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Modelling nesting habitat as a conservation tool for the Eurasian black vulture (*Aegypius monachus*) in Dadia Nature Reserve, northeastern Greece

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Abstract

The Eurasian black vulture (*Aegypius monachus*) is a globally endangered species, vulnerable in Europe and endangered in Greece. We modelled its nesting preferences in Dadia reserve, northeastern Greece using logistic models at multi-scale level combined by Bayesian statistics. Compared with the random sites, the vultures nested at trees with greater diameter (DBH), lower height, and lower total number of trees around the nest tree, steeper slopes and greater distance from forest roads. Our results indicate that conservation and management guidelines for black vultures must aim: (1) to preserve old, isolated mature trees in the reserve, (2) to maintain the zones of strict protection as vulture sanctuary, including most of the suitable nesting habitat, (3) to protect the apparently suitable but still unused habitat in the rest of the reserve from disturbance and logging, (4) to monitor any changes in habitats and use our models to evaluate and predict their effect on vulture nesting in the reserve.

Keywords: Eurasian black vulture; Logistic regression; Bayesian integration; Nest-site selection; Habitat conservation

1. Introduction

The Eurasian black vulture (*Aegypius monachus*) is the largest bird of prey in the western Palearctic. In Europe its breeding distribution is limited to some parts of Spain, France, and southeastern regions (Cramp and Simmons, 1980; Tewes, 1996). The European breeding population has been estimated between 1450 and 1477 pairs, of which 1336 occur in Spain (Tewes et al., in press). Greece is the only southeastern European country holding a breeding population. It is considered to be a globally endangered species (Collar et al., 1994), vulnerable in Europe (Tucker and Evans, 1997) and endangered in Greece (Karandinos and Legakis, 1992). The reasons for its population decline in Greece have been breeding habitat loss, a decrease of food availability paired with changes in livestock-raising practices, and poisoning (Spyropoulou, 1998; Hallmann, 1998b).

In the Dadia Nature Reserve, the only breeding place in Greece (Handrinos, 1985), the breeding population increased steadily from 10 pairs in 1980 to 26 pairs in 2002 (Vlachos et al., 1999; Skartsi, 2002) supported by a feeding station that was established in 1987. This population also includes non-breeding birds. The maximum number of black vultures counted in Dadia between 1987 and 2002 was 89 birds in January 2001 (Skartsi, 2001). The conservation of the population of the black vulture is the central subject of interest in the reserve management.

Habitat loss and alteration are the most serious threats to raptor populations (Newton, 1979). Populations of forest-breeding raptors are sensitive to forest management practices and habitat changes (Niemi and Hanowski, 1997; Fargallo et al., 1998; Donazar et al.,

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2002). Recent studies suggest that the quantification of raptor habitat selection can make possible the prediction of species presence, and thus significantly contribute to the development of conservation measures for endangered species (Newton et al., 1981; Donazar et al., 1993; Austin et al., 1996; Ferrer and Harte, 1997; Suarez et al., 2000; Liberatori and Penteriani, 2001; Loyn et al., 2001).

The habitat of the black vulture consists of rocky areas with steep slopes, usually forested with pines and oaks where air-currents facilitate take-off (Cramp and Simmons, 1980). A few studies have been carried out on the breeding habitat of the black vulture in Europe (Spyropoulou, 1991; Torres-Esquivias and Arenas, 1996; Poirazidis et al., 1996; Tewes, 1996; Fargallo et al., 1998; Atienza et al., 2001; Donazar et al., 2002), but none has attempted to produce nesting habitat models and relevant maps to promote the management and conservation of the species. The present study aimed to facilitate the conservation of the species in the Dadia Nature Reserve by: (a) the identification of habitat characteristics that are critical for the black vultures which breed in this area; (b) building empirical models for the prediction of suitable nesting habitat; (c) the identification and mapping of potential future black vulture nesting areas in the reserve.

2. Study area and methods

2.1. Study area

The Dadia Nature Reserve is situated in the Evros Prefecture, northeastern Greece (Fig. 1), and has been declared as reserve since 1980 by Presidential Decree (Spyropoulou, 1998). It covers a forest complex extending over ca. 43,000 ha (hereafter study area) including two zones of strict protection (core areas), which cover a total of 7250 ha, and are of primary importance

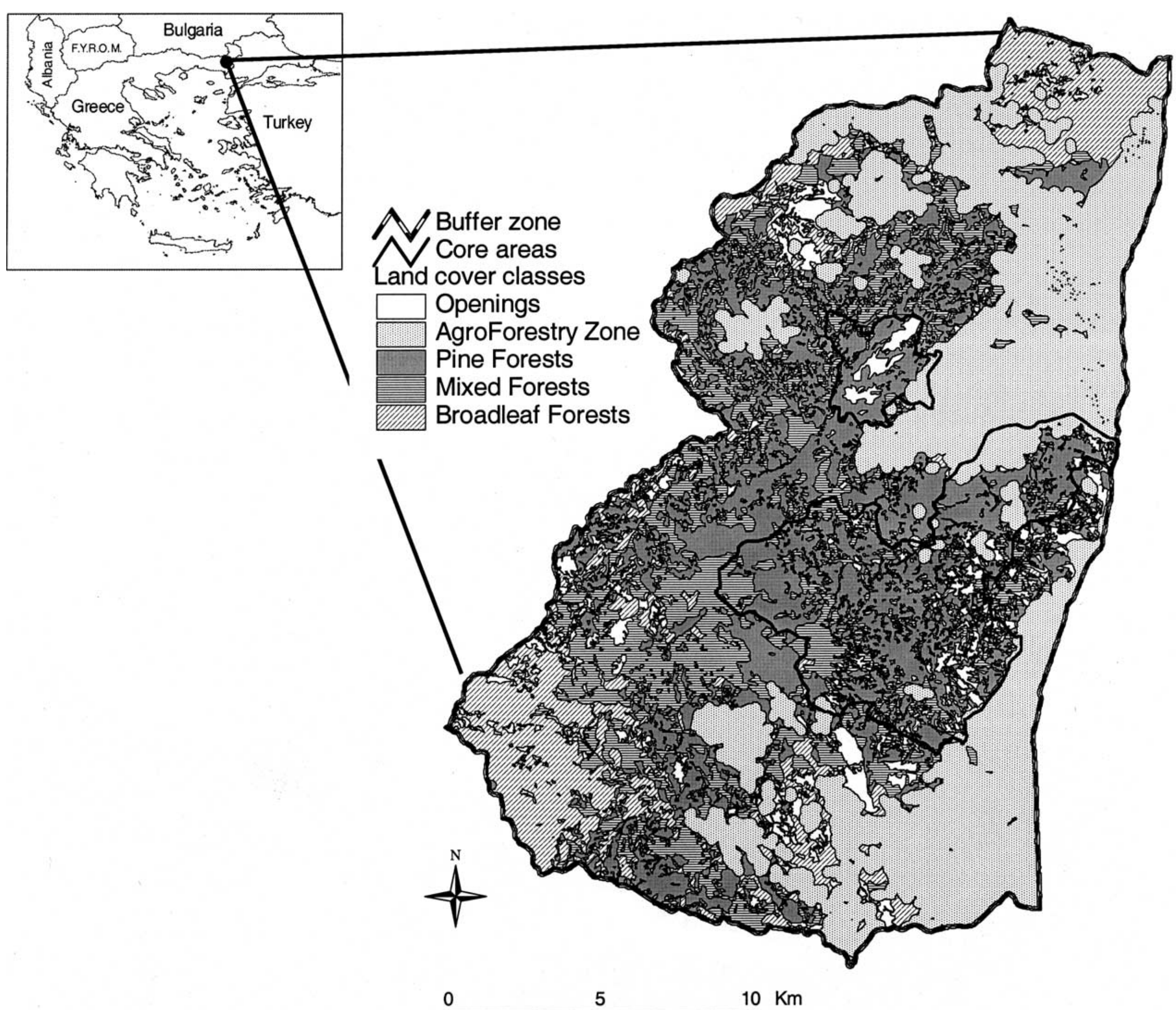

Fig. 1. Map of the study area. Land cover of the Dadia reserve: openings (open1 and open2) (7.2%), agroforestry (33.11%), pine forest (26.96%), mixed forest (mixed1 and mixed2 and mixed3) (18.34%), and broadleaf forest (14.39%). For details see Table 1.

for the breeding population of the black vulture. The study area is characterized by steep valleys covered by extensive oak (*Quercus frainetto*, *Q. cerris*, *Q. pubescens*) and pine (*Pinus brutia*, *P. nigra*) forests, and includes a variety of other habitats, such as cultivations, fields, pastures, torrents and stony hills (Adamakopoulos et al., 1995).

2.2. Nest selection

Black vultures nest both inside and outside the core areas. From 1987 to 2001, 81 nests were recorded both in loose colonies and as independent nests. To develop the habitat-selection model we used two independent data sets, one for calibrating and another for evaluating the model (Guisan and Zimmermann, 2000). The calibration data set was derived from 25 active nest sites in 2001 and the evaluation data set from 56 different nest sites, which were active between 1987 and 2000. The reasons for these choices were: (a) to ensure data independence during the calibration phase (Guisan and Zimmermann, 2002) with respect to individual breeding pairs, which was necessary because both the breeding population was different and the nest sites used by individual pairs differed among years; (b) the use of the 2001 nests for model construction, gave us the opportunity to check the effectiveness of the resulting models and nesting probability maps with data from the rest of the years' nest sites. The particular year (2001) was selected because the environmental data used in the analyses and model construction, were derived from satellite images of the study area taken in July 2001.

2.3. Selection of habitat variables

There are two tendencies in raptor habitat modelling. One paradigm (deductive modelling) is based on former knowledge of the species concerned in the study area, whereas the other (inductive modelling) follows empirical methods (Austin, 1992). In the latter case, the environmental variables identified as significant by the analyses are not necessarily important for the species in question, but are merely associated with the presence of the species in the particular area (James and McCuloch, 2002). If ecological conclusions are to be drawn, the selected variables should be directly related to the biology of the species (Glenz et al., 2001).

In this study, we used a modification of the empirical methods, while using former knowledge of the species. The habitat variables initially selected were empirically known to affect the presence of the black vulture. Nevertheless, due to their semi-colonial nesting and social foraging, a varying number of pairs may simultaneously use some important features of the environment, such as water sources and foraging areas. Initially we used variables, such as distance to shared resources, streams, permanent water, rocks, openings, etc. in the models. During our modelling process, these variables when inserted in the analyses made models very unstable. Thus, to satisfy daily needs, the vulture population in the reserve clearly uses resources outside the Dadia reserve, e.g. for feeding, but these resources do not affect the selection of specific nesting sites.

The habitat preferences of the black vulture were analysed at a multi-scale level. On a first level (nest-site) we analysed the characteristics of the nest-tree and the structure of the forest stand in an area of 0.1 ha (radius 17.85 m) around the nest (Table 1). Tree diameters were measured to the nearest cm at breast height (DBH). Tree and canopy heights were measured using Vertex III equipment (Haglof). All nests were located at the beginning of the breeding season but they were visited after the nestlings had left the nests to avoid disturbance.

On a second level (landscape) we analysed variables related to geomorphology, vegetation type and disturbance. These variables were measured from the Geographical Information System (GIS) images on three scales (at the nest tree points, and in circles of 50 and 150 m around the nests) to study the influence of the scale where selection occurred (Moorman and Chapman, 1996). Unlike other birds of prey, the black vulture does not defend an extensive nesting territory. The distance of 50 m was chosen because it represents the minimum radius of the exclusive territory that is defended by breeding birds (Cramp and Simmons, 1980). The distance of 150 m was approximately half of the minimum nearest neighbour distance measured and was chosen to avoid overlap of neighbouring areas (Table 1).

2.4. Choice of random samples

We made random sampling in areas where the species has not nested so far (1987–2002). We selected a number of samples similar to that of nests (Manel et al., 1999; Osborne et al., 2001). We accepted a random plot only when it was selected within a forested area and taking into account the minimum habitat requirements of the species at the nest-site level. This procedure has been applied in other raptor habitat studies (Titus and Mosher, 1981; Speicer and Bosakowski, 1987; Moorman and Chapman, 1996; Suarez et al., 2000). The minimum habitat requirements of the black vulture in Dadia were: (a) the occurrence of a tree with at least 32 cm DBH, and (b) the presence of young tree stands in areas around big trees (DBH $>$ 32 cm) (Spyropoulou, 1991; Poirazidis et al., 1996; this study). Random sampling was carried out in all forest types, from pines through mixed pine-oaks to pure oak forests. Random samples were determined by the GIS and identified in the field using a Global Position System (GPS).

Table 1
Habitat variables used to characterize nest sites of the black vulture compared with random sites

Abbreviation	Variable description
A. Nest-site level	
Nest tree and random central tree characteristics variables	
DBH	Diameter at breast height (cm)
Hgt	Height of tree (m)
CanHgt	Height of tree canopy (m)
Stand density variables (0.1 ha area)	
DBHmax	Maximum Diameter at breast height in the plot (cm)
RD	Stand density index 1
SDI	Stand density index 2
D4_20	Number of trees in the 4–20 cm diameter class
D22_34	Number of trees in the 22–34 cm diameter class
D36_48	Number of trees in the 36–48 cm diameter class
D50_80	Number of trees in the 50–80 cm diameter class
DM	Mean diameter
Total_tree	Total number of trees
B. Landscape level	
Geomorphologic variables (central point, plot 50 m, plot 150 m)	
ELEV	Elevation (m)
Cvele50	CV in elevation in 50-m radius
Cvelel50	CV in elevation in 150-m radius
Asp_cosine	Aspect (cosine transformation)-eastness (from −1 to +1)
Asp_sine	Aspect (sine transformation)-northness (from −1 to +1)
Slope	Slope (in degrees)
Vegetation variables (central point, 50-m plot, 150-m plot)	
Pinus	Pure Pine or mixed Pine and Broadleaf forest (70–100% *Pinus sp.* cover)
Mixed1	Mixed Pine and Broadleaf forest (40–70% *Pinus sp.* cover)
Mixed2	Mixed Broadleaf and Pine forest (10–40% *Pinus sp.* cover)
Mixed3	Broadleaves forest (isolated *Pinus sp.*)
Broads	Pure Broadleaf forest (no *Pinus sp.* present)
Openl	Openings with Pine trees
Open2	Openings without Pine trees
AgroFo	Agroforestry zone (fields with 150-m forest zone) and urban areas
Disturbance variables (central point) (m)	
Dstpaved	Distance from paved roads
Dstroads	Distance from roads of any type
Dsturban1	Distance from villages
Dsturban2	Distance from isolated buildings or recreational areas
Dstfields	Distance from fields

Since these samples were used for the black vulture habitat modelling where the data followed a binomial mode (presence–absence, see further), a zone of 300 m around the nest sites (the minimum of the nearest neighbour distance of the black vulture in the study area) was excluded from random sampling, as it would include areas where nesting were present. In the remaining area, and to reduce autocorrelation problems (Legendre, 1993), the random points selected were at least 300 m apart.

2.5. GIS coverages

The accuracy and resolution of input maps is one of the key issues related to the distribution model predictions (Guisan and Zimmermann, 2000). The problem of accuracy becomes more important when models are developed for mountainous terrain with heterogeneous topography and mosaic-like vegetation (Guisan and Zimmermann, 2000). Therefore, using fine resolution in data analysis improves the accuracy of the models. Based on topographic maps of the area, we produced a Digital Terrain Model (DTM) of 5-m pixels. Using the Spatial Analyst extension from the ArcGIS® software (Environmental Science Research Institute Inc., Redlands, CA), we created geomorphologic variables of altitude, slope and aspect. This DTM was also used to calculate the coefficient of variation (CV) of altitude in a radius of 50 and 150 m from each nest and at random points. The vegetation and anthropogenic features (habitations, roads, etc.) were taken from detailed maps of the study area, based on ICONOS satellite imagery (1-m pixel resolution) taken in July 2001. These were digitalized on screen using the software ArcGIS. The respective polygons were rasterized at the same resolution as the geomorphologic maps to keep data resolution on a fine scale and to produce the vegetation-type and disturbance variables.

Although all the GIS analyses were made with coverages of 5-m pixel resolution, the probability map was made with a resolution of 50 m per pixel, a scale considered to represent the minimum surface unit needed by the black vulture for breeding. Transformation of the initial GIS raster data layers of 5 m per pixel was made using the Neighbour statistics on a canvas of 10×10 cells, based on the mean value of the initial probability map of 5-m pixel.

2.6. Statistical analysis

Nest density was estimated using the nearest-neighbour distance method (Newton et al., 1977). The regularity in nest spacing was tested by the *G*-statistic (Brown, 1975; Liberatori and Penteriani, 2001), calculated as the ratio between the geometric mean and the arithmetic mean of the squared nearest neighbour distances. This index ranges from 0 to 1 and values >0.65 indicate a uniform distribution of nests.

Data collected at nests and random samples were tested for normality with the Kolmogorov–Smyrnov test. The variable "distance from any roads" was normalized by square-root transformation. The means of the variables with continuous values were compared with *t*-tests. The vegetation-type variables at the plot scales did not follow the normal distribution after transformations (arcsine) and were compared with Mann–Whitney *U*-tests. Vegetation types at the nest sites were analysed with χ^2 tests, because the respective data were categorical. As sample sizes were small (expected values <5), we grouped vegetation types in two categories, the pine forest (with *Pinus* occupying 70–100%) and the rest of the forest (*Pinus* 0–70%). All tests were two-tailed and statistical significance was set at $\alpha = 0.05$.

We used a Generalized Linear Model (GLM) to predict the distribution of potential nest sites. As the response variable of this analysis was binary (presence of nest sites/absence of nest sites), the appropriate form of GLM was the logistic regression (Guisan and Zimmermann, 2000). This approach has been followed by many authors (e.g. Pereira and Itami, 1991; Osborne et al., 2001; see also reviews in Guisan and Zimmermann, 2000; Scott et al., 2002). The habitat variables were divided into four sub-groups: (a) characteristics of nest-trees and their surrounding forest stands; (b) geomorphologic; (c) vegetation-types and (d) disturbance data.

In each case, we used backward stepwise elimination to select the variables in the independent models (Pearce and Ferrier, 2000; Manel et al., 2001). Models were fitted using a likelihood ratio method, and the variables were included in each step using as criterion the level of $P = 0.05$ for entry and $P = 0.10$ for removal. This procedure enhanced the accuracy and predictive power of the independent models reducing the explanatory variables to a reasonable number, as no more than $m/10$ predictors were included in the each model (where m is the total number of the observations) (Guisan and Zimmermann, 2000).

Before running the logistic regression, the variables were tested for multi-colinearity based on the Variance Inflation Factor (VIF) analysis (Montgomery and Peck, 1982). The variables with a tolerance value <0.1 or a VIF >10 were removed from the analyses (Bowerman and O'Connell, 1990). The power of the independent logistic regression models was assessed using the Receiver Operating Characteristics (ROC) plot, a threshold-independent measure. The Area Under the ROC Curve (AUC), varying from 0.5 to 1, provides a measure of overall accuracy based on several different probability thresholds, and can be translated as the probability that the model will correctly distinguish between two cases (Fielding and Bell, 1977; Manel et al., 1999; Osborne et al., 2001). It is presented as $\text{AUC} \pm \text{SE}$ (Standard Error) and is independent of prevalence (Manel et al., 2001).

In the geomorphologic and vegetation-type groups, we tested alternative models to find out which scale should be selected for each variable, aiming at the best separation of nest and random samples, the selection of the fewest variables with the highest significance, and at the highest AUC. All statistical procedures were performed using the SPSS statistical package.

The results of the aforementioned b, c and d models were imported to GIS to produce relevant maps of probability of occurrence for nest sites and were combined using Bayesian statistical inference (Pereira and Itami, 1991; Osborne et al., 2001). This allowed the revision of the probabilities derived from one model on the basis of new probabilities calculated from a second model. The mathematical formulation of the procedure is:

$$\text{Pvar1\_var2} = 1/\{1 + \exp[\log(1 - \text{Pvar1}/\text{Pvar1}) - \log(\text{Pvar2}/1 - \text{Pvar2})]\},$$

where Pvar1 is the probability derived from a first model, Pvar2 is the probability from a second model, and Pvarl var2 the new revised probability estimate.

We assessed the final Bayesian model using a variety of accuracy measures, with the construction of a classification table and a confusion matrix according to Fielding and Bell (1977) (Table 5). To produce the classification table, the interval-scaled outputs of the final Bayesian model (measuring probability of success) were converted to dichotomous 0–1 data through specification of the cut-off point. We used ten cut-off points, defined from 0.1 to 1.0, in order to select the best cut-off point that optimizes presence and absence (Pereira and

Itami, 1991; Fielding and Bell, 1977; Franco et al., 2000).

Validation is an integral part of model development and whenever possible it should be conducted using an independent data set, i.e. data not used to develop the prediction model (Fielding and Bell, 1977; Fielding, 2002). In this study, the validation of the final model was achieved by overlaying the locations of the independent nest sites ($n = 56$ nests) into the final Bayesian model within GIS and extracting scores for those locations. As this map was made using an analysis of 50 m, the new nest sites were rasterised in the same resolution, resulting in 55 nest sites (two nests were close to each other). For comparable results, we chose 55 random samples using the same criteria as in the calibration data.

3. Results

3.1. Spatial distribution of nests

In 2001, the mean nearest neighbour distance between active nests was 646 m and ranged from 279 to 2460 m ($n = 25$). When all nests were considered, their distribution was not regular ($G = 0.48$).

3.2. Nest site level

All variables were normally distributed, except stand density "D36_48" and "D50_80" (Table 1), whose pooled sample was normally distributed. In the univariate analysis, of the 11 variables examined at the nest site level, seven showed significant differences compared with the random samples (Table 2). These results suggested a choice of trees with greater diameter at breast height (DBH), but lower height than at random. The density of the forest and the number of trees with low DBH (4–20 and 22–34 cm) in the samples of 0.1 ha around nests was significantly lower than in the random samples. In contrast, the number of trees with high DBH (>36 cm) was not significantly different between nest- and random samples. The total number of trees was significantly lower around nests.

The model of the backward stepwise logistic regression identified DBH, tree height and total number of trees as significant variables (Table 4). The respective ROC plot (Fig. 2a) indicated an almost perfect performance of the model with an $\mathrm{AUC} = 0.978 \pm 0.016$ ($P < 0.001$).

3.3. Landscape level

3.3.1. Geomorphologic variables

All variables followed the normal distribution. Of 14 variables measured at 25 nests, as well as in circles with radii of 50 and 150 m around nests, a univariate comparison with the random samples showed a significant difference in six, indicating that nests were situated on steeper slopes and at higher altitudes (Table 3).

The variables that were selected by the final logistic regression model were (Table 4): the CV of altitude within the 50-m radius area ("Cvele50"), slope in the 150-m radius area ("Slope_150m"), exposure-sine transformation ("asp_sine_point"), and exposure-cosine transformation ("asp_cosine_point") at the nest-site level. The respective ROC plot (Fig. 2b) indicated very good model performance, with an $\mathrm{AUC} = 0.965 \pm 0.023$ ($P < 0.001$). Based on the results of the logistic regression, we created a probability map of occurrence of nest sites (GEO) based on the geomorphologic variables (Fig. 3a).

3.3.2. Vegetation-type variables

These variables did not follow the normal distribution (even after arcsine-transformations), so they were analysed using the Mann–Whitney U test or the χ^2 test (at the

Table 2
Comparison between parameters recorded at black vulture nest sites and at random sites (both $N = 25$) in Dadia Nature Reserve in 2001, (t-tests)

Variable	Nest sites		Random sites	
	Mean	SD	Mean	SD
Tree variables				
DBH***	49.84	10.69	33.68	11.29
Hgt*	11.46	3.38	13.97	4.11
Stand density variables				
RD***	2.16	1.86	4.80	1.63
SDI***	218.51	188.12	489.61	158.13
D4_20***	17.68	19.29	54.08	37.56
D22_34**	4.76	5.61	11.24	9.67
Total_tree***	25.72	23.84	71.04	38.66

Only significant variables (in comparison in Section 3.2) are shown for conciseness of presentation; full table available on request from the corresponding author.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

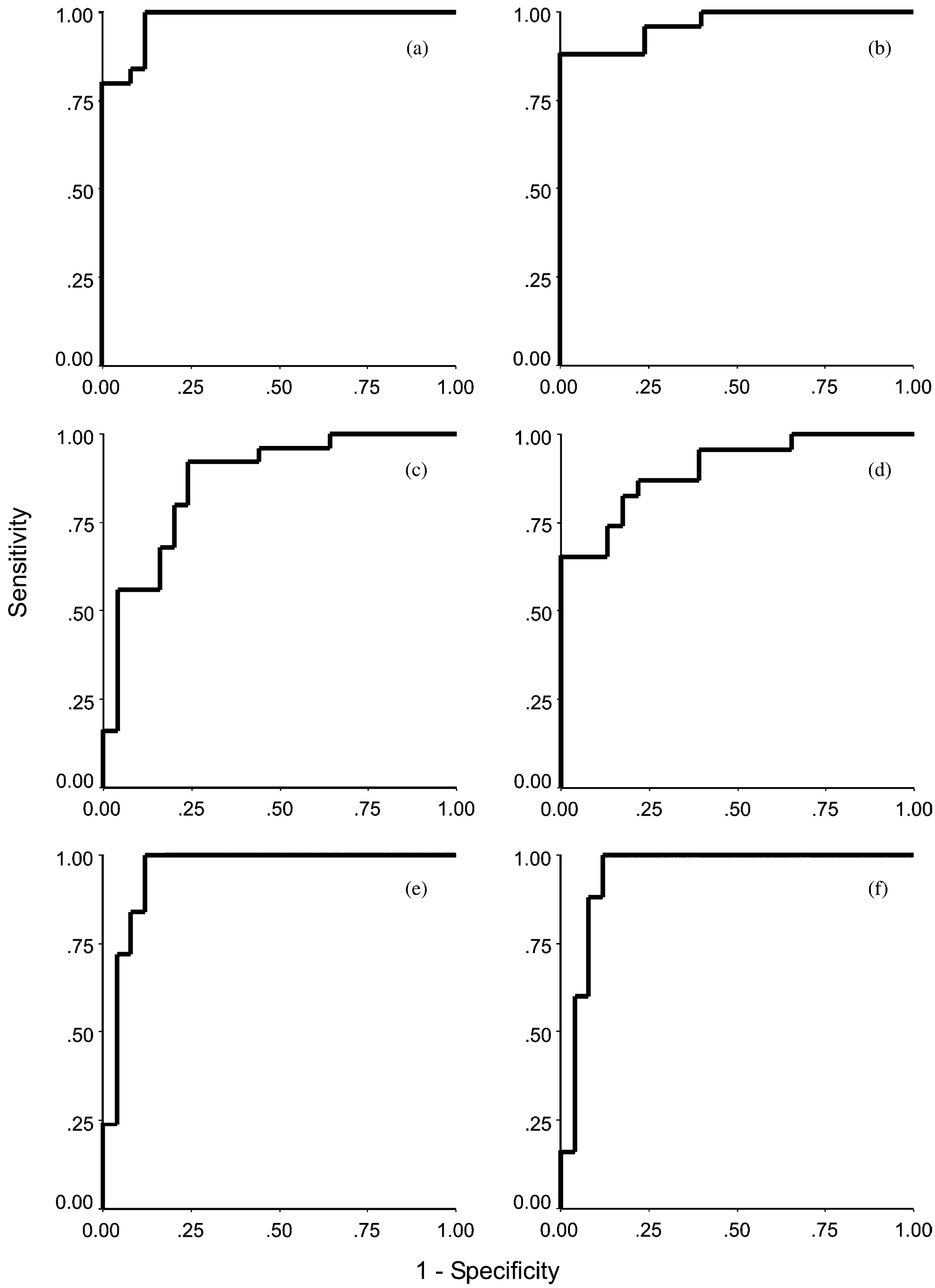

Fig. 2. ROC plots for: (a) Nest-site model, (b) Geomorphologic model (GEO), (c) Vegetation-type model (VEG), (d) Disturbance model (DIS), (e) Bayesian model combining geomorphologic and vegetation models (GEOVEG), and (f) Bayesian model incorporating GEOVEG and the disturbance model (GEOVEGDIS).

nest-tree level). There was no significant difference between the pine forest category (with *Pinus* occupying 70–100%) and the rest of the forest categories (*Pinus* 0–70%) at the nest tree point ($\chi_2 = 0.081$, df = 1, $P = 0.777$). The univariate comparison between 10 variables measured at 25 nest points as well as in circles with radii of 50 m and 150 m around them, and the respective random samples, indicated that (Table 3): there was significantly more broadleaf forest with isolated pines present ("Mixed 3") at nests and in 50-m circles than in the random samples, and in all circular samples around nests there was significantly less pure broadleaf forest ("Broads") than in the random samples.

As in the group of geomorphologic variables, we tested alternative models of logistic regression to choose the best scale that differentiated the samples. The best model was produced when using the data only at the 150-m radius scale (Table 4). The respective ROC plot

Table 3
Comparison between habitat parameters recorded at black vulture nest sites and at random sites (both $N = 25$) in Dadia Nature Reserve in 2001

Variable	Nest sites		Random sites	
	Mean	SD	Mean	SD
Geomorphologic variables				
ELEV_point[a,*]	264.64	68.24	211.84	86.08
ELEV_150m[a,*]	264.20	69.64	212.01	86.33
ELEV_50m[a,*]	264.67	71.57	211.30	87.17
Slope_point[a,***]	23.20	5.18	14.16	7.52
Slope_50m[a,***]	22.49	4.18	14.76	6.93
Slope_150m[a,***]	21.38	3.30	14.38	4.85
Vegetation variables				
Mixed3_50m[b,**]	25.00	40.00	2.00	7.20
Broads_50m[*]	0.00	0.00	13.00	29.70
Broads_150m[b,**]	0.00	0.20	12.00	23.00
Disturbance variables				
Dstroads[a,***]	668.73	438.84	150.42	114.02

Only significant variables (in comparison in Section 3.3) are shown for conciseness of presentation; full table available on request from the corresponding author.
[a] t-Tests.
[b] Mann–Whitney U-tests.
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

Table 4
Logistic regression independent models for black vulture nesting habitat

Variable	Coefficient	Standard Error	Exp (B)
LR model using central tree (nest and random sites) and stand structure variables			
DBH[**]	0.367	0.142	1.444
Hgt[*]	−0.927	0.402	0.396
Total_tree[a]	−0.062	0.034	0.94
Constant[a]	−1.472	2.641	0.229
LR model using geomorphologic variables			
Cvele50[*]	−1.942	0.815	0.143
Slope_150m[**]	1.24	0.398	3.456
Asp_sine_point[a]	1.706	1.048	5.504
Asp_cosine_point[*]	2.586	1.092	13.277
Constant[**]	−18.312	5.942	0
LR model using vegetation variables			
Pinus_150m[*]	0.067	0.026	1.069
Mixed2_150m[*]	0.065	0.031	1.067
Mixed3_150m[**]	0.102	0.034	1.107
Open 1_150m[*]	0.067	0.028	1.069
Constant[*]	−6.189	2.418	0.002
LR model using disturbance variables			
Dstroads[**]	0.01	0.003	1.01
Constant[**]	−2.8	0.872	0.061

[a] NS: Not significant.
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

for this model (Fig. 2c) indicated good performance of the model, with an $\mathrm{AUC} = 0.869 \pm 0.051$ ($P < 0.001$). Based on the vegetation-types analysis, we constructed a probability map of occurrence of nest sites (VEG) for the black vulture (Fig. 3b).

3.3.3. *Disturbance (distance from human settlements)*

All the variables were normally distributed, except the variable distance from any road ("Dstroads"), which was square root transformed. In addition, two nest sites and two random samples with extreme values were

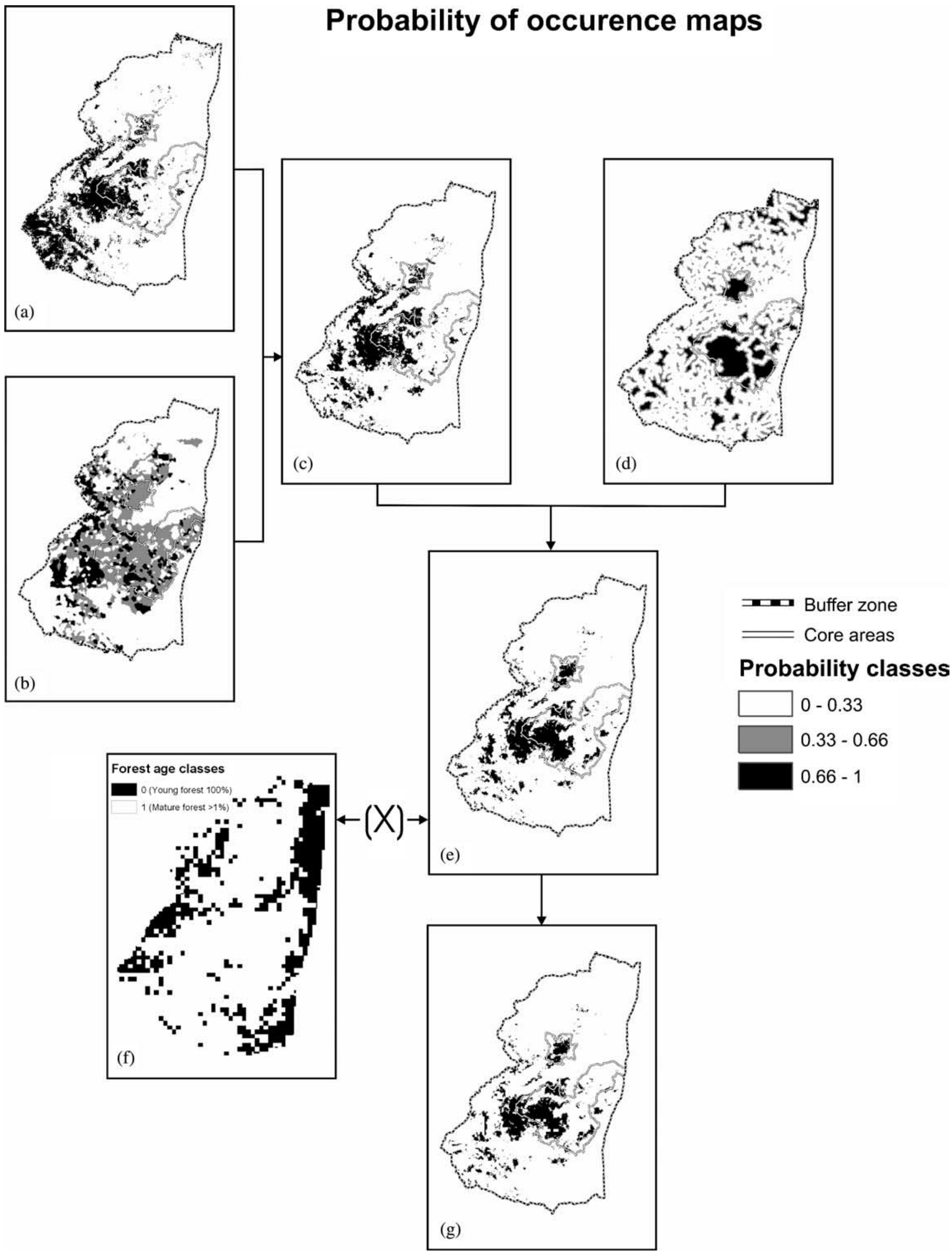

Fig. 3. Maps of probability of occurrence for the nest sites of black vulture based on (a) Geomorphologic model (GEO), (b) Vegetation-type model (VEG), (c) Bayesian model combining geomorphologic and vegetation models (GEOVEG), (d) Disturbance model (DIS), (e) Bayesian model from GEOVEG and DIS (GEOVEGDIS), (f) Boolean map of mature forest, and (g) the final map from GEOVEGDIS X f.

removed from the analyses, as they reduced the effectiveness of both the univariate analysis and the model.

In general, both nest sites and random samples were situated far from human settlements (means of 5338 and 4850 m, respectively). Of the variables used in the univariate analysis, only "Dstroads" showed significantly higher values at nests than in the random samples. No other significant differences were found (Table 3).

The only variable selected by the logistic regression model was "Dstroads" (Table 4). The respective ROC plot (Fig. 2d) indicated very good model performance, with an AUC = 0.902 ± 0.044 ($P < 0.001$). This analysis produced a probability map (DIS) for the black vulture nesting based on the distances from human settlements (Fig. 3d).

3.4. Combining models

Using Bayesian integration, we combined the probability surfaces based on the geomorphologic analysis (used as the prior probability map) and on the vegetation-type analysis (used as the refining probability map). This procedure provided a combined probability surface based on both variable groups (GEOVEG, Fig. 3c). Using the same procedure, we combined the GEOVEG probability surface with that based on the distances from human settlements. These resulted in a nesting probability surface for the black vulture combining all three sub-groups of macro-variables (GEOVEGDIS, Fig. 3e). The respective ROC plot (Fig. 2f) indicated very good model performance with an AUC = 0.946 ± 0.037 ($P < 0.001$).

In order to incorporate the results of the nest-site level model analysis (which showed the preference of the black vulture for mature forest or isolated trees for nesting) in the final combined model, we mapped the mature trees using the following procedure. In the study area, we overlaid a grid of 300×300 m squares (polygon theme) and, using as reference the satellite image, in each square we estimated the percentage cover of mature forest in six classes (0–6): 0 (0% cover), 1 (1–10%), 2 (10–20%), 3 (20–40%), 4 (40–60%), 5 (60–80%), and 6 (80–100%). The isolated mature trees were included in cover class 1. Then the study area was divided into two units, one with mature forest of 0% cover and another of $\geqslant$ 1% cover. This map was rasterised with values 0 and 1, respectively, and a resolution of 50 m (Fig. 3f). The resulting map was combined by multiplication with the final Bayesian map to exclude treeless areas, which are an unsuitable breeding habitat (Fig. 3g). The respective ROC plot was the same as the final Bayesian ROC plot (Fig. 2f).

In the final calibration and validation models the cut-off point, which optimizes presence and absence, was 0.4. Both modes were similar according to accuracy measures (Table 5), with correct classification rates of 92% and 89%, and misclassification rates of 10% and 11%, respectively. The Kappa statistic (Kappa = 0.80 and 0.78, respectively) indicated that the agreement of the models was excellent. The good performance of the final model can also be identified by the AUC value received from the validation model (0.958 ± 0.017, ($P < 0.001$).

4. Discussion

4.1. Selection of the variables

The selection of the variables by the models cannot be assumed to imply a causal effect between the habitat and bird distribution (Austin et al., 1996; James and

Table 5
Measures of classification accuracy for the final models (calibration and evaluation models)

Measure	Calculation	Values in calibration model $N = 50$	Values in validation model $N = 110$
Prevalence	$(a+c)/N$	0.52	0.50
Overall diagnostic power	$(b+d)/N$	0.48	0.50
Correct classification rate	$(a+d)/N$	0.92	0.89
Sensitivity (positive cases correcty classified)	$a/(a+c)$	0.88	0.89
Positive predictive power	$a/(a+b)$	0.92	0.89
Specificity (negative cases correctly classified)	$d/(b+d)$	0.91	0.89
Negative predictive power	$d/(c+d)$	0.88	0.89
False positive rate	$b/(b+d)$	0.08	0.10
False negative rate	$c/(a+c)$	0.11	0.10
Misclassification rate	$(b+c)/N$	0.10	0.11
Odds ratio	$(ad)/(cb)$	84.30	66.69
Kappa statistic	$[(a+d)-((a+c)(a+b)+(b+d)(c+d))/N]/[N-(((a+c)(a+b)+(b+d)(c+d))/N)]$	0.80	0.78
(Normalized Mutual Information)	$[-a.ln(a)-b.ln(b)-c.ln(c)-d.ln(d)+(a+b).ln(a+b)+(c+d).ln(c+d)]/[N.lnN-((a+c).ln(a+c)+(b+d).ln(b+d))]$	0.46	0.49

N is the total number of cases ($a+b+c+d$), a: true positive; b: false positive; c: false negative; d: true negative.
Cut-off point: 0.4.

McCuloch, 2002). Nevertheless, in this study, the habitat variables that were used in the analyses were chosen as having ecological significance for nest site selection by the black vulture. This resulted in very similar selection of habitat variables by the univariate analyses and logistic regression models. This suggests that these variables were the most important for nest-site selection and could thus be used as predictors of their nesting sites. The building of an independent model for each subgroup of habitat variables, and the compilation of these using Bayesian statistics, resulted in the inclusion of all of these important factors in the final model.

Different sets of variables dominate nesting habitat selection at different spatial scales (Pereira and Itami, 1991). According to our independent model results, terrain variables were the most important at the overall landscape level, while vegetation characteristics dominated at a finer resolution. At the nest site level, it seems that mature pines are important for the black vulture, as all nests were made on such trees. The separation of samples at this level was great (AUC = 0.978). In contrast, regarding the vegetation-type model, the separation of samples at the landscape level was less prominent (AUC = 0.869). Vegetation modelling showed that black vultures may not be confined to pure pine forests only, but could also nest in mixed pine-oak stands or in broadleaf forests with isolated mature pines. In Spain, pines are also used in the Sierra de Guadarrama, in Alto Lozoya and in Valle de Iruelas (Fargallo et al., 1998; Atienza et al., 2001; Donazar et al., 2002), but in Sierra Morena oaks are used exclusively (Torres-Esquivias and Arenas, 1996) and in Sierra Pelada oaks used as the main nest tree (Donazar et al., 2002). These results suggest that the key priority for the black vulture is the occurrence of mature nest-trees, and not the type of nest-tree or the surrounding forest.

4.2. Geomorphology

Geomorphologic factors seem to represent the most important category of habitat characteristics for various animal species, especially in areas of highly variable terrain (Pereira and Itami, 1991). According to the geomorphologic model, nest sites were situated on steep slopes and high altitudes. Some of these findings are similar to those reported from central and southwest Spain (Fargallo et al., 1998; Atienza et al., 2001; Donazar et al., 2002). The nesting preference for sparsely vegetated areas with steep slopes seems to be adaptive, as such areas provide better foraging opportunities and protection from predators (Hiraldo and Donázar, 1990; Fargallo et al., 1998). Slope is one of the most important factors affecting nest site selection by the black vulture at Dadia. The black vulture starts breeding in February, when northeast cold winds prevail (Adamakopoulos et al., 1995; Vlachos et al., 1999) and an avoidance of northern exposures would be expected. Exposure was not an important factor in the univariate test at any scale, although the significance of the avoidance of northern orientation increased with the scale. These results could be explained by the fact that most black vulture nests are situated in an extensive internal valley, where particular microclimatic conditions are not greatly affected by the strong northern winter winds. On a larger scale, the effect of exposure could be greater, and the tendency of the black vulture to nest at particular exposures might be checked using information from historical nesting sites in the wider area, outside the limits of the reserve. Unfortunately, this information is lacking.

4.3. Disturbance

The black vulture is considered sensitive to disturbance (Tewes, 1996; Poirazidis et al., 1997; Fargallo et al., 1998) and the avoidance of roads and villages has been documented in other studies (Atienza et al., 2001; Donazar et al., 2002). Human presence in the study area is not intense. Most activities and infrastructure have already existed for many years. Habitations, basic paved roads and agricultural land have not been transformed during the last few decades to an extent that could have affected black vulture breeding, except the forest road network (unpaved roads) which has expanded in the buffer zone especially after 1980.

Although the mean distance of nests from human settlements was considerable (5338 m $\pm$ 1368), which suggests avoidance of disturbance, a significant difference was not detected in the comparison with the random samples (4850 m $\pm$ 2538). We found similar results with the mean distance from agricultural fields (nest sites: 2371 $\pm$ 879 and random sites: 1635 $\pm$ 1796). These results, however, do not necessarily mean that these factors could never affect the breeding of black vultures. It is more likely that human presence does not affect vulture nesting merely because habitations are situated peripherally to the forest (Fig. 1), far from the nesting areas, and human infrastructures occupy only 0.76% of the study area (Poirazidis, 2001). In addition, the steep hills, where most breeding sites occur, discourage the development of human infrastructures and activities in these places.

Black vultures have been reported to breed either in loose colonies or as isolated pairs (Cramp and Simmons, 1980). The use of GIS and maps showing nest site occurrence probabilities indicated that the area suitable for nesting in Dadia reserve reflects the observed nest spacing patterns.

5. Management implications

In 2002 a new LIFE project (administered by WWF-Greece in collaboration with the local authorities) was initiated to improve the reserve's raptor habitats and the thorough management of its black vulture population. The results of this study could be useful for improvements in management of this species.

The results of this study identified some key habitat descriptors, which can be used for the prediction of black vulture nesting sites in the Dadia reserve in the future This is very important for planning habitat conservation. The inclusion of these results in forest management plans will minimize the conflict between forest exploitation and vulture conservation.

Our model suggests that the optimal nesting habitat is mature trees surrounded by openings or with low height vegetation located in steep slopes. This specific vegetation type results from forest fires in the past. The preservation of this microhabitat of the nest sites with the management of the young vegetation around the nests should be carefully examined. As this management activity involves intensive human activity, special care should be taken regarding timing and methods (Donazar et al., 2002).

The final probability map for the occurrence of nest sites shows that much of the nesting habitat was included within the strict protection zones. Management measures enforced by the state are adequate for the conservation of the black vulture nesting habitat in this area. Such measures are: the prohibition of mature tree-cutting and hunting and strict control of access to avoid disturbance. The gradual canopy closure of the forest around the nest sites must be monitored periodically. Livestock grazing, a traditional activity not affecting the breeding of the black vulture, preserves forest openness and reduces the risk of fires (Poirazidis et al., 2002). Nevertheless livestock raising has considerably decreased, therefore development of this activity is desirable.

Apparently suitable breeding habitats, partly used by the vultures, also occur in the buffer zone, especially southwest of the largest core area. The buffer zone is very important for the conservation of the species, as it contains many potential suitable nesting habitats for the black vulture. Our study indicates that conservation of the species and management of these forest areas can coexist. Therefore, special care should be taken in the long-term management of these forests. Suitable nest trees that must be preserved are not only present in pine forests of the reserve but also in a much broader zone including mixed oak-pine and pure broadleaf forests. Logging activities and other disturbance must be restricted to the autumn period, and road access in significant parts of this area must be controlled using bars managed by the Forest Service.

The preservation of landscape heterogeneity, which contributes significantly for diversity, density, and richness of other raptors (K. Poirazidis, *unpublished data*; Bakaloudis et al., 1998; Sanchez-Zapata and Calco, 1999; Anderson, 2001), as well as for other taxa in the reserve (Grill and Cleary, 2003; Kati et al., 2003) have similar results for the presence of the black vulture in Dadia.

Future changes in the habitat suitable for the black vulture nesting are expected in the area due to human activities and natural causes. Such changes must be monitored within the framework of the Systematic Monitoring Plan that has recently been put into action in the Dadia Nature Reserve (Poirazidis et al., 2002). Our model could contribute to the prediction of the suitability of the black vulture habitats when necessary.

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