See text
Allee parameter, *A*	0	0	See text
Steepness parameter, *B*	4	4	See text
% Males in the breeding pool	100%	100%	See text
Carrying capacity (*K*)	*I*: 20,000; *B*: 5,000; *P*: 5,000; *C*: 10,000; *Ce*:10,000	*I*: 1,000; *B*: 500; *P*: 750; *C*: 1,250; *Ce*: 750	See text
Initial population size (*N*)	*I*: 4,464; *B*: 1,698; *P*: 1,424; *C*: 2,430; *Ce*: 2,852	*I*: 608; *B*: 116; *P*: 322; *C*: 470; *Ce*: 594	c, e
Mortality (%) from age 0 to 3 (SD)	14.2 (3.9)	10.0 (2.0)	f, g, h
Mortality (%) from age 3 to 4 (SD)	3.3 (3.7)	11.7 (3.0)	h, i
Mortality (%) from age 4 to 5 (SD)	3.3 (3.7)	11.7 (3.0)	h, i
Mortality (%) from age 5 to 6 (SD)	3.3 (3.7)	40.0 (4.0)	h, i
Mortality (%) after age 6 (SD)	3.3 (3.7)	11.0 (2.0)	h, i

* References: [a] Ferguson-Lees and Christie (2001); [b] Pavokovic and Susic (2006); [c] Arroyo et al. (1990); [d] Del Moral and Martí (2002); [e] Perea et al. (1990); [f] Sarrazin et al. (1994); [g] Sarrazin and Legendre (2000); [h] Grande et al. (2009); [i] Le Gouar et al. (2008); [j] Fernández et al. (1998). See text for specific comments on how parameters were estimated.

I Iberico Massif, *B* Baetic Massif, *P* Pyrenees, *C* Cantabric mountain range, *Ce* Central Massif, *SD* standard deviation

hold (Oro et al. 2008). Therefore, scenarios were based on reasonable options of population management, following Soutullo et al.'s (2008) rationale. To this end, we used similar figures for simulations as those provided by Pavokovic and Susic (2006) in a PVA of Griffon Vultures. We modelled effects of supplementary feeding (decreasing mortality and increasing fecundity) (González et al. 2006; Oro et al. 2008), extensive wind farm development (increasing mortality) (Langston and Pullan 2003; Drewitt and Langston 2006), and catastrophic events such as poisoning (decreasing fecundity and survival) (Gangoso et al. 2009; Hernández and Margalida 2009) and pollutant ingestion (decreasing fecundity but no effect on survival) (Lemus et al. 2008, 2009) (Table 2). Each alternative scenario was also modelled with three intensity levels (*low*, *medium* and *high*) of the magnitude of change of the demographic variables in relation to the baseline model (Table 2). Due to the unpredictability of catastrophic events, the frequency of occurrence, happening in randomly selected iterations, was subjectively set at 20% in order to be conservative, following Pavokovic and Susic (2006). The effect of catastrophic events on survival and/or reproduction was modelled including a severity factor ranging from 0 to 1 (Miller and Lacy 2005). For example, a severity factor with respect to reproduction modelled at 0.90 would mean that, in the period of catastrophe, this parameter will decrease by 10%, whereas an effect on survival at 0.70 would mean that survival rates will decrease by 30% for all age classes. Parameters were modified as shown in Table 2, with all other parameters of the baseline scenario kept unchanged. Stochastic growth rates (*stoc-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 nonparametric alternative to the one-way repeated measures analysis of variance ANOVA, and it is recommended because it makes no assumptions about the distribution of the data (e.g. normality and equality of variance) (StatSoft 2004). Statistical comparisons were performed in STATISTICA v.6.0.

Table 2 Simulated scenarios used in PVA of the Eurasian Griffon Vulture (*Gyps fulvus*) and the Egyptian Vulture (*Neophron percnopterus*) in Spain

Scenario	Juvenile mortality	Adult mortality	Fecundity	Catastrophic events			
				Occurrence	Frequency	Effect on fecundity[a]	Effect on survival[a]
Basic scenario	Baseline scenario[b]	Baseline scenario	Baseline scenario	No	x	x	x
Supplementary feeding low	−10%	−10%	+10%	No	x	x	x
Supplementary feeding medium	−20%	−20%	+10%	No	x	x	x
Supplementary feeding high	−30%	−30%	+20%	No	x	x	x
Wind farms low	+10%	+10%	Baseline scenario	No	x	x	x
Wind farms medium	+20%	+20%	Baseline scenario	No	x	x	x
Wind farms high	+40%	+40%	Baseline scenario	No	x	x	x
Poisoning low	Baseline scenario	Baseline scenario	Baseline scenario	Yes	20%	0.90	0.90
Poisoning medium	Baseline scenario	Baseline scenario	Baseline scenario	Yes	20%	0.90	0.70
Poisoning high	Baseline scenario	Baseline scenario	Baseline scenario	Yes	20%	0.90	0.50
Pollutant low	Baseline scenario	Baseline scenario	Baseline scenario	Yes	20%	0.70	1.00
Pollutant medium	Baseline scenario	Baseline scenario	Baseline scenario	Yes	20%	0.50	1.00
Pollutant high	Baseline scenario	Baseline scenario	Baseline scenario	Yes	20%	0.30	1.00

The signs (+) and (−) indicate an increase or decrease respectively in the parameter of the baseline scenario with the corresponding percentage (see text for details)

[a] The values are severity factors

[b] The parameters of the baseline scenario are those detailed in Table 1

Results

Baseline model

Basic population trends differed between the two vulture species based on Vortex simulations. All five Eurasian Griffon Vulture populations showed a positive trend either taking into account deterministic growth rate (*det-r* > 0 for all populations, range $= 0.093$–0.118), or stochastic growth rate (*stoc-r* range$_{25\ \text{years}} = 0.077$–$0.118$; *stoc-r* range$_{50\ \text{years}} = 0.074$–$0.097$) (ES1).

In the case of Egyptian Vulture populations, they showed differential trends, with three populations showing positive deterministic growth rates (Iberico, Beatic and Central Massif: *det-r* range $= 0.002$–0.022), and two populations showing negative trends (Pyrenees: *det-r* $= -0.020$; and Cantabric mountain range: *det-r* $= -0.014$) (ES2). Furthermore, when the stochastic process for the calculation of the growth rate was taken into account, up to three Egyptian Vulture populations showed negative trends (Baetic, Pyrenees and Cantabric: *stoc-r* range$_{25\ \text{years}} = -0.012$ to -0.026; *stoc-r* range$_{50\ \text{years}} = -0.015$ to -0.028) (ES2).

Supplementary feeding

Population trends significantly changed when management actions aimed at decreasing juvenile and adult mortality and at increasing fecundity were taken into account (for both species Friedman ANOVA $\chi^2_{5,3} = 15.00$, $P < 0.0018$). All Griffon Vulture populations increased according either to deterministic or stochastic population growth rates (ES1).

In the case of Egyptian Vultures, this measure resulted in significant changes in population trends, turning decreasing into increasing projections for all populations (*det-r* and *stoc-r* > 0 in all cases but one; Pyrenean population under low management magnitude *stoc-r* $= -0.002$) (ES2). The magnitude of the change in relation to population trends was higher in Egyptian Vultures than in Griffon Vultures (Fig. 2).

Catastrophic events (poisoning and pollutants)

The effect of catastrophic events showed that the magnitude of change in population trends differed when the demographic parameter lowered was fecundity (with a general lower effect upon population growth rate) or survival (with the highest negative effect on population growth rate) (Fig. 2). In all cases, significant changes were observed when catastrophic events occurred (Griffon Vulture: *poison* Friedman ANOVA $\chi^2_{5,3} = 15.00$, $P < 0.002$; *pollutant* Friedman ANOVA $\chi^2_{5,3} = 10.20$, $P < 0.017$; Egyptian Vulture: *poison* Friedman ANOVA $\chi^2_{5,3} = 15.00$ $P < 0.002$; *pollutant* Friedman ANOVA $\chi^2_{5,3} = 14.76$, $P < 0.002$). In the case of the Griffon

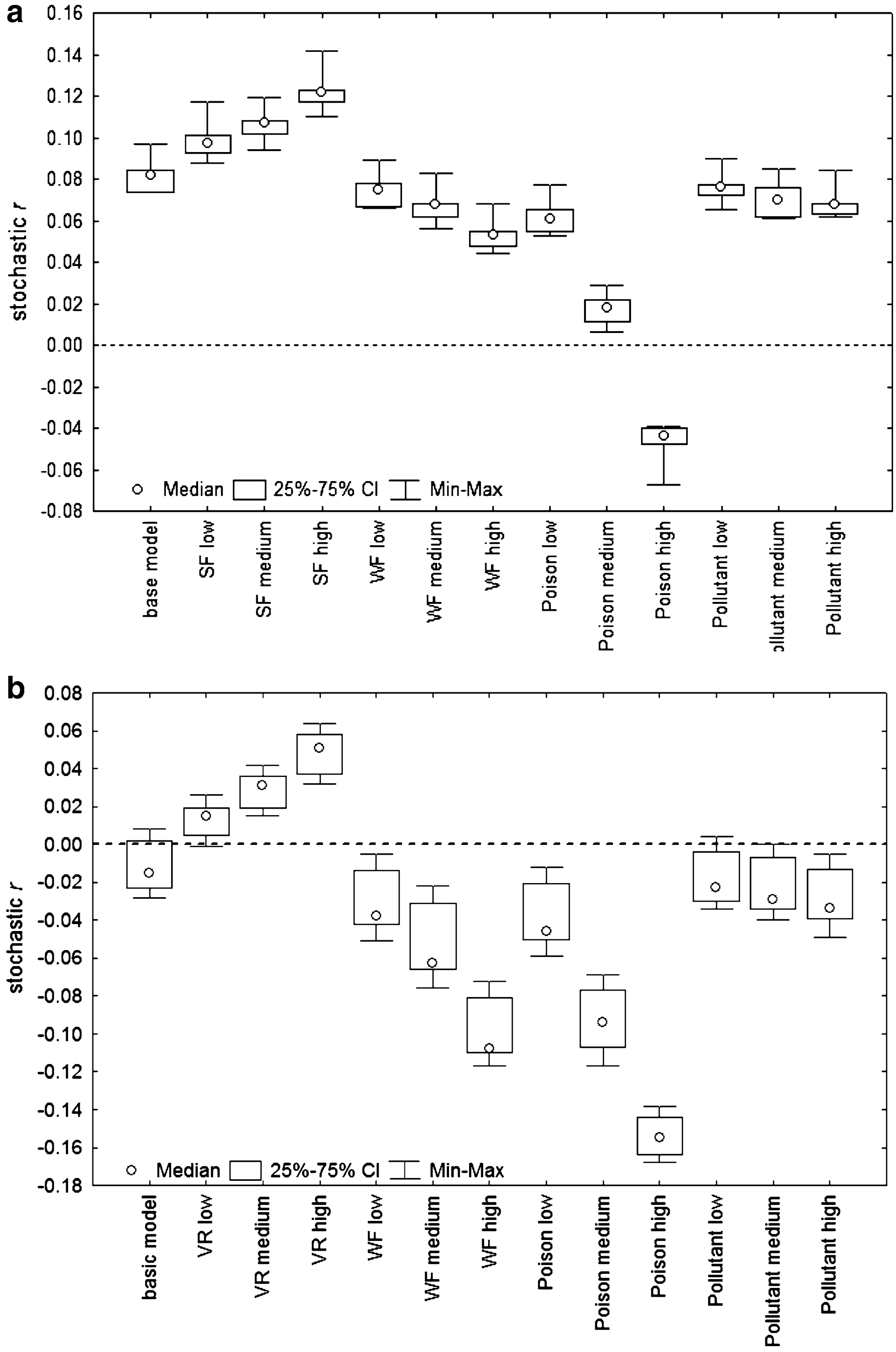

Fig. 2 Comparative stochastic population growth rates (*stoc-r*) under different management scenarios simulated (50 years) in a PVA in Spain for: **a** the Eurasian Griffon Vulture (*Gyps fulvus*), and **b** the Egyptian Vulture (*Neophron percnopterus*) (*SF* supplementary feeding, *WF* wind farms, *CI* confidence intervals). Three intensity levels (*low*, *medium* and *high*) were modelled in relation to the magnitude of change of the demographic variables in relation to the baseline model (see text for details)

Vulture, the occasionally poisoning affected population trends negatively and was the only action that would drive a population to a decreasing trend under the highest intensity levels (poisoning$_{\text{high}}$ *stoc-r* < 0 in all populations, ranging from -0.039 to -0.067 for long-term projections) (ES1). In the case of pollutant accumulation, mostly negative effects on population growth rates were projected (% of change in *stoc-r* varying from $+24.68\%$ to -21.11% for medium-term projections, and between -2.70% to -19.05% in the long term) (ES1), but with much lower effects than poisoning (Fig. 2a). Curiously enough, the effect of stochasticity in catastrophic events results sometimes in apparently contradictory results at lower intensity levels (e.g. *stoc-r* > 0 in the case of Baetic$_{\text{pollutant low}}$ and Cantabric$_{\text{pollutant low}}$) (ES1). However, the effect of stochasticity disappeared as the projected time frame increased (e.g. *stoc-r* < 0 in 50 years projections).

In the case of Egyptian Vulture, poisoning clearly leads to decreasing population trends under all intensity levels (in all cases *stoc-r* < 0 and for all populations) (ES2;

Fig. 2b). This highlights how occasional poisoning incidents (even at low frequencies such as 20%) could drive some populations to extinction in the long term ($PE_{50\ years}$ ranging from 0.000 to 0.990) (ES2). The effect of pollutant accumulation (e.g. antibiotic residues and veterinary drugs) had lower effects than massive poisoning, but caused a decrease in population trends under all intensity levels (*stoc-r* < 0 for all populations) (ES2). The risk of extinction of some populations also occurred in the long term ($PE_{50\ years}$ ranging from 0.000 to 0.040) (ES2).

Wind farms

Vortex simulations showed that actions lowering juvenile and adult survival changed population trends significantly (for both species Friedman ANOVA $\chi^2_{5,3} = 15.00$, $P < 0.0018$). However, similarly to what happens in the *supplementary feeding* scenario, the effect of change varied in relation to the species considered. In the case of the Griffon Vulture, all populations showed decreases in both deterministic and stochastic population growth rates (% of change in *stoc-r* varying from −3.75% to −40.26% for medium-term projections and between −9.46 to −40.54% in the long term) (ES1). However, it should be emphasized that even in the case of increasing bird mortality, all populations still showed positive (but lowered in relation to the basic scenario) population growth rates (*det-r* and *stoc-r* > 0 for all populations under the three different intensity levels) (ES1; Fig. 2a).

In the case of the Egyptian Vulture results were different, with all populations showing negative population trends (in all cases except for $\text{Iberico}_{\text{windfarm low}}$, *det-r* and *stoc-r* < 0) (ES2). The magnitude of the effect increased as the intensity level increased, inevitably driving populations to extinction in the long term ($PE_{50\ years}$ ranging from 0.000 to 0.970) (ES2; Fig. 2b).

Discussion

PVAs are a useful tool for risk-assessment studies (Beissinger and McCullough 2002). In fact, PVAs are especially valuable not only to project population trends in the future under alternative potential scenarios but also for translating the results of sensitivity analyses into sensible management prescriptions (Soutullo et al. 2008). According to the baseline model, our predictions of future population trends match with observational data, thus providing a measure of reliability of the modelling approach used in this study. Griffon Vulture populations have increased in the past 20 years (Del Moral and Martí 2001; Del Moral 2009a) whereas Egyptian Vultures seem to show differential population trends, with some populations slightly increasing whereas others are clearly decreasing (Del Moral and Martí 2002; Del Moral 2009b).

Our results showed that those measures affecting survival had higher negative effects on population growth rate than those affecting fecundity. This is actually expected to occur under closed population dynamics for long-lived species (e.g. Soutullo et al. 2008). Notwithstanding, it is interesting to emphasise that, under similar conditions, the effects of massive poisoning, even occurring at low time frequency, had stronger negative effects on population trends than the pollutant accumulation, or actions affecting only survival, such as wind farms. The result of changes in demographic parameters was highly dependent on initial conditions of the species modeled, essentially mortality rates and the initial population size. For example, whereas an increase of 10–30% in juvenile and adult mortality did not change the direction of population trends of Griffon Vultures, a similar increase in mortality led to a high risk of extinction in the case of the Egyptian Vulture. This is important from a conservation point of view, given that, for the latter, there would be no chance to recover after a sudden increase in mortality.

One of the alternative management scenarios is the use of supplementary feeding, which has the potential to produce long-term changes in the population dynamics and distribution of some bird species (review in Robb et al. 2008). In Spain, scavengers, mostly the Eurasian Griffon Vulture, have relied greatly on artificial maintenance through vulture restaurants or dumps. Consequently, it has generated intense debate about sanitary, social and conservation problems associated with this artificial management (Margalida et al. 2010). The main advantage of supplementary feeding is that it is cheap, easy to implement and it has short-term effects on demographic parameters (mainly increasing juvenile survival and breeding success) (Donázar et al. 2009). Negative effects of the use (and abuse) of supplementary feeding include the occurrence of density-dependent effects resulting in a reduction of productivity (Carrete et al. 2006); buffering effects on dispersal strategies, making birds to stay in the natal population as a consequence of conspecific attraction (Oro et al. 2008); changes in social structure through changes in aggressiveness levels, especially in territorial species such as the Egyptian Vulture (Meretsky and Mannan 1999); or even effects on trophic cascades upon herbivores through facultative scavengers (Cortés-Avizanda et al. 2009). In addition, supplementary feeding could also have negative effects on scavenger populations through the accumulation of pollutant and veterinary drugs from livestock and poison, which has negative effects on reproduction (Green et al. 2004, 2006; Lemus et al. 2008, 2009) and survival (Gangoso et al. 2009; Hernández and Margalida 2009). Accordingly, supplementary feeding has a lot of potential for conservation of scavenger species, but it has to be managed through a coordinated network, acting in accordance with sanitary prescriptions, and following scientific evidence-based recommendations (Deygout et al. 2009; Donázar et al. 2009).

Measures aimed at stopping poisoning are encouraged as this is the most influential threat to vulture populations, not only in southern Europe but also worldwide (Green et al. 2004, 2006). These include economic sanctions and legal punishment for poisoners when applicable. Veterinary drugs and pollutant accumulation should also be decreased. More research is needed to establish the threshold levels of pollutant accumulation that causes deleterious effects not only on scavengers but also in the cattle that enter into the human trophic chain after recovering from veterinary diseases. In fact, this could be an underlying factor that could explain why some species seem not to recover or are recovering at lower rates (e.g. the Egyptian Vulture, but also the Bearded Vulture *Gypaetus barbatus* or the Black Vulture *Aegypius monachus*).

Finally, mortality caused by wind farms does not seem to be the most influential parameter upon population persistence, at least according to our PVAs. Despite the potential negative effects of wind farms on birds and bats (e.g. Langston and Pullan 2003; Barrios and Rodríguez 2004; Drewitt and Langston 2006; but see Farfán et al. 2009; review in Stewart et al. 2007), we are currently undergoing a period of expansion of wind farm energy in Spain, with undetermined consequences over resident and migrant species (Tellería 2009a, b, c). Problems arise when the effects of several threats are combined, including the exposure to poison and veterinary drugs, added to an increase in mortality due to the installation of wind farms close to breeding or feeding areas, as it is happening in some Spanish regions. Therefore, the application of the precautionary principle becomes necessary. The establishment of management actions aimed at improving bird survival and breeding success will probably boost the scavenger populations into an upward trend, which is particularly important in the case of the endangered Egyptian Vulture.

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