Nest-site selection of endangered cinereous vulture (*Aegypius monachus*) populations affected by anthropogenic disturbance: present and future conservation implications

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Abstract

The cinereous vulture *Aegypius monachus* is the largest bird of the western Palaearctic, and is threatened over its entire range of distribution. Considering explicitly the influence of human interference, we studied breeding habitat selection in seven breeding colonies using a geographic information system and multivariate statistical models. Steep areas far from human disturbance constituted the preferential breeding sites in all the colonies. The nesting substrate and climatic conditions varied between colonies, but always corresponded to non-extreme climates, and included tree species of adequate size. Since human activities influenced the breeding habitat choice, there is a potential for management policies that can clearly be of benefit for the conservation of this vulture. These would fundamentally be as follows: (1) forestry activity should be oriented to protecting oak (*Quercus* spp.) and pine (*Pinus* ssp.) stands, especially individual trees of great height, and to replacing eucalyptus (*Eucalyptus* spp.) with autochthonous species; (2) activities (recreational, economic, etc.) around the breeding areas should be scheduled and spatially organized to avoid disturbance, particularly those deriving from the proximity of roads and tracks; (3) the expected effects of global warming should be compensated, identifying future sites where the habitat can be managed, supplementary food can be provided and reserves can be designed.

Introduction

The preservation of biodiversity is faced with many challenges, many of which are related to the difficulty of obtaining empirical data. For this reason, conservation strategies are often directed towards habitats that are important for umbrella species (Simberloff, 1998), with birds of prey being widely used for this purpose (Sánchez-Zapata & Calvo, 1999; Penteriani, Faivre & Frochot, 2001; Sergio, Pedrini & Marchesi, 2003).

Consequently, habitat management practices targeted at the conservation of raptors may benefit quite different components of biodiversity. The present study deals with the case of the breeding areas of the cinereous vulture *Aegypius monachus* Linnaeus, 1766. The conservation of these habitats (Poirazidis *et al.*, 2004) may benefit the species richness of many very different groups, from raptors (Bakaloudis, Vlachos & Holloway, 1998) to invertebrates (Grill & Cleary, 2003; Kati *et al.*, 2003). In Europe, the cinereous vulture nests in forested areas of mountainous zones (300–1800 m a.s.l.), and forages for carrion in diverse habitats (Cramp & Simmons, 1980). It breeds in loose colonies of highly variable density, typically building its nest in large trees (Hiraldo, 1977).

Direct persecution, human disturbance, habitat loss, and poisoning have historically been the factors reducing the populations of cinereous vultures (Donázar, 1993; Sánchez, 1998). The last three factors are still operational (Donázar *et al.*, 2002; Madroño, González & Atienza, 2004), so that the species is vulnerable in Spain and other parts of Europe (Tucker & Heath, 1994; Madroño *et al.*, 2004). The aim of the present study was to provide a tool for conservation by identifying the most suitable habitat management strategies to apply to the breeding habitats for the recovery of cinereous vulture populations. To this end, we studied seven Iberian colonies, comprising 40–45% of the European population (Tewes, Sánchez & Ramírez, 2003; our data), with which we sought to determine (1) the habitats in the study area that the cinereous vulture selects for breeding, (2) the factors involved and their spatial variation (i.e. the differences between the colonies), (3) the possible influence of anthropogenic disturbance on those preferences and (4) which management measures would increase the availability of habitats that are conservation priorities.

Methods

Study area

The study population of nesting cinereous vultures is distributed over Extremadura, a 41 600 km^2 region located in
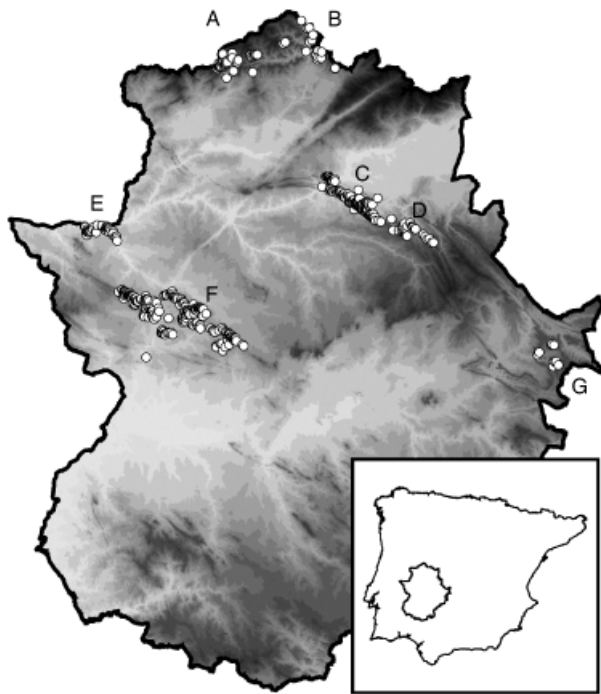
Figure 1 Location of Extremadura in the south-west of the Iberian Peninsula (inset; scale 1:6 000 000), and location of cinereous vulture *Aegypius monachus* nests on a digital elevation model (scale 1:2 000 000). The colonies are A: Gata-Hurdes, B: Granadilla, C: Monfragüe, D: Ibores, E: Tajo, F: San Pedro and G: Cíjara.

the south-west Iberian Peninsula (Fig. 1). The north, south and central areas are bounded by mountain ranges that contain colonies. The southern colonies lie outside Extremadura. The climate is typically Mediterranean, with cool, rainy winters and hot, dry summers. The geology is mainly siliceous, with a scattering of calcareous zones. The human population density is low – *c*. 25 inhabitants km^{-2} – resulting in a land use approximately evenly split into cropland and open-grazing on the one hand, and natural or semi-natural vegetation on the other, mainly dehesa (evergreen oak parkland systems), followed by scrub and true woodland. The commonest tree species are holm oak *Quercus rotundifolia*, cork oak *Q. suber*, Pyrenaean oak *Q. pyrenaica*, pines (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.).

Data sets

In 2000, we censused the *A. monachus* nesting populations with the aid of the Ranger Service of the General Directorate for the Environment (Junta of Extremadura). For each colony, we made a count of the number of occupied nests (existence of brooding adults, or of a fledgling), and recorded the geographical coordinates [1:50 000 maps and 12-channel global positioning system (GPS)].

Habitat selection studies require a comparison of the selected sites (presences) with a randomly chosen control set of non-used sites (absences) (Manly, McDonald & Thomas, 1993). We used the ARC/INFO (Environmental

Systems Research Inc., Redlands, CA, USA) geographic information system (GIS) to generate a random sample of coordinates, twice as many as the number of nests (*n* = 562) and covering the entire region (Pereira & Itami, 1991), excluding the neighbourhoods of the actual nests within a radius equal to the mean distance between nearest nests (*c*. 550 m). We characterized the nesting and random habitats using digital cartography in the GIS. We made the choice of variables according to their potential influence on the nesting preferences of the species, their availability in the form of digital cartography and the representativeness of the potential habitats in the region of Extremadura. We measured 36 environmental variables, corresponding to physiographic, climatic, forestry, landscape and anthropogenic factors (Table 1). Data sources were the Army Geographical Service (1:50 000 maps), the Territorial Weather Centre of Extremadura (315 stations, 1987–1994), the second National Forestry Inventory (1986–1995), the Corine land cover (1999) and the National Institute of Statistics (1989–1991).

Data analysis

We used a GIS to review the classification of the nests into colonies, since historically the field data have followed the traditional mountain range toponymy. We found some inconsistencies with nests far from each other included in the same colony (mainly in Gata, Hurdes and Granadilla), and nests close to each other included in different colonies (mainly in Monfragüe and Ibores). We performed a cluster analysis to delimit the colonies in an objective and spatially explicit manner, assigning each nest to a colony and discarding atypical nests on the basis of their relative position. The algorithm used was simple Euclidean distance clustering ('nearest neighbour clustering'), which defines the distance between two groups as the separation between the two closest objects (StatSoft, 1997).

We applied univariate and multivariate statistical techniques to determine which factors were associated with nest-site selection. Both techniques were based on comparing the values of the factors at the nest sites with those corresponding to random sites. The first consisted of a Mann–Whitney *U*-test to compare the mean values of the variables between nest and random sites. To confirm the existence of spatial differences in habitat between the colonies, we performed a non-parametric Kruskal–Wallis ANOVA with all the variables. The high number of tests involved made it advisable to apply a Bonferroni correction procedure to the individual test significance levels to keep the overall significance level at not greater than 5% (Zar, 1996).

We analysed the relationships between the presence of the nests and the set of explanatory variables by means of logistic regression analysis, one of the families of generalized linear models (GLM) that is appropriate for the analysis of a dichotomous response variable. We followed the forward stepwise procedure of the SPSS program, searching for parsimonious models. As there were many variables, we set the entry probability at 1% and the removal probability at

Table 1 Variables used to characterize the random sites and the nesting sites of the cinereous vulture *Aegypius monachus* (abbreviations in the left column)

Physiography	
ALTITUDE	Altitude in m a.s.l.
SLOPE	Slope in degrees
INVRUGGED	Inverse ruggedness index, calculated as the reciprocal of the spherical variance of the slope
Climate	
INSOP12N	Potential insolation $-12°$ declination (5–26 February; 16 October–6 November)
INSOP12P	Potential insolation $+12°$ declination (5 May–13 April; 8–30 August)
INSOP23N	Potential insolation $-23°$ declination (22 December–13 January; 30 November–21 December)
INSOP23P	Potential insolation $+23°$ declination (29 May–31 June; 22 June–21 July)
TMEAMAX1	Mean maximum temperature of the coldest month (January) in °C
TMEAMAX7	Mean maximum temperature of the warmest month (July) in °C
TMEAMIN1	Mean minimum temperature of the coldest month (January) in °C
TMEAMIN7	Mean minimum temperature of the warmest month (July) in °C
TABSMAX1	Absolute maximum temperature of the coldest month (January) in °C
TABSMAX7	Absolute maximum temperature of the warmest month (July) in °C
TABSMIN1	Absolute minimum temperature of the coldest month (January) in °C
TABSMIN7	Absolute minimum temperature of the warmest month (July) in °C
FROSTDAY	Mean number of days of frost
RAINTOT1	Mean total rainfall in January ($l\,m^{-2}$)
RAINTOT7	Mean total rainfall in July ($l\,m^{-2}$)
RAINMAX1	Maximum rainfall in a day of January ($l\,m^{-2}$)
RAINMAX7	Maximum rainfall in a day of July ($l\,m^{-2}$)
RAINDAY1	Mean number of days of rainfall in January
RAINDAY7	Mean number of days of rainfall in July
Forestry and landscape	
QUEFAPYR	Tree cover in presence of *Quercus faginea* or *Q. pyrenaica* (%)
QUESUB	Tree cover in presence of *Quercus suber* (%)
QUEROT	Tree cover in presence of *Quercus rotundifolia* (%)
CASSAT	Tree cover in presence of *Castanea sativa* (%)
EUCSPP	Tree cover in presence of *Eucalyptus* spp. (%)
PINSPP	Tree cover in presence of *Pinus* spp. (%)
PATCHSIZE	Size of the patch in which the nest is located (ha)
BORDISTAN	Distance from the nest to the border of the patch (km)
Anthropogenic factors	
VILLANND	Distance to the nearest village (km)
VILLAPSI	Human population size index at the site (population interpolated between villages)
ROAD_NND	Distance to the nearest road (km)
TRACK_NND	Distance to the nearest track (km)
ROAD500M	Length of the roads within a radius of 500 m (km)
TRACK500M	Length of the tracks within a radius of 500 m (km)

The values of the variables were determined for the site's location (physiography, climate, vegetation), within a radius of 500 m (communication routes), or as the closest distance (border of the patch, villages and communication routes).

5%. As well as the overall models, we also constructed local colony-by-colony models whenever the number of nests permitted.

The implicit assumption in regression models of independence between samples may not hold with spatial data, as environmental variables are usually spatially autocorrelated (Legendre, 1993). Therefore, we reconstructed the models on matrices of spatially corrected data (Legendre, 1993), replacing each environmental variable with the residual of its linear regression with respect to a spatial trend surface of cubic order.

Prior to the multivariate analyses, we inspected the form (linear, monotonic, etc.) of the response of each predictor variable to determine the most appropriate transformations to include in the models. We performed an analysis of residuals for the re-examination of cases with a great influence on the models, and then removed from the final models the cases with a strongly atypical character.

Results

Nesting populations

The nesting population of the cinereous vulture in Extremadura in 2000 was 562 pairs, located in seven separate

Table 2 The study colonies, number of nests and mean distance to the nearest nest

| Colonies | Number of nests | Distance (m) | | Altitude (m) | Temperature (°C) | | Precipitation (l m^{-2}) | |
		Mean	SD		January minimum	July maximum	January total	July total
Gata-hurdes	42	810.3	1021.5	766.8	2.2	34.5	108.5	22.1
Granadilla	19	1605.9	1366.5	653.6	2.0	34.1	104.3	21.1
Monfragüe	169	418.2	558.9	396.0	2.1	35.2	61.7	8.0
Ibores	30	779.3	623.9	698.5	1.9	34.8	59.9	8.4
San Pedro	249	490.6	372.3	475.0	2.7	34.8	52.3	7.9
Tajo	42	578.9	366.8	219.8	2.5	34.6	61.3	10.4
Cíjara	11	935.7	564.4	728.7	2.0	35.0	52.7	10.0
Overall	562	556.6	606.9					

Also given are the means of the basic orographic and climate characteristics: altitude, minimum winter (January) and maximum summer temperatures (July), and total winter (January) and summer (July) rainfall.

colonies (Table 2). The mean distance to the nearest neighbour was 556.6 m (excluding one atypical nest at 12 km), with a wide range of variation between colonies and a greater density in the larger colonies. Six nests were atypically positioned, i.e. very far from the nearest neighbour, and were excluded from subsequent analyses.

Univariate approach

In general, the environmental conditions differed between colonies ($P = 0.0000$ in all, except for the length of roads, for which $P = 0.2392$). The nesting habitats differed from the random sites (Table 3). At the nesting sites, altitudes and slopes were greater, winter temperatures were lower and summer temperatures were higher, insolation was less, and rainfall was greater throughout the year, and there were greater values of cork oak and eucalyptus and lesser values of holm oak. Lastly, further differences were found in the anthropogenic factors, with the nests occupying sites farther from roads, tracks and villages in areas of lower human population size and less infrastructure.

The colony-by-colony tests showed the same general pattern, but with local variations associated mainly with the forest habitats. Such was the case of the Tagus colony, which, being located in a river valley, had a lower altitude ($U_{42,1157} = 2565.0$, $P = 0.0000$) and a greater density of holm oak ($U_{42,1157} = 11\,912.0$, $P = 0.0000$).

Multivariate approach

The environmental variables presented nonlinear relationships and statistical distributions that made it necessary to use transformations and quadratic terms in the models. In particular, we included the transformed (logarithm or square root) variable of all the descriptors of the nesting substrate, landscape and humanization (except for distance to the nearest village), and the square of all the variables used in the models. It was impossible to create a model for Cíjara because of the small sample size relative to the number of parameters involved, and neither was it possible to use squared terms in the Ibores model. We found evidence in the models of spatial autocorrelation of the environmen-

tal data, although both types of models reflected similar relationships between the nests and their environment. We therefore only present the results of the corrected models (Table 4).

The nesting habitats selected by the total study group of populations (overall logistic model) showed (1) a positive influence of the slope, decreasing at high values, (2) a correlation with a cooler winter and warmer summer climate, (3) an affinity with a greater density of cork oak up to a certain limit, and a negative response to the density of holm oak and (4) the importance of the distance from villages and transport infrastructure (roads and tracks).

The colony-by-colony analyses gave variants of the overall model with better fits to the local conditions – i.e. increments in the explained variance. Such was the case with the altitude, which had no overall influence, but showed a positive relationship in the highest colony (Gata-Hurdes) and a negative relationship in the lowest (Tagus). The major positive overall influence of the slope was also manifest in almost all the colonies (except only for Gata-Hurdes, where its influence was replaced, as noted above, by that of the altitude). Whenever the sample size permitted testing quadratic terms, this relationship was also non-linear. With respect to the nesting substrate, while in the general model the dominant elements were cork and holm oak, this pattern was repeated in certain colonies only, with other species having an influence locally. Lastly, the marked influence of the degree of humanization that was observed overall was repeated locally, with some particularities in different colonies. The most frequent was the correlation with greater distance to transport infrastructure (roads and tracks), which was present in almost all the colonies, separately or conjointly.

Discussion

Areas with steep slopes far from human disturbance constituted the cinereous vulture's preferred breeding sites in the populations studied. For other important factors – fundamentally the nesting substrate and the climate – we found more variable relationships. This indicates that the choice of where to site the nest follows a decision sequence induced by slope and isolation, and reinforced by the

Table 3 Mean and standard deviation (in parentheses) of the variables used to characterize the nest area and the random locations

Variable	Nest site	Random site	*U*-test	*P*	*n* (1)	*n* (0)
ALTITUDE	477.5 (163.6)	448.02 (222.26)	265 856.0	0.0000**	562	1157
SLOPE	13.1 (6.0)	4.16 (5.57)	81 543.5	0.0000**	562	1157
INVRUGGED	168.0 (3.2)	171.58 (2.91)	78 016.0	0.0000**	562	1157
MDI12N	28.8 (1.8)	30.25 (1.55)	151 481.0	0.0000**	562	1157
MDI12P	36.7 (1.7)	38.13 (1.49)	130 113.5	0.0000**	562	1157
MDI23N	24.3 (2.4)	25.98 (2.14)	163 051.0	0.0000**	562	1157
MDI23P	40.6 (2.2)	42.14 (1.71)	156 769.0	0.0000**	562	1157
TMEAMAX1	11.8 (0.3)	12.08 (0.52)	188 242.0	0.0000**	562	1154
TMEAMAX7	34.8 (0.3)	34.69 (0.40)	246 481.5	0.0000**	562	1154
TMEAMIN1	2.4 (0.3)	2.46 (0.40)	286 848.0	0.0001**	562	1154
TMEAMIN7	18.5 (0.3)	18.41 (0.43)	278 169.0	0.0000**	562	1154
TABSMAX1	16.3 (0.3)	16.56 (0.37)	169 350.5	0.0000**	562	1154
TABSMAX7	40.7 (0.3)	40.53 (0.52)	275 204.5	0.0000**	562	1154
TABSMIN1	−2.3 (0.3)	−2.22 (0.45)	302 749.5	0.0255*	562	1154
TABSMIN7	12.6 (0.3)	12.39 (0.41)	229 809.5	0.0000**	562	1154
FROSTDAY	17.4 (2.4)	17.81 (3.54)	312 343.5	0.2155	562	1154
RAINTOT1	62.2 (16.5)	59.86 (18.99)	303 310.5	0.0206*	562	1157
RAINTOT7	9.7 (4.4)	9.54 (4.76)	319 100.0	0.4950	562	1157
RAINMAX1	21.8 (4.4)	19.85 (6.56)	250 875.5	0.0000**	562	1157
RAINMAX7	6.6 (2.9)	5.66 (3.15)	257 059.5	0.0000**	562	1157
RAINDAY1	6.3 (0.6)	6.10 (0.85)	289 828.0	0.0003**	562	1154
RAINDAY7	0.7 (0.5)	0.68 (0.57)	318 902.0	0.5771	562	1154
QUEFAPYR	0.2 (2.0)	2.02 (9.00)	304 613.5	0.0292*	562	1157
QUESUB	7.2 (9.9)	2.01 (7.77)	179 062.0	0.0000**	562	1157
QUEILE	5.1 (9.3)	9.70 (13.75)	271 174.0	0.0000**	562	1157
CASSAT	0.1 (1.5)	0.33 (3.48)	321 232.0	0.6442	562	1157
EUCSPP	2.3 (6.7)	1.24 (7.14)	279 929.0	0.0000**	562	1157
PINSPP	2.8 (12.0)	2.25 (10.04)	299 684.0	0.0071*	562	1157
PATCHSIZE	12 724.5 (20 918.5)	148 286.75 (283 522.70)	241 158.5	0.0000**	562	1153
BORDISTAN	0.3 (0.3)	0.42 (0.60)	270 491.0	0.0000**	562	1157
VILLANND	8.1 (3.5)	5.04 (3.10)	162 943.0	0.0000**	562	1157
VILLAPSI	1636.0 (1413.0)	3721.84 (8179.26)	208 414.0	0.0000**	562	1154
ROAD_NND	3.6 (2.2)	1.71 (1.51)	149 667.5	0.0000**	562	1157
TRACK_NND	1.3 (0.9)	0.85 (0.86)	200 659.0	0.0000**	562	1157
ROAD500M	0.0 (0.1)	0.20 (0.40)	257 041.5	0.0000**	562	1157
TRACK500M	0.1 (0.3)	0.39 (0.54)	22 9900	0.0000**	562	1157

Mann–Whitney *U*-test to test their differences and sample sizes. Abbreviations of the variables as in Table 1.

*Significant differences for an individual error of 5%.

**Differences that remain significant after an overall Bonferroni correction at 5%.

availability of a suitable substrate with a non-extreme climate.

It is important to note that the spatial and temporal variation of many of the factors involved in the relationships that were identified have been or can be altered by human action. This knowledge is therefore needed to guide measures of conservation, restoration and/or *de novo* creation of habitats that are important to bringing the species out of its current threatened status, and in general for the conservation of the biodiversity associated with Mediterranean forest and scrub.

Physiographic factors

The cinereous vulture populations selected breeding habitats for their physiography, as has been found in other places (Fargallo, Blanco & Soto-Largo, 1998; Atienza, Muñoz & Moral, 2001; Donázar *et al.*, 2002; Poirazidis *et al.*, 2004). Air currents facilitate the cinereous vulture's take off (Cramp & Simmons, 1980), and as the currents are more frequently available on hillsides, this would explain the choice of these sites for the construction of nests. The altitude, however, differed considerably between the two colonies with extreme values (Gata-Hurdes and Tagus), so that, in both these colonies, the functional effect of slope, originated by orogeny (elevation in Gata-Hurdes) or fluvial erosion (depression in the Tagus), would seem to come before altitude in determining site selection because it was the only common factor. Nevertheless, this order of importance does not imply that the two factors are independent, as the influence of slope increased with altitude as reflected in the greater partial correlation in the models ($r_s = 0.90$,

Table 4 Partial correlation (*R*) of the variables included in the overall and colony-by-colony logistic models of nesting habitat selection, computed on the corrected data matrix (Wald $P \leq 0.01$ in all cases; quadratic terms in parentheses)

	Overall	Gata-Hurdes	Granadilla	Monfragüe	Ibores	San Pedro	Tajo
ALTITUDE		0.1620	(−0.0957)				−0.1847
							(0.1629)
SLOPE	0.2009		0.1339	0.1284	0.3220	0. 1606	0.1048
	(−0.1295)			(−0.0803)		(−0.1034)	
MDI12P	(−0.0540)	(−0.1590)					
TMEAMAX1	(−0.1876)	0.1621		0.0857			
		(−0.1603)		(−0.0885)			
TMEAMAX7	(0.2127)			(−0.2286)			
TMEAMIN1				0.0846		−0.0851	
						(0.0978)	
TABSMAX7							(−0.1898)
RAINTOT1	−0.0957			−0.1694		(−0.1706)	
RAINTOT7	(0.0866)					0.2155	
RAINDAY1						0.1314	(0.1320)
						(−0.1419)	
RAINDAY7	−0.0538					−0.1554	
						(0.1285)	
QUEFAPYR			−0.0659				
QUESUB	0.1071					0.1807	
	(−0.0821)					(−0.1338)	
QUEILE	−0.1141				−0.1701	−0.1168	
CASSAT	−0.0558						(0.0774)
EUCSPP					0.2067		
PATCHSIZE			(−0.0836)		0.1526	(−0.0785)	
BORDISTAN	(0.0722)						
VILLANND	0.1528					(−0.1945)	
VILLAPSI	−0.1600	−0.1239			−0.2784	0.1195	
						(−0.1279)	
ROAD_NND	0.1149		0.1432	0.6990		0.0735	0.1780
							(0.1913)
TRACK_NND	0.1486	0.1659			0.1557	0.1014	
Explained variance	0.722	0.916	0.909	0.942	0.761	0.844	0.899

Given at the end of each model is the explained variance (R^2) of Nagelkerke (Hosmer & Lemeshow goodness-of-fit test $P > 0.10$ in all cases). Abbreviations of the variables as in Table 1.

$P = 0.0374$, $n = 5$). Again, the need for air currents explains these differences, because at the higher altitudes (cooler and wetter areas) hillside currents (slope lift) predominate over thermals (thermal lift) (Hiraldo & Donázar, 1990; Donázar *et al.*, 2002).

Climatic factors

Considering soaring flight, and that the nests of tree-nesting vultures are more exposed than those of cliff-nesting vultures (Donázar, 1993), it is not surprising that we found that climate influenced nest site selection. The use of slopes contributes to the exposure of nests to climatic factors as they have no cover, which seems the probable reason that, considered overall, they were subject to cooler conditions in winter and warmer conditions in summer (maximum temperature). However the results of the colonies with extreme conditions showed a tendency to avoid the coolest zones at great altitudes where the winter climate is harsh (Gata-Hurdes) and the warmest zones at low altitudes where the summer climate is hottest

(Monfragüe). It seems therefore that the seasonal harshness of temperatures is a limiting factor at both extremes in mediating nest site selection. The behaviour – common in the cinereous vulture – of shading the chicks (Bernis, 1966) seems to explain the abnormally prolonged presence of the adult of this species in the nest (Donázar, 1993), causing a conflict in the parental investment of time between thermoregulation and foraging to feed the chick.

The nest sites of the two large colonies (Monfragüe and San Pedro) both had lower altitudes and lower total winter rainfall. The results indicate that, at the beginning of the breeding season (winter), the pairs prefer to nest in the least rainy areas, and that this preference is more important in mountainous zones of lower altitude. The direct cause of failure would be the shorter time available for foraging, as the conditions for flight are worse in winter, and flight ceases altogether with rain (Donázar, 1993). Its greater importance at low altitudes could be due to an increase in the time waiting for suitable thermals (Pennycuick, 1972; Hiraldo & Donázar, 1990). Indeed, similar climatic

conditions in Ibores did not result in similar influences – a difference that would be explained by the greater elevation. With respect to the Tagus colony, despite its lower altitude, it occupies slopes that correspond to a fluvial depression, and not to orographic elevations as in the other colonies. This is the probable origin of its different relationships with the habitat in these and other factors (see below).

Forestry and landscape

The large body size of vultures imposes constraints on the availability of a suitable substrate for the nest (Newton, 1979). This makes management of habitats in general, and of wooded habitats in particular, of special importance. In general, the nests were preferentially located at greater distances from the patch borders, although there was no relationship with patch size. This could be related to disturbance, as will be discussed below. In these patches, trees constituted the only nesting substrate. Overall, we found a positive association with cork oak and a negative association with holm oak, although both tree species were used (approximately in the proportion 3:1). The Tagus was an example of the latter case. In this colony, the sclerophilous holm oak extends down the slope of the fluvial depression to the riverbanks. As noted above, available slopes were selected at various altitudes, so that the observed proportion of tree species used for nesting would be the result of their differing availability due to phyto-topographic factors (Devesa, 1995). At the opposite extreme of elevation, pines were used for nesting where they were available (81% of the nests of northern Extremadura were on *Pinus pinaster*), again showing that the large size of the nests in general makes the existence of trees of adequate size more important than the type or the density (Bernis, 1966; Fargallo *et al.*, 1998; Donázar *et al.*, 2002; Poirazidis *et al.*, 2004). Eucalyptus, on the other hand, were not used as nesting substrate, but stands of eucalyptus may be used if they include a few large individuals of appropriate species (Donázar *et al.*, 2002). This was the case in Ibores, where the nests were associated with a greater density of eucalyptus, but actually occupied oaks. It has to be noted, however, that when eucalyptus stands reach great height, they hinder entry to the nests located on other tree species, and may eventually lead to abandonment (Sánchez, 1998).

Disturbance

The study populations showed a clear preference to select nest sites that were isolated from human dwellings and movement. This relationship is obviously a covariable with the slope, as flat areas are preferred by humans, but human avoidance seems to be independent of slope. Indeed, this negative association has been observed in other colonies (Fargallo *et al.*, 1998; Atienza *et al.*, 2001), having a particularly marked impact from traffic along forest tracks (Sánchez, 1998; Donázar *et al.*, 2002). Tree-nesting raptors are more sensitive to all types of anthropogenic disturbance than cliff-nesting raptors (Cramp & Simmons, 1980), and

the cinereous vulture generally avoids areas with human disturbance (Cramp & Simmons, 1980). It has been found that disturbance can be minimized in some strictly protected areas (Poirazidis *et al.*, 2004), but this is not a generalized situation. We observed obvious influences in many colonies under a variety of conditions – even though the two largest colonies had been included in Special Protection Areas for Birds (SPA, European Birds Directive 79/409/EEC) for a long time (since 1989), and Extremadura is a region with a low human population density. A counterintuitive result related the Sierra de San Pedro colony to closeness to villages and a greater density of humans. While this mountain range is located between the three largest towns of Extremadura (Badajoz, Cáceres and Mérida), it still possesses natural habitats in a good state of conservation, probably due to their orography and use for forestry and hunting. It is also one of the oldest SPAs in Extremadura. We therefore believe that this relationship is a geographical artefact stemming from the simplified assumption that the disturbance effect is due only to distance. Accessibility to the breeding areas represented by transport infrastructure seems to be the most likely factor of disturbance in the observed preferences.

Management implications

The results of the present study contribute to knowledge of the cinereous vulture's biology. Principally they allow one to identify sources of anthropic disturbances when and where these disturbances are most prejudicial for the species. Knowledge of these factors will improve our management capacity to direct conservation strategies that improve the status of these habitats. The present analysis of many colonies under diverse conditions improves the expectation of the generality of the resulting models, although this aspect remains to be tested. Whatever the case, the present results point to guidelines for the conservation of the cinereous vulture populations that could be developed at three levels: (1) protection of the current suitable conditions; (2) correction of negative factors acting on the populations and (3) the compensation of future negative effects.

Conservation of current breeding habitats must principally be targeted at stands of trees large enough to support the nests, with particular attention being paid to those species that are currently being used. Their present distribution and abundance in Extremadura is not only due to the ecological characteristics of these species, but also to traditional usage and to the deforestation and re-afforestation policies of the 20th century (Alvarado, 1983). This involved first the replacement of oaks by pines and eucalyptus, and then replacing the eucalyptus by other species. This latter substitution of eucalyptus has to be regarded as an appropriate measure for the conservation of the cinereous vulture, besides being a step to the restoration of autochthonous forest ecosystems. But these actions should not be allowed to affect the rest of the tree species, especially large individual trees. Also, the scheduling of forestry activities should avoid the breeding period (January to August) in

the proximity of the colonies, as this is one of the major current reasons for failure. Indeed, in all the colonies the breeding sites were selected far away from roads and tracks, which were a sure source of disturbance, and therefore constitute the most important element of correction for the conservation of the cinereous vulture. This should be put into effect by (1) regulating the construction of transport communication infrastructure, (2) controlling people's access to these areas (tourism, sports, etc.) and (3) scheduling and spatially organizing the associated economic activities (mainly forestry and hunting) during breeding at the nesting sites. Predictive mapping techniques applying statistical models will provide a useful tool to implement these measures spatially, also allowing the identification of potential breeding areas (Poirazidis *et al.*, 2004).

On a longer time scale, the probable scenario of global climate change makes it advisable to adopt compensatory measures in order to avoid subsequent threats to the cinereous vulture populations. The principal foreseeable agent to consider is global warming, because nests in trees are very exposed to the weather, and the soaring flight of these large birds imposes on them a dependence on orography and climate. This means that added costs are to be expected in breeding, which will in the last instance affect the dynamics of the populations negatively – a greater thermoregulatory cost in both adults and chicks. The present understanding of island biogeography (MacArthur & Wilson, 1967), the studies carried out with other species (Peterson *et al.*, 2001; Meynecke, 2004), and the breeding biology of the cinereous vulture make one expect a shift of their nesting habitats to greater altitude. The consequences will be: (1) a reduction of the total area available, (2) the disappearance of breeding areas and (3) greater distances between the breeding and the foraging areas. To palliate these effects, it will be necessary to have cartographic models of the potential distribution of new nesting areas under different climate scenarios. This will facilitate the future management of the newly emerging breeding areas, which are presently unsuitable, orienting the re-design of reserves that were established without taking climate change into account (see, e.g. Araujo *et al.*, 2004), and select the best sites for providing supplementary feeding. Indeed, because the cinereous vulture's dependence on orography and climate only seems to be attenuated by an over-abundance of food, this could be a measure to use to mitigate the added breeding costs (Cramp & Simmons, 1980; Donázar *et al.*, 2002).

Acknowledgements

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