

# Effects of wind farms and food scarcity on a large scavenging bird species following an epidemic of bovine spongiform encephalopathy

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## Summary

1. Wind farms are emerging as a major cause of mortality of large scavenging bird species, which may be catastrophic when they operate in concert with other threats. As a study model, we examine the impact of wind turbines on the population dynamics of a soaring bird species, when acting in conjunction with a sudden decrease in food availability following the European bovine spongiform encephalopathy (BSE) epidemic.

2. In Spain, vultures have been provided with supplementary food at traditional vulture restaurants for centuries. In 2006/2007, these feeding stations were closed as part of disease control measures. At the same time, wind farms were deployed within the vulture foraging range. We used capture–recapture data and direct observation to monitor the impacts of these changes on the vulture population.

3. The number of breeding pairs decreased by *c.* 24%, adult survival by 30% and fecundity by 35%. However, the population recovered as soon as the perturbations ceased, the vulture restaurants were reopened, and the most problematic wind turbines were closed. Population recovery was faster than predicted by a retrospective stochastic population model.

4. Our analyses indicate that fecundity and survival were influenced predominantly by wind turbines. Food scarcity promoted a shift in foraging behaviour that drove vultures to fly into the path of wind turbines as they sought out new food sources in a landfill site. Elasticity and sensitivity analyses of the population model showed that mortality of adult birds had a much greater effect on population declines than mortality of immature birds, whereas reduction in fecundity had negligible effects.

5. The most likely explanation for the rapid recovery of the vulture population is that the observed decline in breeding pairs was not solely because of increased mortality. The decline probably included dispersal away from the area and a greater incidence of skipped breeding during the perturbation years. Subsequent immigration from large nearby populations was probably a factor in population recovery.

6. *Synthesis and applications.* Where specific wind turbines are causing substantial mortality, their closure is an effective management response. For vulture populations dependent on supplemental feeding stations, the feeding sites should be relocated away from the most problematic wind turbines, or other anthropogenic sources of mortality, to prevent negative impacts. We recommend the establishment of scattered, low-value food sources to replicate historical conditions and to avoid the problems associated with high concentrations of individuals in one place.

**Key-words:** bovine spongiform encephalopathy, *Gyps fulvus*, mortality, population model, rescue effect, scavenging birds, wind farms

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## Introduction

Subsidising wild animal populations, either unintentionally or as part of conservation management, is known to have profound effects on the population dynamics of many species (Gomper & Vanak 2008; Robb *et al.* 2008). While supplemental feeding can increase survival of highly threatened populations, and thus maintain population viability, it can also inevitably create dependence. A sudden discontinuation of supplementary feeding can have unexpected cascading effects on populations and communities (Votier *et al.* 2004). This is especially true for scavenging species, for example, gulls, shearwaters or vultures, whose diets incorporate supplementary food in substantial proportions (Martínez-Abraín, Maestre & Oro 2002; Oro *et al.* 2008). The effects of food cessation can be particularly severe for species under pressure from anthropogenic sources of mortality.

The risk of death from collision with wind farm turbine blades has increased in recent years (e.g. Lucas, Janns & Ferrer 2007; Martínez-Abraín *et al.* 2009). From 2005 to 2009, installations of wind farms increased by 45% and 74% in the European Union and the United States, respectively (Lucas, Janns & Ferrer 2007), because wind farms are considered an environmentally friendly alternative energy source (Kuvlesky *et al.* 2007; but see Carrete *et al.* 2009). However, wind farms are reported to cause mortality in many flying animal species (Langston & Pullan 2003; Barrios & Rodríguez 2004; Sterner, Orloff & Spiegel 2007). Preliminary studies indicate that wind turbines can reduce the abundance of many bird species, particularly ducks, waders, songbirds and raptors (Stewart, Pullin & Coles 2007). Wind farms can also impede migratory birds if they are located in key flyways (Larsen & Guillemette 2007; Tellería 2009a), and they can force local populations to disperse (Madders & Whitfield 2006; Farfán *et al.* 2009). Wind farms are usually located in windy areas, often coinciding with colonies of scavenging raptors (Tellería 2009b) that use the same wind currents to maximise gliding efficiency.

Previous research on the impacts of wind farms on birds has been limited to recording species found dead under turbine blades. For example, thirty-eight unpublished reports and papers, cited in Sterner, Orloff & Spiegel (2007), recorded bird mortality caused by wind farms in the United States and Europe but did not provide any analysis of the effects of such mortality on population dynamics, nor did they consider the impact of wind turbines in the context of other threats. This may be due to the fact that the number of birds at risk is generally unknown and hence the number of dead birds cannot be used to estimate mortality rate. However, many bird species are affected by wind power development, and managers lack sufficient information on which to base risk mitigation measures (Carrete *et al.* 2010; Janss *et al.* 2010). For example, in Navarra (northern Spain), Lekuona & Ursúa (2007) reported that *c.* 50 species of birds are susceptible to collision risk, 13 of them raptors comprising 71% of the casualties recorded.

In this study, we assess the impacts of wind turbines and food availability on a population of Eurasian griffon vultures *Gyps fulvus*, Hablitzl 1783, in Spain as a model species for large

scavenging birds. Specifically, we analyse demographic, population-level consequences in the context of wind farm deployment and food scarcity (see García-Ripollés, López-López & García-López 2004). Traditional vulture restaurants have been used in Spain for centuries as ad hoc facilities for the disposal of cattle that have died from natural causes; these facilities rely on the scavenging ecosystem services provided by wild vultures. Following the 2001 European bovine spongiform encephalopathy (BSE) epidemic, the provision of vulture restaurants with livestock carcasses was temporarily banned to reduce the risk of disease spreading (Camiña & Montelío 2006; Donazar *et al.* 2009).

Griffon vultures are long-lived species with delayed maturity and a low reproductive output per season (Sarrazin & Legendre 2000), making populations especially vulnerable to high adult mortality following environmental and anthropogenic perturbations (Reed *et al.* 2003; Drewitt & Langston 2006). Both wind farms and supplemental feeding can have complex consequences if the placement or closure of vulture restaurants alters the spatial patterns of movement such that vultures are rendered more vulnerable to wind turbines. Here, we distinguish the effects of wind turbines and food scarcity on the fecundity and survival of vultures, and we examine how stage-specific population parameters drive population dynamics.

## Material and methods

### STUDY POPULATION

The study population is located in eastern Spain within the province of Castellón; this population was almost driven to extirpation during the 1960s, probably due to the widespread use of poison to control mammalian carnivores. Since 1995, exhaustive government-funded monitoring of colonies has been conducted during the incubation and fledging periods. In 2009, vulture colonies in the province of Castellón occupied a surface area (calculated as a Minimum Convex Polygon) of 3166 km<sup>2</sup>. The main feeding grounds of the study population were located in the neighbouring province of Teruel, where vulture restaurants continued to operate throughout 2006. Traditional vulture restaurants in Castellón were closed from April 2006 to October 2007 following European regulations in response to the BSE epidemic (Camiña & Montelío 2006; Donazar *et al.* 2009). A subset of vulture feeding stations (i.e. a type of vulture restaurant set-up specifically for conservation purposes by the environmental authorities) reopened in late 2007. The temporary loss of supplementary food affected the 2006 and 2007 breeding seasons (Table 1). Currently (2010), there are four large vulture restaurants in the area and nine more in the neighbouring province of Teruel, which are used heavily by the vultures.

Wind turbine deployment began in the northern part of the vulture range in September 2006, affecting the 2007 and 2008 breeding seasons (Table 1). Wind turbines were operative until May 2008, when 50 turbines (of 260) were closed because they had been identified as the cause of high vulture mortality (Table 1).

### CAPTURE-RECAPTURE TO ESTIMATE SURVIVAL

Vultures were trapped each year from September to December in 2005–2009, using a large cage placed at one vulture restaurant that was operated remotely. Vultures were aged based on their plumage

**Table 1.** Annual calendar showing the state of major vulture restaurants and wind farms causing the bulk of mortality in the study area. The year runs from June to June to show the breeding (January–June) and post-breeding (June–December) periods. Before 2005, restaurants were open and windfarms were not yet deployed

	2005–2006		2006–2007		2007–2008		2008–2009	
	June–Dec	Jan–June	June–Dec	Jan–June	June–Dec	Jan–June	June–Dec	Jan–June
Restaurants	Open	Closed	Closed	Closed	Open	Open	Open	Open
Wind farms	Inactive	Inactive	Active	Active	Active	Active	Inactive	Inactive
Breeding period		X		X		X		X

and marked with a Darvic leg ring with an alphanumeric code. Because of the low number of sub-adults captured, only birds with adult plumage were included in the survival analysis ( $n = 422$ ). Resighting of marked birds predominantly occurred at feeding and nesting sites between September and December. In total, 1195 resightings of adult vultures occurred from 2006 to 2009, corresponding to 557 individual resightings. Examination of dead vultures sent to rehabilitation centres because of collision with turbines revealed that 70% were adults and 30% were immature birds (data up to May 2009). As a direct estimate of mortality was only obtained for adults from the capture–recapture data, we reduced the survival rate of immature age classes to half that estimated for adults (i.e. whereas during 2007 and 2008 adult survival rate was reduced by 30%, the survival rate for other stages was reduced by only 15%).

Adult local survival was estimated from presence–absence data of marked individuals using a standard Cormack–Jolly–Seber (CJS) capture–recapture model, with survival and recapture probabilities varying with time ( $\phi_t$  and  $p_t$ , respectively, see Lebreton *et al.* 1992) using the program M-SURGE (Choquet *et al.* 2004). We used the Akaike Information Criterion corrected for small sample size for model selection [ $AICc = AIC + (2K(K + 1))/(n - K - 1)$  where  $AIC = \text{model deviance} + 2K$ ,  $K$  is the number of identifiable parameters in the model, and  $n$  is the sample size; Burnham & Anderson 2002; ]. We used a conservative threshold  $\Delta AICc$  score ( $\geq 4.0$ ) to distinguish between two statistically equivalent models (Burnham & Anderson 2002). A goodness-of-fit test was performed to assess the fit of the general CJS model using the program U-CARE (Choquet *et al.* 2009). As the goodness-of-fit test failed to show any statistically significant deviation of the CJS model to data, we did not correct for overdispersion. The effort of resighting vultures, measured as the number of days of fieldwork out of each year (and denoted in the models by ‘ $e$ ’, Table 3), was used to model the resighting probability.

We ran several capture–recapture models to test biological hypotheses about the two potential mortality factors: wind farms and restaurant closure. As these two factors affected different years (see Table 1), we could test for the relative importance of each factor as well as possible synergistic effects of both types of perturbations (see Fig. 1). The hypotheses considered were ( $w1$ ) as follows: survival decreased only when wind farms were in operation (2007–2008); ( $w2$ ) survival decreased when wind farms were in operation but particularly during their first year of operation (2007) because in subsequent years some vultures learned to avoid turbines (2008) (personal observations, see also Mateos 2009); ( $r$ ) survival decreased only in the first two years (2006–2007) when vulture restaurants were closed; ( $r*w1$ ) there was a statistical interaction between the effects of restaurant closure (2006–2007) and wind farm operation in years 2007 and 2008, so that mortality differed between the periods when wind farms were operating and restaurants were closed and when wind farms were active but restaurants were open; ( $t$ ) survival rates vary with time without a clear influence of mortality factors (only one of the possible

relationships is shown in Fig. 1); and (constant) survival probability did not vary with time (noted by ‘.’ in the models, see Table 3).

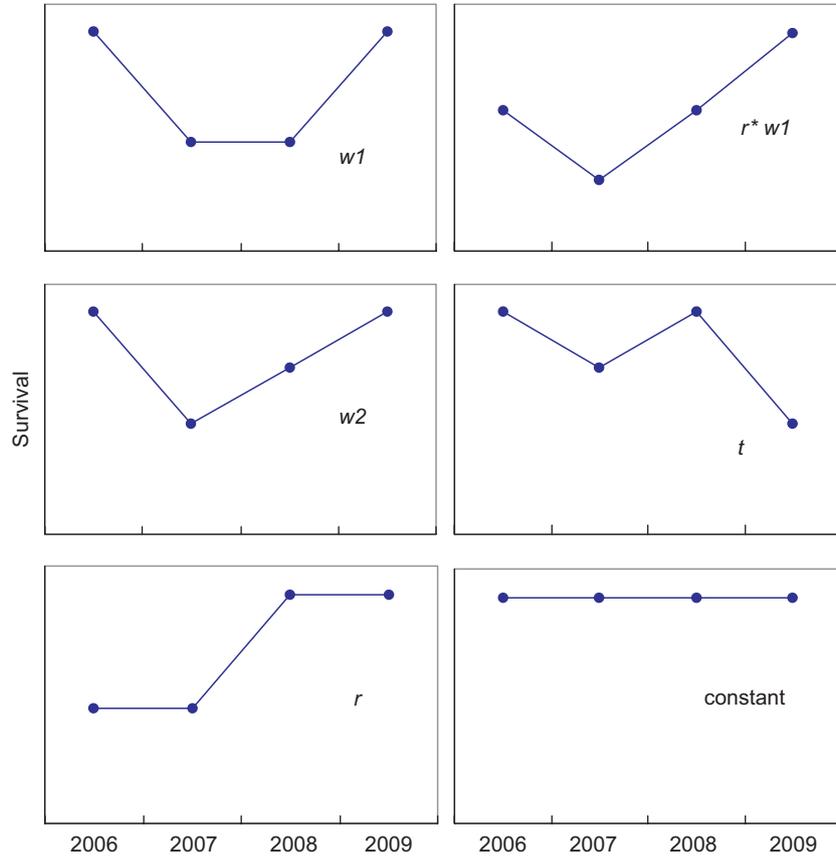
#### DISENTANGLING THE EFFECTS OF WIND TURBINES AND FOOD SCARCITY ON FECUNDITY

To separate out the effects of wind farms and food scarcity on fecundity, we contrasted several biological hypotheses using general linear models (with the identity link, assuming that sample data on fecundity came from a normally distributed population) and compared and selected models by means of theoretical information criteria (Akaike Information Criterion). To account for the possible decrease in fecundity because of density dependence (see ‘Population model’), we included the number of breeding pairs (‘density’) in all our models as a covariate. The possible synergistic effects of food scarcity and wind farm activity on fecundity were tested by including a model with an interaction term between both variables. Food scarcity and wind farm activity were considered as factors with values 0 and 1 corresponding to their state in each of the eight semesters considered (see Table 1). Finally, we assumed that the closure of vulture restaurants could affect subsequent reproduction in the period January–June 2007 only (Donázar, Margalida & Campión 2009).

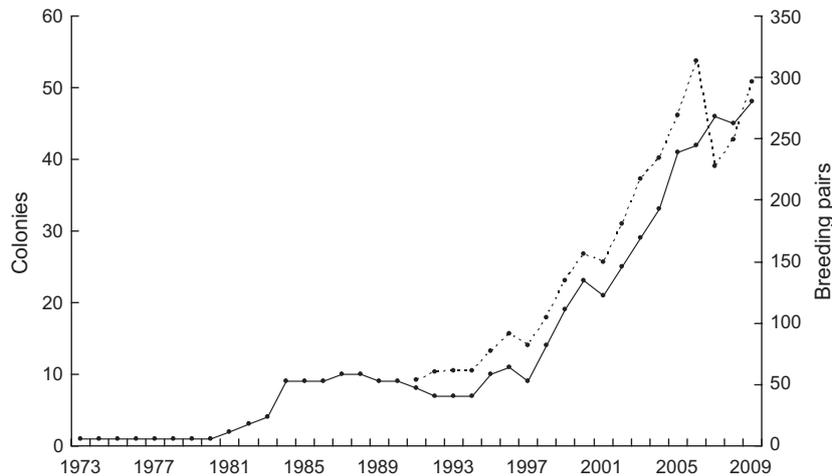
#### POPULATION MODEL

We assumed an age-structured population model to simulate the growth of the population. Our model consisted of four age classes (0–1 years, 1–2 years, 2–3 years and 4 years or older), after Sarrazin & Legendre (2000). Sexual maturity in griffon vultures can be achieved in 3–11% of the population even before birds achieve full adult plumage after 5–6 years of age (Blanco & Martínez 1996; Blanco, Martínez & Traverso 1997). Hence, only the composite age class (4+ years) can reproduce. The data from 1995 to 2006 (i.e. before anthropogenic perturbations) indicated that density dependence was operating because fecundity decreased as population abundance increased with time (Figs 2 and 4). Our model is used to shed light on mechanisms by recreating observed population dynamics, so we used an explicit multiplier in each year that reduced fecundities to those observed (Fig. 4) as population size increased (Fig. 2). As we did not observe any equilibrium population level in the data, we did not assume a carrying capacity. Rather, the fecundity was decreased to match observed fecundities over the time period of observed increases in population abundance (Figs 2 and 4).

While the matrix model was parameterised with empirical fecundity data for the entire study period, the adult survival probabilities were estimated from the capture–recapture data from 2006 onwards (Table 2). In this way, local mortality and possible fecundity decreases caused by density dependence, wind turbines and food scarcity were taken into account (Fernández, Azkona & Donázar 1996). Adult survival prior to the onset of perturbations was assumed to be



**Fig. 1.** Graphical representation of hypotheses tested to explain changes in annual survival of vultures from 2006 to 2009 depending on the mortality factors involved (wind farms ‘w’, restaurants ‘r’ and time ‘t’; see also Table 1). Maximum values in each panel represent the survival values for the species in the absence of additive mortality.



**Fig. 2.** The number of griffon vulture colonies (solid line) and breeding pairs (dashed line) observed in the study area during the last 25 years (censuses of population density were carried out from 1991).

equal to the survival rate for the first year of the perturbation period (i.e. 2006) when food was already scarce but wind turbines were not operating yet (Tables 1 and 2). Survival rates for the juvenile and immature birds for both periods were taken from Sarrazin *et al.* (1994) and Sarrazin & Legendre (2000), and the proportion of breeders was obtained from López-López, García-Ripollés & Verdejo (2004) for the study population. In our pre-breeding matrix model,

we assumed that fledgling survival ( $S_0$ ) was not affected by the human impacts because fledglings tend to disperse far from their natal places (Bildstein *et al.* 2009). Note that this assumption is conservative with respect to the impact of human perturbation on population dynamics.

The model was constructed in RAMAS<sup>®</sup> Metapop 5.0 (Akçakaya & Root 2005) and run 1000 times for a 15-year period. Deterministic

**Table 2.** Mean parameter values used in the population model with time-dependent survival ( $S_i \pm SE$ ) and time-dependent fecundity. For simplicity, fertility values shown for the pre-crisis (1995–2005) and crisis (2006–2009) periods are the arithmetic means (and standard deviations)

Period	$S_0$	$S_1$	$S_2$	$S_3$	$S_4$	Fertility
1995–2005	0.858 $\pm$ 0.039	0.858 $\pm$ 0.039	0.858 $\pm$ 0.039	0.987 $\pm$ 0.006	0.939 $\pm$ 0.026	0.80 $\pm$ 0.02
2005–2006	0.858 $\pm$ 0.039	0.858 $\pm$ 0.039	0.858 $\pm$ 0.039	0.987 $\pm$ 0.006	0.939 $\pm$ 0.026	0.61 $\pm$ 0.07
2006–2007	0.858 $\pm$ 0.039	0.7293 $\pm$ 0.039	0.7293 $\pm$ 0.039	0.8393 $\pm$ 0.006	0.656 $\pm$ 0.037	0.61 $\pm$ 0.07
2007–2008	0.858 $\pm$ 0.039	0.7293 $\pm$ 0.039	0.7293 $\pm$ 0.039	0.8393 $\pm$ 0.006	0.656 $\pm$ 0.037	0.61 $\pm$ 0.07
2008–2009	0.858 $\pm$ 0.039	0.858 $\pm$ 0.039	0.858 $\pm$ 0.039	0.987 $\pm$ 0.006	0.939 $\pm$ 0.026	0.61 $\pm$ 0.07

declines and increases were applied via multiplication factors to reflect the observed reductions in survival and fecundity rates during the perturbation period (Table 2). We did not include demographic stochasticity because the population was rapidly increasing and was not expected to be affected by small population size, but we included environmental stochasticity in all vital rates. To simulate environmental stochasticity, survival rates and fecundities were randomly selected at each population run from a log-normal distribution, with means and standard deviations estimated as described later and reported in Table 2.

Standard deviations were estimated using the variance of the survival estimates from our survival analyses for the adult age class and from Sarrazin *et al.* (1994) for the other age classes. Although these variance estimates came from other populations, they are plausible for this species because long-lived survival is a conservative life-history trait and adult survival (which was estimated here from empirical data) is the most sensitive parameter for those species. We computed fecundity ( $F$ ) as  $F = SR \times S_0 \times P \times Fe$ , where  $SR$  is the proportion of female fledglings (here assumed to be 0.5),  $P$  is the proportion of breeders (0.8),  $S_0$  is the first-year survival rate (0.858  $\pm$  0.039), and  $Fe$  is the fertility (i.e. number of fledglings per breeding pair for the pre-crisis period, 1995–2005, Table 2). Standard deviations for fecundity were assigned as 0.02 during the period before the perturbations and 0.07 thereafter (Table 2), based on available standard deviations for  $Fe$  and  $S_0$ . While these standard deviations are most likely to be underestimates, they reflect relative differences in variability in the fecundities of pre- and post-perturbation periods for comparison.

The stable-age distribution was used to distribute the initial population sizes across age classes. Because only the number of adult breeding females was available in 1995, we used this number (77 breeding pairs) for the initial number of breeding females and set the initial population size in the remaining age classes accordingly.

The final output of our models was summary trajectories with 95% confidence intervals and annual stochastic population growth rates with 95% confidence intervals. Annual stochastic lambdas were calculated in a separate model in *R* (<http://www.r-project.org/>) by projecting the population for 15 years, for 1000 replications. Values in the vital rates matrix were randomly drawn from a log-normal distribution for each parameter, as described earlier, to estimate population size under environmental variation in each time step and replication. Population growth rates were then calculated for each time step in each replication, following the procedure described in Morris & Doak (2002) and averaged (with standard errors) across replications.

## Results

### SURVIVAL PROBABILITY ANALYSIS

The goodness-of-fit test failed to show a statistically significant departure of the CJS model to the data ( $\chi^2_8 = 6.048$ ,  $P = 0.642$ ). Models with a temporally varying resighting probability performed better than models with a constant resighting probability (for instance model 7 performed better than model 9, see Table 3). Including the effort in resighting probabilities reduced the number of parameters and allowed estimation of the survival parameter for the last interval (2008–2009), which cannot be calculated from the last parameter of recapture in the CJS models. Furthermore, the resighting effort explained more variability than the time-dependent model for resighting probabilities (model 5 compared with model 7, Table 3). Although the constant survival model performed

**Table 3.** List of models to estimate adult survival of vultures in the study area under the different hypotheses involving the two mortality factors (restaurants and wind farms, see Fig. 2)

Rank	Model	$K$	Deviance	AICc	$\Delta$ AICc	Model weight
1	$\phi_{\omega 1}, p_e$	<b>4</b>	<b>14.524</b>	<b>743.036</b>	<b>0.00</b>	<b>0.504</b>
2	$\phi_{\omega 2}, p_e$	5	14.462	745.024	1.99	0.186
3	$\phi_{\omega 1}, p_t$	6	13.876	746.497	3.46	0.089
4	$\phi_{\cdot}, p_t$	5	16.307	746.869	3.83	0.074
5	$\phi_{t_s}, p_e$	6	14.462	747.084	4.05	0.067
6	$\phi_{r^* \omega 1}, p_e$	6	14.462	747.084	4.05	0.067
7	$\phi_{t_s}, p_t$	8	13.860	750.633	7.60	0.011
8	$\phi_{r_s}, p_e$	4	27.146	755.658	12.62	0.001
9	$\phi_{t_s}, p_{\cdot}$	5	25.605	756.167	13.13	0.001
10	$\phi_{\cdot}, p_{\cdot}$	2	42.030	766.473	23.44	0.000

$K$ , number of estimable parameters.

The best model of the set considered is shown in bold.

better than the time-dependent survival model (models 4 and 7, respectively), the model with only two survival values (one for the mortality in wind farms and the other under natural conditions, model 1:  $[\phi_{wl}, p_e]$ , see Table 3) provided the lowest AICc value. The model with an intermediate survival in the second year affected by wind farm mortality performed well, suggesting some type of behavioural learning to avoid turbines (see Fig. 1, model 2 in Table 3) but did not improve the AICc of model 1, with two survival rates. The hypothesis that the closure of vulture restaurants had an effect on survival was not supported (model 9). A model with a statistical interaction between the presence of wind turbines and lack of restaurants performed poorly (model 6, Table 3). Resighting rates (from the time-dependent model, model 6 in Table 3) ranged from 0.503 (standard error, SE = 0.026) to 0.666 (SE = 0.028); adult survival was much higher during years without wind turbines (0.939, SE = 0.026) than during years with such a perturbation (0.656, SE = 0.038) (Table 2). According to model values, adult survival showed a 30% decrease during the population crash period (2006–2008).

#### DISENTANGLING THE EFFECTS OF WIND TURBINES AND FOOD SCARCITY ON FECUNDITY AND SURVIVAL

The population recovered from its historical fall by the mid-1980s and began to grow rapidly in the 1990s (Fig. 2). From then on growth was exponential up to 2006, holding *c.* 300 breeding pairs in 2009 (Fig. 2). However, in 2007, the number of breeding pairs decreased by 24.1% compared to the previous year, immediately after the deployment of wind turbines and the closing of traditional vulture restaurants. Faced with food scarcity, vultures unexpectedly began to feed for the first time in a landfill. According to annual monitoring data obtained in the study area, fecundity decreased slightly (2% annual decrease) during the period 1995–2005, but there were two abrupt fecundity reductions of 12.8% and 33.3% from 2005 to 2006 and 2005 to 2007, respectively. When disentangling the effects of wind turbines and food scarcity on fecundity, the model with a lower AICc was the one that explained fecundity solely as a function of the presence/absence of wind farms (Table 4). This is similar to the result obtained when dis-

entangling the effects of food scarcity and wind turbine activity on survival (Table 3). This model was much better than the other models considered in the analysis because it captured most of the Akaike weight (0.77). In 2006, when wind farms were not operating but food was scarce, fecundity dropped by 16% in relation to the average of the years without perturbations (0.80 fledglings/pair), whereas in 2008, when wind farms were operating but food became available, the decrease in fecundity was 24%. The greatest decrease in fecundity occurred in 2007 when both perturbations were in operation (35% decrease), despite a lower number of breeding pairs than in 2006 and 2008, which should increase the amount of food available per capita. This suggests that the effect of wind farms on fecundity was more pronounced than the effects of food availability.

#### POPULATION MODEL

Our simulations faithfully reproduced the observed population growth pattern from the year 1995 to the beginning of the crisis period in 2005 (Fig. 3). During the perturbation years (2006–2009), the observed and simulated trajectories differ only in 1 year (2008). However, the simulated mean trajectory and its 95% confidence bounds ran below the observed population growth during half of the study period (Fig. 3).

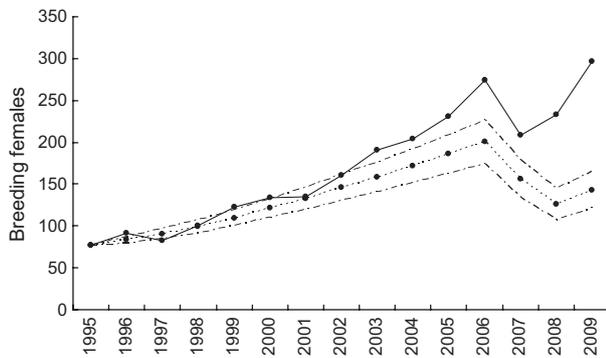
Elasticity analyses showed that the growth rate of the population was most sensitive to changes in adult survival, as found in previous studies of scavenger bird species (see e.g. Mertz 1971; Ferrière *et al.* 1996). If only adults were killed by wind turbines, then adult survival would need to be  $> 0.78$  (compared with the estimated 0.939 in the absence of wind turbine mortality) for the population to have a finite rate of increase of at least 1. If only immature vultures (2-year-old birds) were killed by the wind turbines, their survival could drop to at least 0.15 (compared with the estimated value of 0.858 in the absence of wind turbine mortality) and still maintain a population finite rate of increase of at least 1. The influence of fecundity on deterministic lambda was negligible, although a steep fecundity decline was observed directly after the perturbations (Fig. 4). It is important to note that these results apply to the deterministic model under an assumption of exponential growth and do not necessarily apply to the real population, although they

**Table 4.** Comparison and selection of general linear models explaining fecundity as a function of wind power turbine and vulture restaurant activity

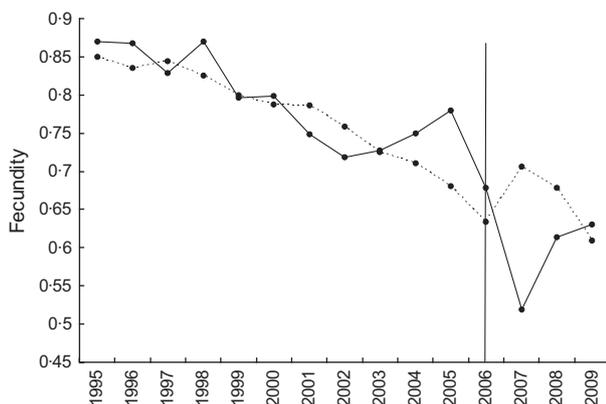
Model	AICc	K	$\Delta_i$	$w_i$
Fecundity–Wind farms + Restaurants	–40.97	5	3.12	0.16
Fecundity–Wind farms*Restaurants	–39.11	6	4.98	0.06
<b>Fecundity–Wind farms</b>	<b>–44.09</b>	<b>4</b>	<b>0</b>	<b>0.77</b>
Fecundity–Restaurants	–31.66	4	12.43	0.00
Fecundity–Density	–32.03	3	12.06	0.00

AICc, Akaike Information Criterion corrected for small sample size; K, number of estimable parameters;  $\Delta_i$ , change in AICc for each model in relation to the model with the lowest AICc value;  $w_i$ , Akaike weight.

The best model is shown in bold. All models included number of pairs ('density') as a covariate to account for a possible density-dependent effect on fecundity.



**Fig. 3.** Time-dependent stochastic model (dotted line) fitted to the observed growth of the griffon vulture population under study (solid line) during 1995–2009. Broken lines are 95% confidence intervals of the mean trajectory of our simulations.

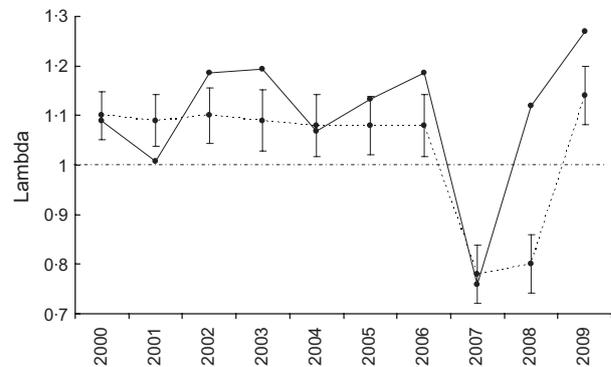


**Fig. 4.** Changes in fecundity (i.e. breeding success or number of fledglings/pair) observed (solid line) over the last 15 years in the griffon vulture population under study, compared to the expected trend taking into account a density dependence effect on fecundity (dotted line). The vertical line separates the years before and after the anthropogenic perturbations.

provide insight to ‘ideal’ conditions. The comparison of stochastic lambda (which incorporates both stochasticity and density dependence) with observed lambda showed that the recovery of the population in 2008–2009 (after the end of perturbations) was much faster than expected (Fig. 5).

## Discussion

Food scarcity after the BSE crisis triggered a change in the foraging behaviour of vultures. Faced with reduced supply of carcasses, many individuals moved to exploit a garbage dump, another predictable but lower-quality food source, not exploited previously (own data, see Appendix S1 in Supporting Information). The presence of wind turbines on the main flight pathway of vultures to the landfill was the main cause of vulture mortality and was responsible for the observed population crash. Wind farms are increasingly identified as a source of mortality for large soaring bird species world-wide, and griffon vultures are one of the resident species most commonly affected



**Fig. 5.** Observed growth rate (solid line; mean value and 95% CI) and predicted change in the annual stochastic growth rate of the griffon vulture population (dotted line) comparing the years before (showed only since 2000), during and after the anthropogenic perturbations. The broken line shows the value of  $\lambda = 1$  (population stability).

by collisions with wind turbines in southern Europe (Barrios & Rodríguez 2004, 2007; Lekuona & Ursúa 2007; Lucas *et al.* 2008), in part because they have been shown to continue using foraging areas despite the presence of wind farms (Madders & Whitfield 2006). The rapid and strong negative demographic impact of vulture mortality is best explained by the sensitivity of the population growth rate to changes in adult survival, as expected for long-lived species (Carrete *et al.* 2005; Oro *et al.* 2008). On the contrary, the reduction in observed fecundity was unlikely to have a substantial effect on population growth of vultures (also suggested by elasticity analysis).

The large drop in breeding pair numbers (2006–2008) is most probably explained by dispersal out of the study area after perturbations (see an example in Cam *et al.* 2004), reproductive skipping of adults (i.e. adults present in the area that do not breed because of the loss of a pair member) faced with a high mortality, a typical adaptation of long-lived species to unpredictable environments (Orzack & Tuljapurkar 1989; Pilastro, Tavecchia & Marin 2003) or a combination of both factors (dispersal and reproductive skipping), in addition to actual mortality. According to life-history theory, long-lived species faced with food scarcity reduce breeding effort before their survival rates decline, because that maximises their lifetime fitness (Aebischer & Wanless 1992; Saether & Bakke 2000). Dispersal probably took place towards the largest and closest colonies (see Le Gouar *et al.* 2008). Importantly, we found that both fecundity and local adult survival were more severely affected by wind turbine activity than by decreased food availability, and hence, the peak of the population crash occurred when the most problematic wind turbines were active (in 2007 and 2008). The most relevant effect of food scarcity was indirect, driving a change in foraging habits in vultures rendering them more vulnerable to wind turbines. The number of vultures recorded flying over the wind farm close to the landfill increased from only *c.* 9 individuals per hour to *c.* 51 before and after the food crisis (authors’ unpublished data).

The vulture population recovered rapidly once the main threats ceased. As our study population was an open population, immigration might have facilitated a rescue effect

(e.g. Cam *et al.* 2004). The study population is located in close proximity to the large vulture population of Teruel province, which supports 21% of the Spanish vulture population; this population has experienced dramatic growth during the last decades ( $\lambda = 2.2$  during the period 1979–2009; see Del Moral & Martí 2001 and Del Moral 2009). Hence, the resilience shown by the study vulture population is most probably explained by the combination of an intrinsic factor (reproductive skipping) and an extrinsic factor (immigration), acting as buffering mechanisms against the negative impacts of anthropogenic stressors, as reported for other long-lived species (Klomp & Furness 1992; Oro 2003; Votier *et al.* 2008).

#### MANAGEMENT RECOMMENDATIONS

Vulture mortality from wind farms in the study area continues to be a concern, but it has not directly prevented the recovery of the population. However, if other stressors such as food scarcity coincide with wind farm activity, the latter can threaten a population that is in the exponential growth phase, leading to a decreasing population in the short term. If both factors act synchronously (which can happen whenever food provisioning to vulture restaurants decreases or fails unpredictably), the impact of wind farms can be strong and rapid (Fig. 4). However, in this study, the response of the population to management (halting wind turbines that caused the bulk of mortality and opening new vulture restaurants) was rapid, and vulture population growth immediately reached high lambda values. The cessation of the 50 turbines located close to the landfill resulted in a 50–60% reduction in the number of vultures found dead between June 2008 and January 2010 (G. Valenciana, unpublished data), compared with previous years.

We suggest that the location of vulture restaurants could be changed to alter foraging habits of vultures, thereby reducing mortality from wind farms. This management solution is cheaper and more feasible than closing entire wind farms or closing or removing individual wind turbines, which can incur high economic costs. In addition, the establishment of other scattered food sources would help to avoid the concentration of vultures around vulture restaurants and the complex demographic problems that follow (Bretagnolle *et al.* 2004; Carrete, Donázar & Margalida 2006a; Carrete *et al.* 2006b; Oro *et al.* 2008; Carrete *et al.* 2009). Vulture restaurants are an inefficient way of promoting population growth (Bretagnolle *et al.* 2004; Carrete, Donázar & Margalida 2006a) and create undesirable population effects, such as reduced dispersal and the formation of polyandrous trios that ultimately reduce vulture productivity (Carrete *et al.* 2006b). We suggest that future management should aim to stabilise vulture populations by replicating food sources that mimic historical conditions. This could include making available carcasses from extensive and small-size livestock operations through the establishment of numerous scattered feeding stations supplied with small quantities of food (Cortés-Avizanda, Carrete & Donázar 2010), reproducing the original food unpredictability vultures have evolved with.

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## Supporting Information

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

**Appendix S1.** Vultures attending a landfill during the food shortage period due to the closure of traditional vultures restaurants following the 2001 Bovine Spongiform Encephalopathy crisis in Europe.

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