Population dynamics and spatial distribution of Griffon Vultures (*Gyps fulvus*) in Portugal

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Summary

The global decrease of vulture populations has been attributed to several factors, such as food availability, poisoning, human disturbance, or habitat suitability. We studied the effect of factors that vary both spatially and temporally on the nest site distribution of the Griffon Vulture *Gyps fulvus* in northeast Portugal, and influence the population dynamics of these cliff-dwelling birds. Several demographic parameters were studied in the field, and the age structure of the population was determined. Additionally we investigated how food availability affected population fluctuations. The vulture population was most sensitive to juvenile mortality according to our model results. Our models showed that a decrease in the present food supply resulted in a decrease in vulture abundance and, moreover, negatively affected the spatial distribution of the species by decreasing the number of breeding pairs per colony. The total quantity of sheep and goat biomass, a greater distance to the nearest unpaved road, and the presence of Egyptian Vultures *Neophron percnopterus* at the breeding colonies showed a significant positive relationship to the numbers of Griffon Vulture breeding pairs. It is recommended that the available food supply in the most important foraging areas should be monitored and protected. Furthermore, to manage the community of cliff breeding raptors adequately, future research should identify and protect the most suitable breeding areas for each species. Human disturbance should be kept to a minimum by protecting breeding areas, especially in an area like Riba-Côa where species such as the Egyptian Vulture, Bonelli's Eagle *Hieraaetus fasciatus* and Griffon Vulture breed so close to each other.

Introduction

Vultures are seriously threatened in Europe (Tucker and Heath 1994, Donázar *et al.* 2002a, BirdLife International 2007), the Middle East (Newton and Newton 1996), Asia (Green 2006, Green *et al.* 2006), and Africa (Thiollay 2006). Some studies have highlighted the importance of factors such as human disturbance (Gavashelishvili *et al.* 2006), poisoning (Donázar *et al.* 2002a, Green 2006), or food availability (Thiollay 2006). However, other studies (Donázar *et al.* 2002b, Parra and Tellería 2004, Poirazidis *et al.* 2004, Monadjem and Garcelon 2005; Gavashelishvili *et al.* 2006, Moran-Lopez *et al.* 2006) focused on the importance of factors that varied spatially, affecting nest site selection and local breeding success. There is therefore an urgent need to analyze the effect of factors that vary spatially, as well as temporally in relation to their effects on vulture populations.

The global population status of the Griffon Vulture *Gyps fulvus* Hablizl, 1783, has not been quantified accurately, but the species is not believed to approach the thresholds for the population decline criterion of the IUCN Red List. The current status of the species is therefore evaluated as ''Least Concern'' (BirdLife International 2007). Nevertheless, the Griffon Vulture is extinct in many parts of its former distribution (Slotta-Bachmayr *et al.* 2004). The main threats

to the viability of Griffon Vulture populations are similar throughout their range (Donázar and Fernández 1990). Food abundance especially is considered an essential factor in the population dynamics of vultures (Parra and Tellera 2004, Thiollay 2006). For instance, Parra and Tellería (2004) found a functional relationship between food availability and vulture abundance; the number of vultures was greater in areas with higher food availability, whilst other studies confirmed the importance of food availability affecting population growth over time (Donázar and Fernández 1990). Suitable habitat for nesting places (Ruxton and Houston 2002) is an important variable, often linked to differences in colony size, influencing population growth (Parra and Tellera 2004). However, the Griffon Vulture populations in Iberia appear to be healthy (Dónazar and Fernández 1990). The Riba-Côa area in northeast Portugal is one of the most important regions in the country for cliff breeding birds, and Griffon Vultures appear to have a stable breeding population (A.E. Monteiro, pers. obs.).

This study examines the population dynamics of Griffon Vultures in the Riba-Côa area by constructing a simple mathematical model with the support of available census data. The main objectives of this study are: 1) to examine the population dynamics of the Griffon Vulture and to test whether food availability affects population fluctuations over time, and 2) to investigate which variables determine nest site selection, and how these variables explain the spatial distribution of Griffon Vultures.

Methods

Study area

Fieldwork was carried out between June and October 2005 in northeast Portugal, in the Riba-Côa area, and part of the Parque Natural do Douro Internacional (centre 41°14′N, 6°41′W). The river valley forms the border with Spain and includes several river canyons. The main rivers are the Douro (national and international sections), the Águeda (international section) and the Côa. The total length of these valleys is 115 km. The area has a mean annual temperature of 15–20°C and an annual rainfall of *c.* 1300 mm. As a result of the inaccessibility and remoteness of the area and the large availability of cliffs along the sides of the main valleys, the area holds approximately 365 pairs of Griffon Vultures and approximately 150 pairs of Egyptian Vultures (A. Berliner, pers. comm.). Moreover it is a vital breeding area for Bonelli's Eagle *Hieraaetus fasciatus* with *c.* nine breeding pairs (approximately 10% of the national population), Golden Eagle *Aquila chrysaetos* with *c.* 29 pairs, and Black Stork *Ciconia nigra* with *c.* 17 pairs (A.E. Monteiro, pers. obs.).

Population modelling

To study the population dynamics and the role of food availability on the Griffon Vultures in Riba-Côa we constructed a model based on several demographic parameters (e.g. mortality and reproduction) and the age structure of the population. To evaluate fluctuations in breeding pairs over time and to calculate productivity we used census data from 1996 to 2005. To quantify the age structure we selected 15 breeding colonies (with one observation site per colony) where we counted and classified all visible Griffon Vultures into four age classes (juveniles: < 1yr, immatures: 1–2 yr, sub-adults: 3–4 yr, or adults: ⩾ 5 yr) according to their physical characteristics (Elosegi 1989). The selection of observation sites was based on the number of birds present within the colony, as it was crucial to classify as many birds as possible. All sites were visited on rainless days with good light and visibility. Each site was visited three times (once every month), either in the morning (06h00-10h00) or late afternoon (17h00-21h00), depending on light conditions. All observations were made by telescope from a distance (> 100 m) to minimize disturbance.

Spatial distribution

To study habitat preferences and consequently analyze which factors determine Griffon Vulture distribution, an intensive literature study was conducted to extract the most important variables. Studies on Griffon Vultures are rare, and therefore also findings and estimates from studies carried out on other vulture species were used for this part of the analysis as well as for the population modelling. In total 23 potential variables were identified concerning geography, disturbance, food availability, and intra- and interspecific relations. These variables were measured at the 15 observation sites and in 15 additional sites where Griffon Vulture numbers used to be high, but are now low or birds are absent. Variables were mainly measured with the aid of Arc View 3.1, using data derived from topographic maps (IGEOE 2000) and aerial photography (CNIG 2003). Information about other raptor species (number of breeding pairs in 2005) was supplied by the Instituto da Conservação da Natureza.

The geographic variables measured were 'cliff slope' (of the observation site) and the 'altitudinal difference'. The altitudinal difference (m) was measured by taking the average of the height difference from the top to the bottom of the three steepest places at each observation site. Additionally, the slope of these three steepest places was calculated and averaged.

Variables concerning human disturbance included: 'distance to nearest paved road', '- nearest unpaved road', '- nearest village' and '- nearest power line' (km). These distances were measured from the centre of each breeding colony (observation site). Unfortunately we were unable to analyze the effect of these variables with regard to the distance to the colony edge, as it was extremely difficult to determine where the exact boundaries of the colonies were. Therefore, all measurements were taken from the centre of the colony, which was the location with the highest concentration of nests. Furthermore, the total length (km) of the above mentioned infrastructures situated within a 500 m radius around the observation sites was measured. The total surface area (m²) of different land use types (olive groves, vineyards and cereal fields) within a 500 m radius was also measured, since some land use types are more intensively cultivated than others and can create more disturbance. Lastly, the human density was calculated within a 25 km radius circle around the observation sites (2001 data supplied by Instituto Nacional de Estatística Portugal).

To measure food availability all livestock biomass present in a 25 km radius from the centre of each observation site was calculated. Arroyo and Garza (1995) showed that the foraging area of Griffon Vultures is not a perfect circle around a breeding site. Moreover, they showed that 70% of the Griffon Vulture records, while foraging, were made < 25 km away from the corresponding colonies. Livestock biomass present in a 25 km radius was calculated using 1999 census data (Instituto Nacional de Estatística Portugal). Cows, sheep and goats represent the major food source for vultures in the area (Parra and Tellaría 2004). To calculate the available meat biomass available to vultures, first the number of animals that died per year was calculated (1% of all cattle per year and 2.5% of all sheep/goats per year; Bort *et al.* 1993). The number of dead animals from each species was multiplied by a standard body weight (550 kg for cattle, 55 kg for sheep and goats; Parra and Tellería 2004). Next, the standard body weight was multiplied by a conversion factor of 0.66, to correct for the weight of young animals (S. van Wieren pers. comm.). Griffon Vultures eat only meat, organs and intestines (Mundy *et al.* 1992), so the potential available biomass available to vultures is 31% of the total body weight for cattle (Friedman and Mundy 1983) and 27% for sheep and goats (Donázar and Fernández 1990). The total available 'food biomass' (cattle plus sheep and goat) was also used as an explanatory variable in the analysis.

Variables concerning intraspecific relationships included: 'distance to nearest occupied cliff' (by Griffon Vultures) and 'number of Griffon Vulture breeding pairs in a 2 km radius around each site'. Variables concerning the interspecific relationships included: 'distance to nearest Egyptian Vulture nest', '- Bonelli's Eagle nest' and '- Golden Eagle nest' in km. Besides this, the numbers of nests from these three species were counted within a 500 m radius circle around the selected sites.

The different radii used in this study for the different variables were similar to the ones used for studying Griffon Vultures in Arroyo and Garza (1995) and, moreover, ensured a full dataset, avoiding zero counts. For instance, livestock or human densities could not be calculated reliably when using a radius of only 500m, and are probably more important at a larger spatial scale.

Analyses

The population age structure was calculated from the proportion and the total number of birds present in the four age classes. We also calculated several demographic parameters. The average annual productivity used in this study was calculated according to Cheylan (1981):

$$Productivity = \frac{N° \ of \ fledgling \ young}{N° \ of \ breeding \ pairs}$$

We estimated annual mortality rates (AMR) by calculating the number of birds in one age class (A) that failed to move into the subsequent age class (B), using the formula:

$$Annual \ Mortality \ Rate = \frac{(N° \ of \ birds \ class \ A \ - \ N° \ of \ birds \ class \ B)}{(N° \ of \ birds \ class \ A \ / \ 100)}$$

Only the mortality rates of juveniles and immatures were calculated this way. Immature and sub-adult birds remain in their own age class for two years before progressing to the subsequent age class (Elosegi 1989). Therefore we created two subgroups of immatures (1st and 2nd year immatures), each with their own AMR and two subgroups of sub-adults (1st and 2nd year sub-adults). Mortality rates for sub-adult and adult birds were estimated using the model. To our knowledge there is no information available concerning egg and hatchling mortality of Griffon Vultures. Therefore, the productivity parameter in combination with information on the breeding biology of Lappet-faced Vultures *Torgos tracheliotus* (Newton and Newton 1996) was used to estimate the different mortality factors. To do so we calculated the number of nests that is necessary to sustain the present population.

$$N° \ of \ active \ nests = \frac{N° \ of \ Juveniles}{Productivity}$$

Furthermore, we calculated the proportion of the adult population that is actively involved in the breeding process.

$$\% \ breeding \ adults = \left(\frac{N° \ of \ active \ nests \ * \ 2}{N° \ of \ adults}\right) * 100$$

To incorporate food availability into the model we calculated the quantity of food required for the population in order for it to survive. We estimated that all birds, except juveniles, eat on average 164.25 kg of meat per year (450 g of meat per day in reported in Mendelssohn and Leshem 1983, Donázar and Fernández 1990 for other Griffon Vulture populations). Juveniles require an average of 320 g/d (Donázar and Fernández 1990) until they are able to forage for themselves and have permanently left the nest after about 210 days (Mundy *et al.* 1992). After this they require 450 g/d, which results in an average of 137 kg per year. These amounts fall within the range reported by Komen (1991) for hand-rearing nestlings of the larger Cape Griffon *Gyps coprotheres*, with 791g/d during the period of maximum growth.

The population model was built in Stella (Dynamic modelling software; Version 8.0 for Windows 2003). We had to make several assumptions:

- Breeding is restricted to adult birds only (for Griffon Vultures: Blanco *et al.* 1997, Cape Griffon: Borello and Borello 2002).
- Migration is not included since no accurate data are available for this species.
- For simplicity and lack of data we assumed that the natural mortality and reproduction rates are similar in each consecutive year (but see Borello and Borello 2002 for Cape Griffon).
- Food requirement (in kg/yr) is assumed to be similar for adults, sub-adults and immatures, since body size between age-classes does not vary much.
- No direct mortality due to food shortage was included as there were no figures available concerning mortality and the different mortality causes.
- According to Slotta-Bachmayr *et al.* (2004) Griffon Vulture breeding success varies in accordance with food availability. We therefore made the percentage of breeding adults dependent on food supply such that in a period of food shortage the number of breeding adults will decrease linearly. When there is no food limitation the number of breeding adults becomes dependent on the number of adults.

A schematic representation of the model is given in Figure 1. All simulations were run for 100 years unless otherwise indicated. A sensitivity analysis was performed to identify the parameters to which the population reacts strongly. The analysis was performed by running the model with the default settings, after which the model was run again while the value of one parameter was increased and then decreased by 20%. The influence of the tested variable was calculated from the average percentage of change in the total population size resulting from the test runs compared to the default run. This process was repeated for all parameters in the model.
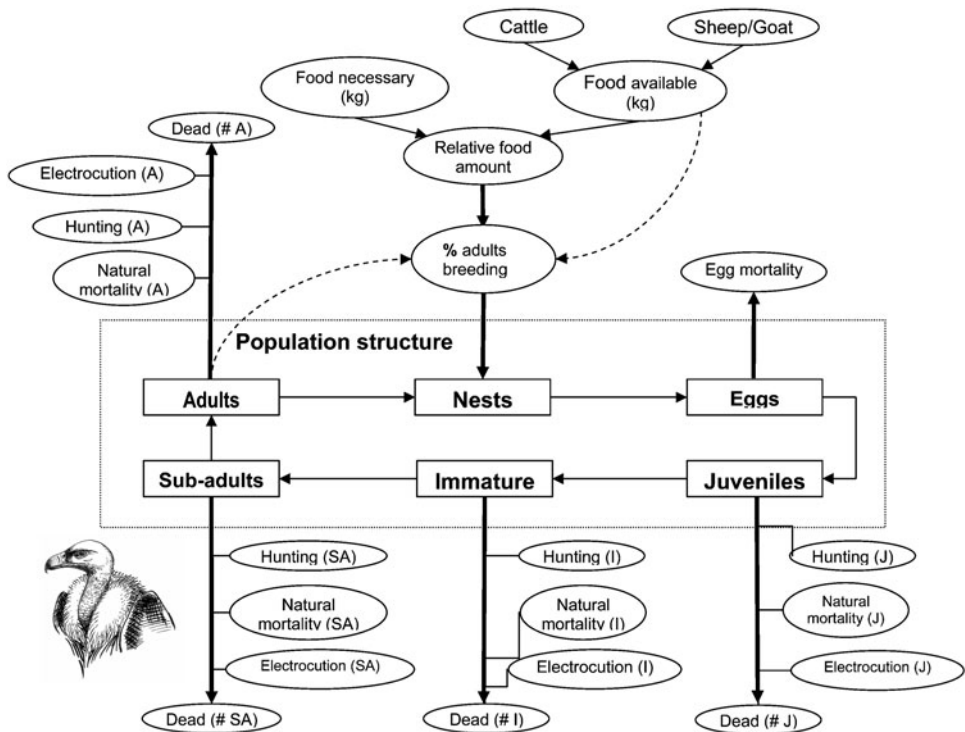

Figure 1. Conceptual design of the Griffon Vulture population model with the impact of food availability on breeding adults.

Analysis of the spatial distribution data was carried out using the statistical software package SPSS v. 12. Several steps were taken to extract the most important variables that could explain the spatial distribution of Griffon Vultures. Variables that showed significant differences between occupied and non-occupied sites were directly included in further analyses. From the remaining variables, when two variables were similar (for example, total length of paved roads and distance to nearest paved road), only the normally distributed variables were included. To analyze the relationship between the number of breeding pairs and the environmental variables, only data from the occupied cliffs were used, using 'number of breeding pairs in a 2 km radius' as the dependent variable, which followed a normal distribution. The remaining predictor variables were checked for multicollinearity with the use of a correlation matrix. When two variables correlated significantly, one of them was excluded from the model, and priority was given to variables that had shown a significant relationship with vulture occurrence in similar studies. With the remaining set of variables, a backward multiple linear regression was carried out and those that did not contribute significantly to the model were removed. Simultaneously the variance inflation factors (VIF) were calculated, which indicate the more subtle forms of collinearity. We selected the final model based on the VIF (Field 2005), and the highest R^2 Adjusted.

Results

Population modelling - Calculation of demographic parameters.

Analyzing the census data for the period 1996 to 2005 (Fig. 2), resulted in an average number of breeding pairs of 343 (SD. $\pm$ 35.7), producing an average of 238 juveniles/yr (SD. $\pm$ 36.7). This yielded an average annual productivity of 0.69 juveniles per breeding pair (SD $\pm$ 0.07). In total 1863 birds were observed in the field (including double counts) and classified into their appropriate age class. However, the first month of observations produced a biased picture of the population's age distribution: a relatively low number of adults was observed when compared to the number of juveniles (N° of juveniles > 50% of adults). To minimize errors in observation bias we therefore calculated the age structure using only the data of the last two months when number of juveniles < 50% of adults. Using this approach the total population was approximately 1,306 birds, and the juveniles constituted about 18.2% of the total population (Table 1).
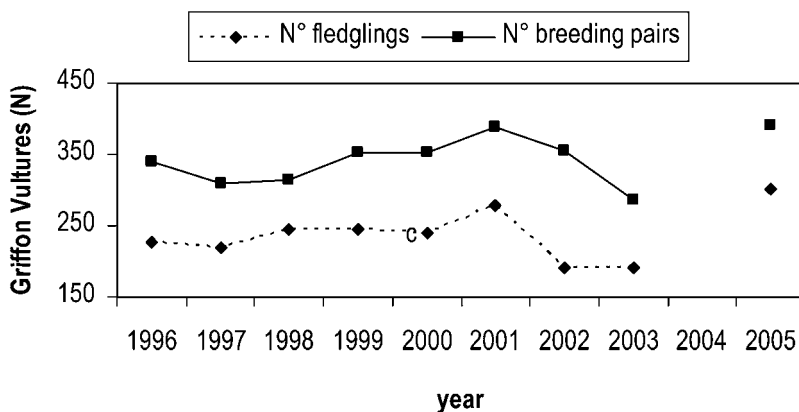

Figure 2. Census data for the Griffon Vulture population in Riba-Côa, north-eastern Portugal, between 1996 and 2005.

Table 1. Age structure of the Griffon Vulture population in the Riba-Côa area, 2005.

Age class	% of population	N° of birds in population
Adults	67.9	887
Sub-adults	6.3	82
Immatures	7.6	99
Juveniles	18.2	238
Total	100	1306

With 238 juveniles present in the population and an average annual productivity of 0.69 there should, on average, be *c.* 345 nests and consequently *c.* 690 adult birds actively breeding. This indicates that the proportion of breeding adults is 77.7% of the total number of adult birds.

Using data from Lappet-faced Vulture and educated guesses it was estimated that 90% of the breeding pairs actually produced an egg after nest building, that egg mortality was 11% and hatchling mortality 14%. The AMR for juveniles was calculated to be $(237.66-55) / (237.66/100) = 76.9\%$. For immature birds two different AMR were calculated: $(55-44) / (55/100) = 20\%$ for 1st year immatures, and $(44-42) / (44/100) = 4.5\%$ for 2nd year immatures.

The total amount of livestock biomass available for the vulture population in the Riba-Côa area is 260,600 kg/yr. According to our calculations, a population of approximately 1,306 birds with an age structure distribution equivalent to the Riba-Côa population would require 80% of this amount to fulfil its food requirements (Table 2).

Population model

With the population dynamics model we started by making an assessment of the AMR for the sub-adults and adults. Because census data showed a stable population over the years we had to estimate a mortality rate that would reflect this trend. Ultimately, an AMR of 0.04 and 0.045 for adults and sub-adults, respectively, provided a stable population over time (Fig. 3).

After incorporating food availability into the model we tested its effect on population numbers by creating a situation with several years of food shortage. Food shortage started in year 15 and ended in year 20. During this time the available food biomass for the vultures was reduced by 50%. Food scarcity resulted in a population drop of 11% *(n = 1,170 in yr 15 to n = 1,038 in year 20; Fig. 4)*. Due to fewer adult birds breeding (59% of adult population in year 18), the number of juveniles decreased by 25% during these 5 years. Fewer juveniles resulted in a lower recruitment into the subsequent age classes, with at the end a 7% drop in adult birds. The effect of the reduced recruitment rate, and therefore the subsequent smaller adult class some years later changes the population structure over several decades. After food biomass returned to its original quantity more adult pairs came to breed (84% of adult population), which resulted in an increase in the number of juveniles. The number of adults at the end of the simulation (100 years) was still 2% smaller than at the beginning of the simulation when food was not limiting the breeding performance.

Table 2. Food requirement of the Griffon Vulture population in the Riba-Côa area.

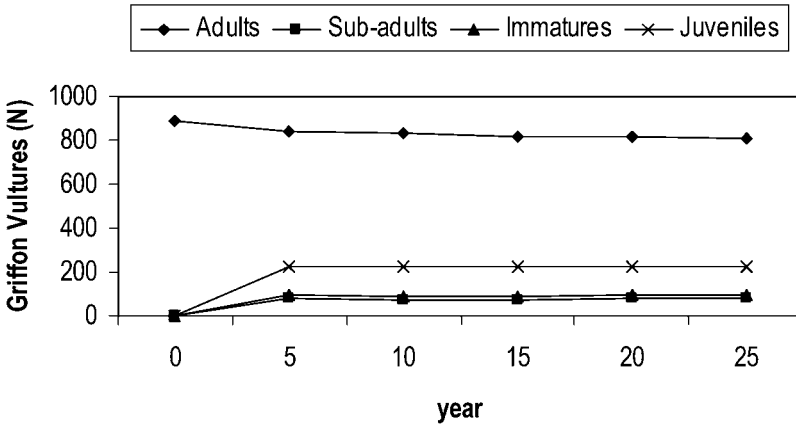| Age class	kg / day	kg / year	N° of birds	biomass (kg / yr)
Adults	0.45	164.25	887	145,690
Sub-adults	0.45	164.25	82	13,469
Immatures	0.45	164.25	99	16,261
Juveniles	0.37	136.75	238	32,547
Total				207,966

Figure 3. Predicted fluctuations of the Griffon Vulture population over time (25 years). Annual mortality rate for adult birds = 0.04 and for sub-adults = 0.045.
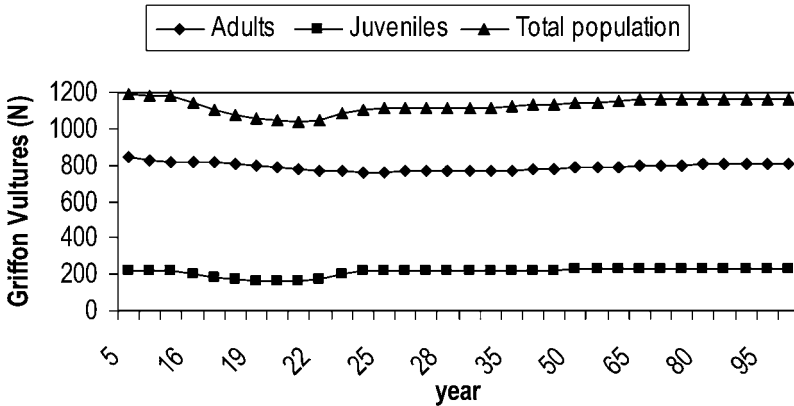

Figure 4. Predicted Griffon Vulture population fluctuations, adults and juveniles, in response to a 5-year period of food scarcity, in which food biomass was reduced by 50% during years 15 to 20.

The sensitivity analysis (Table 3) showed that changes in the natural mortality of juvenile birds resulted in the greatest fluctuations in total population size. With an increased mortality rate of 20% for juvenile birds the vulture population decreased to 564 birds. A decreased mortality rate of 20% resulted in an expansion of the population to 1993 birds. This is a mean difference of 48%. Mortality rates altered in a similar way for adult birds resulted in a mean difference in total population size of only 10% while similarly altered hatchling and egg survival resulted in mean differences of 15%.

Spatial distribution

For five of the 23 variables significant differences were found when comparing occupied with non-occupied sites, namely: distance to the nearest occupied cliff, cliff slope, sheep and goat biomass within a 25 km radius, distance to nearest village and human density in a 25 km radius (Table 4). This univariate analysis indicates factors that can explain the difference in nest

Table 3. Results from the sensitivity analysis with the column 'Rate (%)' showing the values with a 20% decrease and 20% increase, and their subsequent effect on the size of the total population, together with the mean effect (%) calculated from the comparison with the default run.

Parameter	Rate (%)	Total population (N)	Mean difference (%)
Adult mortality	0.032	1,373	10
	0.048	1,032	
Sub-adult 2 mortality	0.036	1,167	< 1
	0.054	1,164	
Sub-adult 1 Mortality	0.036	1,167	< 1
	0.054	1,163	
Immature 2 mortality	0.036	1,168	< 1
	0.054	1,163	
Immature 1 mortality	0.16	1,197	2
	0.24	1,145	
Juvenile mortality	0.615	1,993	48
	0.923	564	
Hatchling survival	0.688	949	15
	1.032	1,457	
Egg survival	0.712	949	15
	1.068	1,457	

densities between the colonies. However, non-significant factors can still be important in a multiple regression, but the analysis is hampered by collinearity between independent factors. In order to build a good regression model we calculated a correlation matrix and omitted variables from the model with large VIF values. A total of 16 variables were included in the Spearman correlation matrix. The following variables were removed from further analysis, because they correlated highly with other variables: 'distance to nearest occupied cliff', 'distance to nearest village', 'distance to nearest paved road', 'human density', 'altitudinal difference', 'olive grove 500 m radius', 'vineyard 500 m radius' and 'cereal field within 500 m radius'. After carrying out a multiple linear regression and checking for co-linearity the following variables were removed: 'cliff slope' and 'distance to nearest Golden Eagle nest'. The remaining model has an R^2_{adj} of 0.443, which means that 44 % of the variability in the number of breeding pairs is accounted for by this set of explanatory variables (Table 5). One observation site contained a much higher number of breeding pairs than the other sites, which does not seem to be explained by the variables measured. Possibly the dependent variable is influenced by another (more important) predictor variable that we failed to measure in the field. The outlier was removed from the analysis to see if this increased the explanatory power of the model. This resulted in model 2 (Table 5) with an R^2_{adj} of 0.804. The contribution of each explanatory variable to the R^2_{adj} was calculated by removing every single variable separately from the linear regression analysis and calculating the change in the R^2_{adj} (ΔR^2_{adj}, Table 5). In both models sheep and goat biomass accounted for the largest part of the variance. The variables 'distance to the nearest Bonelli's Eagle nest' and 'distance to the nearest Egyptian Vulture nest' negatively affected the number of Griffon Vulture breeding pairs and also accounted for a large part of the explained variance (Table 5). Surprisingly, the correlation with the distance to power lines was negative, indicating a higher density of breeding pairs near power lines.

Discussion

Using the Griffon Vulture population in the Riba-Côa area as an example, we showed the potential effect of several factors that varied spatially or temporally, on population change. The population appears to be stable. Census data acquired between 1996 and 2005 showed some

Table 4. Mean values (standard deviation) of environmental variables at occupied and non-occupied sites. Test statistic (*t* or *U*) and significance level (*P*) for group differences are given.

Variable	Unit	occupied (*N*=15)	non-occupied (*N*=15)	Test	Test statistic (t or U)	*P*
Distance to nearest occupied cliff	km	0.73 (0.73)	3.7 (3.4)	t-test	−3.30	0.003
Clif slope		1.62 (0.5)	2.36 (0.71)	t-test	−3.28	0.003
Altitudinal difference	m	85.8 (44.6)	67.1 (26.2)	t-test	1.18	0.247
Nearest unpaved road	km	0.43 (0.22)	0.32 (0.17)	t-test	1.59	0.123
Nearest paved road	km	2.37 (1.53)	1.6 (1.11)	t-test	0.144	0.163
Nearest power line	km	2.88 (1.8)	1.89 (1.15)	t-test	1.28	0.214
Nearest village	km	2.95 (0.86)	1.82 (1.14)	t-test	3.41	0.002
Total length unpaved roads	km/500m radius	0.86 (1.1)	0.94 (0.53)	Mann-Whitney U	90	0.367
Total length paved roads	km/500m radius	0	0.09 (0.26)	Mann-Whitney U	97.5	0.539
Total length power lines	km/500m radius	0.17 (0.46)	0	Mann-Whitney U	97.5	0.539
Human density	N/25km radius	26,277 (5,381)	23,291 (2,524)	Mann-Whitney U	53	0.013
Cows	kg/25km radius	35,394 (11,259)	32,989 (7,104)	t-test	0.7	0.490
Sheep & goat	kg/25km radius	33,607 (7,450)	42,031 (2,137)	Mann-Whitney U	28	0.001
Total food biomass	kg/25km radius	72,592 (19,226)	74,233 (6,885)	Mann-Whitney U	104	0.724
Nearest Egyptian Vulture nest	km	0.44 (0.63)	0.33 (0.29)	t-test	0.24	0.813
Nearest Bonelli Eagle nest	km	1.98 (1.5)	3.39 (3.16)	t-test	−1.56	0.135
Nearest Golden Eagle nest	km	0.75 (0.82)	1.02 (1.01)	t-test	−1.02	0.318
Number Bonelli Eagle nest	N/500m radius	0.27 (0.59)	0.6 (1.30	Mann-Whitney U	109	0.812
Number Golden Eagle nest	N/500m radius	0.6 (0.63)	0.6 (0.91)	Mann-Whitney U	104	0.676
Number Egyptian vulture nest	N/500m radius	1 (1.25)	0.93 (0.590	Mann-Whitney U	101	0.569
Olive-yards	m²/500m radius	34,470 (56,377)	12,855 (17,752)	t-test	1.37	0.190
Vine-yards	m²/500m radius	10,490 (22,867)	13,131 (25,593)	t-test	−0.29	0.772
Cereal	m²/500m radius	3,906 (10,861)	1,934 (6,065)	t-test	0.61	0.548

Table 5. Regression coefficients given for model 1 (outlier included) and model 2 (outlier excluded), with p-values, R^2 adjusted and ΔR^2 adjusted.

Variables	Model 1	P	ΔR^2 adjusted	Model 2	P	ΔR^2 adjusted
(constant)	−101	0.053		0.352	0.983	
Cow biomass	0.001	0.083	0.182			
Sheep/goat biomass	0.004	0.017	0.497	0.002	0.002	0.543
Distance to nearest unpaved road	139	0.017	0.492	48.460	0.007	0.331
Cliff slope				−7.130	0.288	0.008
Distance to nearest powerline	−13.8	0.070	0.208			
Distance to nearest Bonelli's Eagle nest	−15.1	0.073	0.203	−14.550	0.001	0.672
Distance to nearest Egyptian Vulture nest	−39.3	0.024	0.420	−20.990	0.012	0.225
Distance to nearest Golden Eagle nest				−12.280	0.027	0.166
df	14			13		
R^2 adjusted	0.443			0.804		

variation in number of breeding pairs per year but numbers remained relatively constant or even slightly increased over the study period. The average productivity of 0.69 juveniles per breeding pair per year differs from that of Griffon Vulture populations elsewhere. Sarrazin *et al.* (1994) found a productivity of 0.82 for a successfully reintroduced Griffon Vulture population in the Causses, France, but this latter population probably thrived under favourable conditions and seemed unaffected by intra-specific competition (Sarrazin *et al.* 1994). Martínez *et al.* (1997) found a mean productivity of 0.5 for the breeding population inhabiting the gorges of the Riaza River; Spain. This variation in breeding success, between areas, could be explained by differences in food availability, intra-specific competition (density of breeding pairs), or climate. Moreover, large year-to-year variation has also been recorded for the Cape Vulture, with fledging success varying from 64–75% to 27–43% dependent on the year of study (Borello and Borello 2002). Nevertheless, reproductive rate does not seem to be the central demographic parameter influencing the population dynamics of Griffon Vultures. It is believed that species with a large body size, a low reproduction, and a long life expectancy depend heavily on high adult survival for their population success (Mertz 1971). This is partly in agreement with our results for the population in Riba-Côa. Estimates of mortality rates for adult- and sub-adult birds were as low as 0.04 and 0.045 and seem to be comparable to the annual mortality rate of 0.02 for adults found by Sarrazin *et al.* (1994), although the latter study was carried under favourable conditions for Griffon Vultures. Nevertheless, the sensitivity analyses showed, surprisingly, that the vulture population was most sensitive to changes in juvenile mortality. Egg and hatchling survival also seemed to have a great effect on the size of the population followed by the adult mortality. In agreement with Sarrazin *et al.* (1994) the period between incubation and becoming an immature seems to be a critical period for Griffon Vultures, and one that seriously affects the population size. The juvenile mortality rate calculated in this study seems to be high with 77% of all juveniles dying in their first year. In France, mortality rates for first year birds were low, < 30% (Sarrazin *et al.* 1994), but this study was carried out in a re-introduction programme using special protection measures. However, higher mortality rates have been found for juvenile Cape Vultures with 83% (Piper *et al.* 1981), although Piper et al. (1999) confirmed that this latter mortality rate was probably overestimated, and re-estimated mortality for first year young, now based on colour rings, between 44% and 71%, decreasing to 19–56% under supplemented feeding. Borello and Borello (2002) also reported high nestling mortality rates for Cape Vultures

in which only 38% of all eggs laid produced fledged juveniles. It is impossible to identify the cause of death for juvenile Griffon Vultures in Riba-Côa, but we assume that high mortality is a consequence of their inexperience. Newly fledged Griffon Vultures often use flapping flight, which is energetically costly and may result in exhaustion, dehydration and starvation (Sarrazin *et al.* 1994). Griffon Vultures are partial migrants, with especially immature birds migrating annually (Mundy *et al.* 1992). This migratory behaviour could have influenced our assessment of juvenile mortality as it is possible that a number of immature birds migrated before our age-structure observations started. This would have resulted in an under-estimated immature population and consequently an over-estimate of juvenile mortality. Although the population structure seems plausible, with a satisfactory adult-juvenile ratio, monitoring the population more intensely and frequently (e.g. by using monitoring colour rings for population dynamics, or GPS tracking to determine home ranges), and for a longer period of time would presumably result in a more accurate population age structure.

Parra and Tellería (2004) showed that fluctuations in the number of Griffon Vulture breeding pairs were positively correlated with changes in livestock abundance, supporting a functional relationship between food availability and vulture abundance. Following this, we found that a 50% decrease in available food biomass resulted in a rapid decrease in vulture numbers of 11% over 5 years. Nevertheless, once food availability was restored, the population grew steadily but slowly back to its original size due to an increase in adult breeding birds. We should point out here that, when building the model, we assumed that breeding activity is restricted to adult birds only. However, sub-adults have been occasionally recorded breeding in many species of large raptors. This could be explained by reduced intra-specific competition when populations decrease, or by sub-adults being able to attain breeding condition when environmental factors are favourable (Newton 1979). This suggests that after a period with food scarcity the actual percentage of birds breeding could be higher than indicated by the model, resulting in a more rapid increase in vulture numbers.

According to our calculations, the Riba-Côa vulture population consumes an extremely high proportion (80%) of the available biomass in the area (25 km radius around each observation site). Although Arroyo and Garza (1995) showed that 70% of the Griffon Vulture forage-records were made less than 25 km away from the corresponding colonies, it is possible that the vultures in the Riba-Côa area travel greater distances to find sufficient amount of food. In this context it is important to note that we assumed that 27–31% of the total carcass weight is consumed by Griffons, although Mundy *et al.* (1983) recorded values as high as 65% (assuming that all carcasses are found and are eaten completely). It is therefore recommended to study the fraction of dead livestock that vultures can find, and the fraction of body mass that is actually consumed from the carcasses. Nevertheless, on our present calculations, this result could be a sign that food availability in the Riba-Côa area is currently limiting the growth of the population. More importantly, however, it seems that a small reduction in livestock biomass (e.g. active destruction of carcasses due to some epidemic disease) could have immediate negative effects on the vulture population size. This relationship was also found by Parra and Tellaría (2004) for Griffon Vultures in Spain. The creation of artificial feeding sites (vulture restaurants) in the area could relieve the vulture population (and other scavengers inhabiting the area) from this limitation and significantly increase their survival rates, especially of juvenile birds (Piper *et al.* 1999).

Habitat quality probably regulates raptor populations and determines the species' settlement pattern, such as also shown for Egyptian Vultures (Sarà and Di Vittorio 2003). The spatial distribution model showed that biomass of cattle, sheep and goats, distance to the nearest unpaved road, distance to nearest power line, distance to the nearest Bonelli's Eagle nest, and distance to the nearest Egyptian Vulture nest are the main factors determining the selection of a cliff as a nesting site. Food availability and human disturbance have also been correlated with population fluctuations in other studies or with other species (Cinereous Vulture: Poirazidis *et al.* 2004, Griffon Vulture: Xirouchakis and Mylonas 2005, multiple species: Thiollay 2006).

The fact that numbers of breeding pairs increased with decreasing distance to the nearest power line (Table 5) can be explained by the high density of power lines throughout the study area, as it is highly suitable for hydroelectric energy production. Simultaneously, the steep cliffs and altitudinal differences are also favourable for Griffon Vultures, and therefore the relationship between power lines and Griffon Vulture distribution can be considered as an indirect, confounding effect, as they occur in similar areas. The presence of power lines does not seem to affect the distribution pattern of Griffon Vultures negatively in the Riba-Côa area. This is also demonstrated by one of the observation cliffs in the study area where a large number of breeding pairs occurred next to a hydro-electric dam. Moreover, only 6 birds per year are killed by collision with power lines in Portugal (Janss and Ferrer, 1999). The problem of electrocution by power lines cannot currently be assessed accurately for Griffon Vultures (Slotta-Bachmayr *et al.* 2004, see also Donázar *et al.* 2002a), although for other cliff breeding birds, especially Bonelli's Eagle, electrocution is one of the main causes of mortality in some regions as they use the power lines as perching sites for hunting (Janss and Ferrer, 1999). The number of breeding pairs of Griffon Vultures increased with increasing distance to the nearest unpaved road, which confirms that they have a preference for relatively undisturbed and inaccessible areas (Pain *et al.* 2003). Surprisingly, the vultures seem to be quite tolerant of human disturbance since one of the largest colonies is located next to a hydroelectric dam with roads and frequent visits by tourists. Despite this, we believe it is necessary that breeding areas are protected, to keep the level of disturbance as low as possible, as disturbances by recreation can be a problem at breeding sites (Slotta-Bachmayr *et al.* 2004).

Our results indicate that, in the Riba-Côa area, Griffon Vultures seem to nest near other cliff breeding raptors like Bonelli's Eagle and Egyptian Vulture. When the distance to the nearest other cliff breeding raptor nest increased, the number of Griffon Vulture breeding pairs decreased. This relationship was strongest with the Egyptian Vulture, which could be explained by the fact that the species have similar habitat requirements. In some cases the Egyptian Vultures were seen feeding on food leftovers from juvenile Griffons which lead us to believe that the Egyptian Vulture, to some extent, benefits from the presence of Griffon Vultures. However, prior research showed that an increase in Griffon Vulture abundance may negatively affect other cliff-nesting raptors, since their eyries are frequently taken over by Griffon Vultures (Donázar and Fernández 1990). This process has also been observed in Riba-Côa (A.E. Monteiro, pers. obs.); Griffon Vultures repeatedly occupied the nests of Bonelli's Eagles forcing the Bonelli's Eagle to settle elsewhere. Our results suggest that cliff breeding birds in Riba-Côa breed in close proximity, but their interspecific relationships are unknown.

Despite the endangered status of several cliff breeding raptors, there are considerable gaps in our knowledge concerning many aspects of their biology, limiting the implementation of adequate management plans. The results of this study provide useful empirical data regarding the population dynamics and spatial distribution of the Griffon Vulture population in Riba-Côa area. We conclude that the Griffon Vulture population is extremely sensitive to small variations in mortality rates, of juvenile birds especially. Although food availability is just one of several factors affecting the growth of these Griffon populations (Griffon Vultures: Sarrazin *et al.* 1994, Parra and Tellaría 2004, other species: Thiollay 2006) it currently appears to be important in both survival and spatial distribution of the Riba-Côa population. Therefore, future research should focus on categorizing the most important foraging areas that are used by the Griffon Vulture population in order to monitor and possibly safeguard their food supply. In addition, human disturbance should be kept to a minimum by protecting breeding areas, especially in an area like Riba-Côa where species such as the Egyptian Vulture, Bonelli's Eagle and Griffon Vulture breed so close to each other. The challenge is to combine spatial analyses (e.g. Garcia-Ripolles *et al.* 2005) with dynamic population models, in order to be able to understand the underlying causes behind differences in population development, and the spatiotemporal distribution of vultures.

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