Application of a predictive model to detect long-term changes in nest-site selection in the Bearded Vulture *Gypaetus barbatus*: conservation in relation to territory shrinkage

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In this study we examined long-term variation in the selection of nesting cliffs for the recovering population of the Bearded Vulture *Gypaetus barbatus* inhabiting the Spanish Pyrenees. We focussed on variables indicating a high probability of cliff occupancy as determined by a previously published model. Although the breeding population increased from 53 to 93 territories between 1991 and 2002, the breeding range expanded only slightly. New and old nesting cliffs had similar habitat features in relation to topography, altitude and degree of human influence, but the distance between occupied cliffs was reduced (from 11.1 to 8.9 km). Thus the probabilities of occupation predicted by the model were lower for newly colonized locales. Our study shows that territory compression may occur without serious modification of nesting habitat quality. These results may arise from the lack of strong territorial behaviour by Bearded Vultures and the availability of high-quality cliffs. The relatively low quality of sites in adjacent mountains may prevent the expansion of the breeding range, but conspecific attraction may also play a role. Our study confirms that monitoring changes in key variables important to habitat selection is useful in determining long-term trends in settlement patterns in heterogeneous environments. The results also suggest that the available nest-site selection model may accurately predict cliff occupancy by Bearded Vultures in those areas where the distance to the nearest neighbour is not a limiting factor. In particular, the model may be useful in establishing priority areas for reintroduction.

**Keywords:** cliffs, conspecific attraction, despotic competition, habitat quality, Pyrenees.

Explanatory and predictive models are powerful tools in the study of spatial distributions of populations and their use is growing exponentially in animal ecology (Guisan & Zimmermann 2000, Guisan *et al*. 2002, Rushton *et al*. 2004). Models establish statistical relationships between a response and explanatory variables that usually quantify environmental characteristics such as climate, landscape features, and degree of human influence (e.g. Bustamante & Seoane 2004, Guisan & Thuiller 2005, Gavashelishvili & McGrady 2006). This procedure is increasingly employed in wildlife conservation, mainly to determine the probability of future site occupation for expanding populations (Mladenoff *et al*. 1995, Buckland *et al*. 1996, Jerina *et al*. 2003, Hirzel *et al*. 2004) and to examine habitat suitability for released populations within reintroduction programs (Bustamante 1998). The accuracy of predictive models is strongly dependent on population equilibrium, biotic interactions and stochastic local events. Although such complexity frequently limits the generality of the results (Guisan & Zimmermann 2000, Guisan *et al*. 2002), an increasing number of studies take this into account (e.g. Fielding & Haworth 1995, Lindenmayer *et al*. 1995, Rodriguez & Andrén 1999). Predictive

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models are now a potentially valuable tool to detect long-term trends in those key variables capable of explaining the distribution of organisms.

Here we use a previously published predictive model to determine long-term changes in nest-site selection in an endangered population of the Bearded Vulture, Gypaetus barbatus. This species is a large scavenger living in rugged areas where it feeds mainly on bone remains from wild and domestic ungulates (Margalida et al. 2007a). It builds large nests in sheltered caves and ledges of cliffs (see Hiraldo et al. 1979 for review of general biology). The Bearded Vulture lived formerly in all the mountain regions of the Old World from southern Europe to the Middle East and central Asia, but at present its distribution has been much reduced, mainly due to human persecution (Margalida et al. 2008). In Europe, by far the largest population occupies the Pyrenean range between France and Spain (Heredia 2005). Because the Bearded Vulture is considered endangered in Europe (Annex I, EU Wild Birds Directive 79/409/EEC, Appendix II of the Bern Convention, Bonn Convention and CITES) with fewer than 130 breeding territories in the European Union in 2005, reintroduction projects have been carried out, for example in Andalucía (Simón et al. 2005) and the Alps (Terrasse 2004), or are in preparation (e.g. Sardinia, the Balkans).

Nesting habitat selection by Bearded Vultures was studied in 1991 in the Spanish Pyrenees by assessing physiography, land use, climate, human disturbance and intraspecific density (Donázár et al. 1993). Cliffs having a high probability of occupancy were those situated in rugged areas (i.e. a high degree of topographic irregularity), at an average altitude, far from villages and far from the nearest conspecific territory (see below for details). Between 1990 and 2000 the Bearded Vulture population of the Spanish Pyrenees grew annually at a rate of 5% (Heredia & Margalida 2002). This increasing trend is unusual as populations of this species are decreasing over most of their distribution (Del Hoyo et al. 1994). However, the area in which the Pyrenean birds are found has not increased at the same rate: less than 10% of their former breeding range has expanded during the last two decades (Heredia 2005).

In this paper, we have the advantage of the above mentioned 1991 predictive model to assess whether nest-site selection patterns of the Bearded Vulture have changed in parallel with population growth. The results may contribute to the long-term management of the most important European population of this endangered species and, moreover, may help to determine the validity of nest-site selection models as a tool for future conservation actions, especially those involving reintroduction programs.

METHODS

Population trends and cliff characterization

The basic information on the distribution of territories and nests of Bearded Vultures in the Pyrenees has been obtained from two sources: unpublished databases compiled by R. Heredia from 1977 to 1991 (see Donázár et al. 1993) and monitoring programs established by regional governments (Navarra, Aragón and Catalunya) from 1991 to the present. In all the regions, the monitoring has been able to detect the occupation of new territories thanks to repeated visits to locations with at least minimum requirements for the establishment of new pairs (Margalida et al. 2003c). Each year, breeding sites known from previous studies, named old cliffs, and new sites located after 1991, named new cliffs, were visited at least once a week between the months of November and August. To locate the nests, observations began in September coinciding with the start of nest building (Margalida & Bertran 2000) and ended during fledging (June–August). During each visit, a pair’s breeding behaviour and whether the birds were building nests, incubating, or rearing a chick was recorded. The sampling effort for the two periods (i.e. 1977–91 and 1991–2002) was similar.

Statistical procedures

Comparisons were done on the basis of four groups of sampling locations (b and c correspond to those used by Donázár et al. 1993, see Table 1):

(a) New (n = 36): cliffs with nests occupied between 1991 and 2002. If a territory had more than one nest, we only considered the one used the first time.

(b) Old (n = 111): all cliffs with nests occupied at least once between 1977 and 1991.

(c) Random (n = 111): unoccupied cliffs from the existing range, selected by pseudo-random generation of co-ordinates and choosing the nearest point on a cliff without a nest.

(d) Peripheral (n = 40): cliffs without Bearded Vulture nests selected at random in the former range of the species and located in zones more than 20 km from the nearest pair. These cliffs were in the Eastern Pyrenees and the
Table 1. Variables used to characterize Bearded Vulture nesting cliffs and random cliffs. In random cliffs, distances were measured from a point in the centre of the cliff (modified from Donázar et al. 1993).

**Topography**
RELIEF: Topographic irregularity index. Total number of 20-m contour lines, cut by four 1-km lines starting from the nest in directions N, S, E and W.

**Cliff local characteristics**
ALTITUDE: Altitude of the nest above the sea level (m).
CLIFF: Cliff height, measured as the number of 20-m contour cut by a 50-m line perpendicular to the cliff face at nest level.
ORIENTATION: Orientation of the cliff face at the level of the nest. Orientations were scored in increasing shelter from cold humid winds from the NW, which are dominant in the area: 1 = NW, 2 = N or W, 3 = NE or SW, 4 = E or S, 5 = SE.

**Environmental characteristics of the surrounding area**
FOREST: Extent (%) of forested areas in a 1-km radius around the nest.
DISTANCE VILLAGE: Distance to the nearest inhabited village (km).
INHABITANTS: Number of inhabitants in the nearest village.

**Human disturbance**
KILOMETRES ROADS: Kilometres of paved and unpaved roads in a 1-km radius of the nest.
DISTANCE PAVED ROAD: Shortest linear distance between the nest and the closest paved road (km).
DISTANCE ROAD: Shortest linear distance between the nest and the closest road, paved or unpaved (km).
HEIGHT PAVED ROAD: Altitudinal difference between the nest and the closest paved road, measured at the point the road is closer to the nest (m). If the nest is lower than the road, a negative value is obtained.
HEIGHT ROAD: Altitudinal difference (m) between the nest and the closest road (paved or unpaved). If the nest is lower than the road, a negative value was obtained.

**Intraspecific relationships**
NEAREST NEIGHBOUR: Linear distance between the nest and the closest nest of the nearest neighbour (km).

Table 2. Descriptive statistics (mean ± sd) and significance of the differences in mean values between some groups obtained with the Mann–Whitney test of the variables characterizing the new breeding cliffs (n = 36) occupied by the Bearded Vulture in the Spanish Pyrenees between 1991 and 2002, old cliffs occupied before 1991 (n = 111), randomly selected cliffs (n = 111) and cliffs in peripheral mountains (n = 40).

<table>
<thead>
<tr>
<th>Variable</th>
<th>New (n = 36)</th>
<th>Old (n = 111)</th>
<th>Random (n = 111)</th>
<th>Peripheral (n = 40)</th>
<th>P (Mann–Whitney U-test)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RELIEF</td>
<td>77.0 (19.9)</td>
<td>83 (18.0)</td>
<td>67.8 (15.4)</td>
<td>58.8 (13.0)</td>
<td>ns</td>
</tr>
<tr>
<td>ALTITUDE</td>
<td>1424.2 (358.9)</td>
<td>1333 (361.2)</td>
<td>1316.56 (516.0)</td>
<td>1078.7 (955.3)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>CLIFF</td>
<td>321.7 (124.5)</td>
<td>367.2 (116.7)</td>
<td>268.8 (94.1)</td>
<td>13.5 (4.7)</td>
<td>ns</td>
</tr>
<tr>
<td>ORIENTATION</td>
<td>3.3 (1.0)</td>
<td>3.1 (1.3)</td>
<td>3.0 (1.2)</td>
<td>3.3 (1.2)</td>
<td>ns</td>
</tr>
<tr>
<td>FOREST</td>
<td>167.0 (97.0)</td>
<td>167.9 (111.5)</td>
<td>155.4 (102.7)</td>
<td>49.5 (32.7)*</td>
<td>ns</td>
</tr>
<tr>
<td>DISTANCE VILLAGE</td>
<td>2.60 (1.4)</td>
<td>3.1 (2.4)</td>
<td>2.8 (2.0)</td>
<td>2.2 (1.3)</td>
<td>ns</td>
</tr>
<tr>
<td>INHABITANTS</td>
<td>88 (139)</td>
<td>175 (259)</td>
<td>116 (205)</td>
<td>156 (186)</td>
<td>ns</td>
</tr>
<tr>
<td>KILOMETRES ROADS</td>
<td>1.5 (1.6)</td>
<td>1.5 (2.2)</td>
<td>2.4 (2.9)</td>
<td>4.6 (3.6)</td>
<td>ns</td>
</tr>
<tr>
<td>DISTANCE PAVED ROAD</td>
<td>2.3 (1.7)</td>
<td>2.1 (1.6)</td>
<td>2.3 (1.7)</td>
<td>1.6 (1.2)</td>
<td>ns</td>
</tr>
<tr>
<td>DISTANCE ROAD</td>
<td>1.0 (0.9)</td>
<td>1.0 (0.9)</td>
<td>1.0 (1.0)</td>
<td>0.3 (0.2)</td>
<td>ns</td>
</tr>
<tr>
<td>HEIGHT PAVED ROAD</td>
<td>431.4 (267.6)</td>
<td>494.7 (252.3)</td>
<td>390.6 (330.3)</td>
<td>239.2 (247.2)</td>
<td>ns</td>
</tr>
<tr>
<td>HEIGHT ROAD</td>
<td>325.0 (257.8)</td>
<td>250.8 (291.0)</td>
<td>254.0 (310.7)</td>
<td>83.0 (147.6)</td>
<td>ns</td>
</tr>
<tr>
<td>NEAREST NEIGHBOUR</td>
<td>8.9 (8.4)</td>
<td>11.1 (6.4)</td>
<td>8.1 (6.0)</td>
<td>53.3 (21.5)</td>
<td>0.001 ns</td>
</tr>
</tbody>
</table>

*Calculated on a sample size n = 19 as consequence of limited data available.

Basque Mountains. They are habitually visited by immature and adult birds during their dispersal stage (R. Heredia, D. Campión, A. Margalida, unpubl. data).

We first used Wilcoxon Mann–Whitney tests to check if there were statistical differences in environmental variables comparing peripheral to random cliffs. Next, we compared the differences in environmental variables between new and old nesting cliffs, and between new and random cliffs (Table 2). Finally, we compared average probability of cliff
occupancy predicted by the model between old, new and random cliffs. We used generalized linear models (GLMs) to analyze the binary response variables ‘cliff occupation’, assuming a binomial distribution of errors and using a logit link function (see Donázar et al. 1993). The final model included four variables: relief, distance to the nearest occupied nest (log-transformed), altitude and distance to the nearest village (log-transformed): linear predictor = −33.9 + (0.091*relief) + (1.644*log distance to the neighbour territory) + (0.099*altitude) − (4.024*10⁻⁶ *altitude²) + (0.945*log distance to the nearest village). The result was that in 1991 the Bearded Vulture selected those areas with the most irregular topography as nesting cliffs, far from other breeding pairs, at an average altitude, and away from human habitation.

The predictive ability of a model tends to be optimistically biased when evaluated with the same data used to build it. Because of that, and because of the fact that old nesting cliffs and random cliffs, rather than new nesting cliffs, have been used to build the model, the probability of occupancy predicted by our model on new cliffs cannot be compared with other cliffs. To avoid the bias, we estimated the probability of a cliff being occupied by Bearded Vultures by cross-validation. We divided each sample (old, new and random cliffs) into five groups with 20% of the observations in each. The first group of observations in each sample was used as a test and the remaining four groups of old cliffs and random cliffs (80% of original model data) were used to fit new model parameters. This model was used to predict the probability of occupation in the test group of observations (20% of data). Each of the groups of observations was dropped in turn from model construction and used as test data. The dataset was reordered 20 times and the whole procedure repeated, so the probability of cliff occupancy was estimated 20 times by 20 different predictive models based on observations before 1991 that did not contain that particular observation. We estimated the mean predicted probability for each cliff and compared samples (old, new and random) with the Wilcoxon Mann–Whitney test. The predictors included in all models were the same used in the model of Donázar et al. (1993); we only estimated new parameters in each case. The whole procedure was repeated, fitting a model without distance to the nearest neighbour to estimate the effect of this variable on the probability of cliff occupancy.

**RESULTS**

The Bearded Vulture population of the Spanish Pyrenees grew from 53 territories occupied in 1991 to 93 in 2002. Despite this increase, the distribution area changed only slightly during this period: two new territories were located up to 40 km westwards. The rest of the new territories were found within the former breeding area, mainly within the central nucleus of the mountain range. The cliffs located in peripheral zones, without Bearded Vulture territory, showed several significant differences from those existing in occupied breeding areas (Fig. 1). They tended to be smaller (mean height) and were usually located in less steep and lower altitude zones. In addition, they were nearer, in distance and altitude, to roads and they had a greater neighbouring human population.

The new territories occupied from 1991 to 2002 showed similar habitat characteristics to those occupied before 1991 (Table 2). The only exception was the variable ‘nearest neighbour’. New territories were situated at a significantly shorter distance to other occupied territories than they were before (mean: 8.9 km vs 11.1 km). In relation to randomly selected cliffs, new nest sites were in areas that were more rugged, and in cliffs that were higher than average. In addition, new nesting cliffs were not significantly further from the nearest occupied nest (mean: 8.9 km) than were random cliffs (mean: 8.1 km; Table 2). These results are similar when comparing old nests with random cliffs (Table 2).

The application of models including the variable ‘nearest neighbour’ determined that newly occupied cliffs had intermediate probability values between old nesting cliffs and random cliffs (Fig. 1); the two comparisons gave significant differences (new vs old Z = 2.89, P = 0.0038; new vs random Z = −3.16, P = 0.0016). Previously occupied cliffs had, as expected, a higher probability of occupancy than random cliffs (Z = 8.537, P < 0.0001). When probabilities were calculated on the basis of the model without ‘nearest neighbour’ (Fig. 1), new cliffs did not differ significantly from old cliffs (Z = 1.11, P = 0.267), but both old cliffs and new cliffs had significantly higher occupancy probabilities than random cliffs (respectively, Z = −3.592, P = 0.0003, Z = 6.949, P < 0.0001). Therefore, during the last decade Bearded Vultures have been selecting a similar kind of cliff as previously chosen in relation to topography and distance from human habitation, the main factors affecting cliff selection. The distance...
between neighbouring territories decreased in parallel with the increase in population density (from 4.4 to 2.5 territories/1000 km² between 1991 and 2002).

**DISCUSSION**

Our results show that the selection of nest sites has not changed with the population increase of the Pyrenean Bearded Vulture. For those variables determining the probability of cliff occupancy (ruggedness, altitude and distance to nearest human habitation), newly established territories between 1991 and 2002 had similar values to those of traditional territories occupied previously. These new pairs, however, occupied cliffs among the existing old territories so that the distance between neighbours has reduced by around 20%, which proves territory shrinkage (Both & Visser 2000, Ridley et al. 2004). In addition, cliffs remaining unoccupied by Bearded Vultures after 1991 in the periphery of the Pyrenees had both lower values in key variables (e.g. relief, altitude, distance to village) and lower probability of occupancy than those occupied in the Pyrenean range during the same period.

These findings seem to contradict what would be expected from a distribution by despotic competition, classically described for birds of prey and other territorial birds (e.g. Ferrer & Donázar 1996, Newton 1998). It could be argued that there is still availability of good-quality breeding sites in the Pyrenees and that, consequently, the population has not reached the saturation threshold necessary to observe the occupation of marginal territories by newly established birds. This holds true if the comparison is limited to the examination of the quality of nesting cliffs where no long-term changes were evident. A different picture, however, arises when distance between neighbouring territories is considered. As this variable was significant in the model fitted in 1991, we can deduce that saturation is taking place and that there is a decrease in territorial quality via reduction in the distance between breeding pairs. In parallel, it has been demonstrated that the productivity of the Pyrenean population has sharply declined during the last decade as a consequence of the increasing breeding density (Carrete et al. 2006a), a clear symptom of population crowding, as is the appearance of unusual mating systems (Carrete et al. 2006b). Today, the density attained by Bearded Vultures in the Spanish Pyrenees (226 km²/one territory) is the highest recorded for the species in its European breeding range. Equivalent figures are 333 km²/territory for the French Pyrenees, 240 km²/territory for Corsica and 2065 km²/territory for Crete (Xirouchakis & Nikolakakis 2002, Terrasse 2004). To these numbers (93 pairs in 2002), a non-breeding population of around 200 individuals should be added to the Spanish Pyrenean population (Heredia 2005).

Why do Bearded Vultures tolerate shrinkage of territories? In territorial birds of prey, an increase in the density of breeders usually results in a higher level of agonistic encounters; large territories are vigorously defended against conspecifics (Newton 1979, 1998, Ridley et al. 2004). Territorial defence in the Bearded Vulture appears, however, to be restricted to the areas surrounding the nest (less than 500 m radius according to the majority of authors; Hiraldo et al. 1979, Brown 1988, Bertran & Margalida 2002, Margalida & Bertran 2005). Outside these limits, there is habitual tolerance between neighbouring pairs. Tolerance towards conspecifics may be evolutionarily favoured as a consequence of the large distances between territories, which would not favour selection for aggressiveness against intruders (see also Margalida et al. 2003b). In fact, the strategy for finding unpredictable food makes it necessary to forage over extensive areas that overlap neighbouring pairs (Brown 1988). Human manipulation of the availability of resources (e.g. feeding stations) may also be a determining factor explaining this ‘packing’ of the population. During the 1990s, nearly 30 feeding stations were established in the Spanish Pyrenees.
There, more than 50,000 kg of bones per year are left for the Vultures (Regional Governments, unpubl. data). Consequently, it could be that this increase in the availability of resources has resulted in the reduction of territorial behaviour and facilitated the compression of territories. Monitoring of feeding stations reveals a predominant use by immature birds (70%; Heredia 1991), but it is not possible to disregard the fact that these feeding stations are important factors for adult birds at specific times of the breeding cycle. Feeding stations can strengthen conspecific attraction, reducing the probability that new breeding birds will occupy territories in areas distant to the central zone of the mountain range (Serrano & Tella 2003).

Finally, the packing process could be also motivated by the scarcity of suitable breeding sites in mountain areas surrounding the Pyrenees. As our analyses demonstrate, potential nesting cliffs in those regions are of lower quality (in terms of altitude, topography and human influence) than those existing within the main mountain range. Human presence is known to affect strongly the distribution patterns of Bearded Vultures and other large raptors, not only in relation to the safety of breeding nest sites (Donázar et al. 2002, Margalida et al. 2007b), but also in relation to foraging grounds (Bautista et al. 2004, Gavashelishvili & McGrady 2006). Previous analyses have shown that the breeding success of Pyrenean Bearded Vultures is affected by human activities and infrastructures (Donázar et al. 1993, Arroyo & Razin 2006). Therefore, it is reasonable to think that the low probability of cliff occupancy outside the Pyrenees is determined, at least partially, by the intense human influence on these peripheral mountain regions. In this sense, the Pyrenees could progressively become more of an ecological island for the Bearded Vulture surrounded by areas that are inadequate due to the increasingly intense human influence on the environment. Consequently, the risk of extinction in this population will remain high as a consequence of stochastic demographic and environmental phenomena and of the scarce genetic variability (Godoy et al. 2004).

The conservation efforts for the population of Pyrenean Bearded Vultures should facilitate the geographic expansion of the species towards other mountainous zones of the Iberian Peninsula. Two complementary actions, the creation of new populations through reintroduction plans, and the promotion of the dispersion of non-breeding individuals using changes in the availability of food, could favour the maintenance of a metapopulation structure permitting genetic exchange and, fundamentally, determining unequal probability of extinction for different sub-populations. To determine the suitability of the areas of reintroduction, where constraints linked to territoriality do not exist, a model such as that determined in 1991, without the distance to nearest neighbour variable, seems particularly relevant. In fact, the aforementioned model has been used to predict nesting probability in areas where the Bearded Vulture is being reintroduced, such as the Alps and Andalucía (e.g. Bustamante 1996). In a broader sense, our study shows that the probability of presence determined by predictive models may be sensitive to social behaviour, in this case flexibility in territoriality. This shows the necessity for modelling procedures to take into account variables quantifying intraspecific relationships between individuals (Alexander et al. 2006).

The basic information about the recent distribution (1991–2002) of the Bearded Vulture comes from databases generated by the Ministry of Environment, Organization of Land and Housing of the Autonomous Region of Navarra, the Department of Environment of the General Council of Aragon and the Department of Environment and Habitat of the Autonomous Government of Catalonia. Our thanks to all the people who have directly or indirectly participated in different phases of this work: I. Afonso, I. Antón, R. Antor, M. Arilla, J. Bertran, J. Bolado, A. Bonada, D. Campión, J. Canut, D. García, D. Gómez, R. Heredia, J. Jové, J. Martín, J.M. Miranda and A. Senosiain. B.E. Arroyo, G.R. Bortolotti, M. Carrete, F. Hiraldo, A. López-Sepulcre and two anonymous reviewers contributed suggestions which improved the manuscript. This work was financed by the Ministry of Environment of the Autonomous Government of Andalucía, within the Project ‘Studies of viability for the reintroduction of the Bearded Vulture in Andalucía’. Support was also obtained from the BBVA Foundation through its award for scientific research in Conservation Biology (2004).

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