Comparison of nestsite selection patterns of different sympatric raptor species as a tool for their conservation

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Abstract

Comparison of nest–site selection patterns of different sympatric raptor species as a tool for their conservation.— In this study the nest–site selection patterns of four tree–nesting sympatric raptor species in Dadia National Park (Greece) were compared in order to provide a sound conservation tool for their long–term management in the area. The species studied were the Black vulture (*Aegypius monachus*), the Lesser–spotted eagle (*Aquila pomarina*), the Booted eagle (*Hieraaetus pennatus*) and the Goshawk (*Accipiter gentilis*). Twenty–six variables illustrating the landscape context and vegetation structure of nesting sites were analysed. Multivariate–ANOVA and Discriminant Function Analysis were used to test for significant differentiations in nest–site characteristics among the species. The species studied were initially differentiated by geomorphology and distance to foraging areas. Once these were determined their nesting areas were established according to forest structure. Our results indicate that forest management should integrate the preservation of mature forest stands with sparse canopy and forest heterogeneity in order to conserve suitable nesting habitats for the raptors. Specific conservation measures such as restriction of road construction should be implemented in order to protect the active nests and provisions should be made for adequate nesting sites for the Black vulture, which is sensitive to human disturbance.

Key words: Sympatric raptors, Discriminant analysis, Nesting habitat separation, Conservation guidelines.

Resumen

Comparación de los patrones de selección del lugar de nidificación de distintas especies rapaces simpátridas, como herramienta para su conservación.— En este estudio se han comparado los patrones de selección del lugar de nidificación de cuatro especies de rapaces simpátridas que construyen sus nidos en los árboles, en el Dadia National Park (Grecia), con el fin de obtener una buena herramienta de conservación para su gestión a largo plazo en esta zona. Las especies estudiadas fueron el Buitre Negro (*Aegypius monachus*), el Águila Pomerana (*Aquila pomarina*), el Aguililla Calzada (*Hieraaetus pennatus*) y el Azor Común (*Accipiter gentilis*). Se analizaron 26 variables que ilustraban el contexto paisajístico y la estructura de la vegetación de los lugares de nidificación. Se utilizaron el ANOVA multivariante y el Análisis de Función Discriminante para comprobar las diferencias significativas en las características de los lugares de nidificación según las especies. En primer lugar, las especies estudiadas se diferenciaron en cuanto a la geomorfología y la distancia a los lugares de alimentación. Una vez determinados ambos parámetros, se establecieron sus áreas de nidificación según la estructura forestal. Nuestros resultados indican que la gestión forestal debería integrar la conservación de zonas de bosque maduro con un dosel escaso y la heterogeneidad forestal, para conservar hábitats de nidificación adecuados para estas rapaces. Deberían tomarse medidas específicas de conservación tales como la restricción de construcción de carreteras, para la protección de los nidos activos y se debería proveer de lugares adecuados para la nidificación del buitre negro, que es muy sensible a la presencia humana.

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Palabras clave: Rapaces simpátridas, Análisis discriminante, Clasificación de hábitats de nidificación, Pautas de conservación.

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Introduction

Because they are at the top of their food chain, raptors are considered biologically important, environmentally sensitive (Olendorff et al., 1989) and indicators of the health of the ecosystem (Newton, 1979; Donázar et al., 2002; Sergio et al., 2005). Their unfavourable conservation status has attracted public interest (BirdLife International, 2004) and they can act as a conservation flagship (Simberloff, 1998).

The identification of suitable habitats, habitat use and the ecological demands of sympatric species (e.g. Titus & Mosher, 1981; Reynolds et al., 1982; Kostrzewa, 1989; Restani, 1991; Moorman & Chapman, 1996; Selas, 1997; Katzner et al., 2003) should be taken into consideration in the decision–making process in order to reduce conflict between raptor conservation and forest management (Olendorff et al., 1989; Niemi & Hanowski, 1997; Penteriani et al., 2001; Donázar et al., 2002). Such an approach could contribute to safeguarding against the long–term degradation of the protected raptor species' habitats.

Dadia–Lefkimi–Soufli National Park (hereafter Dadia NP) in North–eastern Greece has a high biodiversity value and a particularly high number of breeding raptor species (Poirazidis, 2003b). However, timber exploitation practices over the last decades have decreased forest diversity, and have also altered the stand structure and the size class composition of the forests, thus affecting raptor nesting sites both temporally and spatially (Adamakopoulos et al., 1995; Poirazidis et al., 1996).

In this study a comparison was made of the habitat selection patterns of four forest–dwelling and tree–nesting sympatric species whose precarious situation calls for special consideration within the overall Dadia NP management plans. These species were: i) the Black vulture (*Aegypius monachus*), a colonial, globally threatened species (SPEC 1) with Dadia NP hosting the last breeding population in the Balkans (Skartsi & Poirazidis, 2002; Skartsi et al., in press); ii) the Lesser–spotted eagle (*Aquila pomarina*); and iii) the Booted eagle (*Hieraaetus pennatus*), both with an unfavourable conservation status as well as a declining population trend in Europe, including Greece (SPEC 2) and iv) the Goshawk (*Accipiter gentilis*), which despite enjoying a safe conservation status (BirdLife International, 2004) has a special preference for mature forests (e.g. Reynolds et al., 1982; Block et al., 1994; Kenward, 1996) and can act as a value indicator for the forests in Dadia NP. The breeding population of all four species in Dadia NP ranges from 20 to 25 pairs and different food habits have been observed (Hiraldo, 1976; Cramp & Simmons, 1980; Veiga, 1986; Widen, 1987; Vlachos & Papageorgiou, 1996; Toyne, 1998).

The aims of this study were to investigate: i) the intra–specific and inter–specific distribution patterns of the four raptor species; and ii) the differences in nesting site selection patterns in order to integrate these findings into a long–term forest conservation management plan to improve the birds' conservation status.

Methods

Study area

The study area is situated in the Evros Prefecture, in North–eastern Greece (40° 59'' to 41° 15'' N, 26° 19'' to 26° 36'' E). In 1980 the area was declared a nature reserve and in 2003 a National Park. It constitutes a forest complex extending over 432.86 km^2, including two strictly protected zones (core areas) that cover a total of 72.93 km^2 (fig. 1). Elevation ranges from 20 m to 640 m (above sea level) and the climate is sub–Mediterranean (for details see Poirazidis et al., 2004). The study area is characterised by the presence of extensive oak and pine forests (74.5%) and includes a variety of other habitats such as cultivations (8.3%), pastures and forest openings (9.2%), creeks and stony hills.

Raptor survey and nest sites

Systematic surveys were conducted during the years 1999 and 2001 in order to locate the occupied breeding territories and active nests, using the onset of the breeding season as a starting point for each species. This period ranged from February (for the Black vulture) until late May. Additional information for Black vulture nesting sites was collected within the framework of a systematic monitoring plan of Dadia NP (implemented by WWF Greece; Skartsi & Poirazidis, 2002). Nest–site characteristics were only measured at the active nest sites found in 2001. Territory mapping (Poirazidis, 2003b) suggests that the sample represents about 80% of the local populations of the four species. However, for the estimation of the nearest neighbouring nest distances the total breeding population was used. In this case, when nest sites could not be found in active territories in 2001, those from previous years were used.

Collection of nesting habitat data

A total of 25 variables were measured to describe nest–site characteristics. They were classified into two groups, describing the horizontal (topographical–landscape) and vertical (vegetation) structure of the nesting habitat (table 1). In the horizontal dimension, variables included geomorphologic measures as well as nest site distances from sources of potential disturbance and from environmental characteristics (Mosher et al., 1987). Variables were calculated using ArcGIS software (ESRI), on the basis of a recent (2001) GIS map of the study area (Poirazidis, 2003a). The geomorphologic variables, altitude, slope and aspect were created using the Spatial Analyst exten-

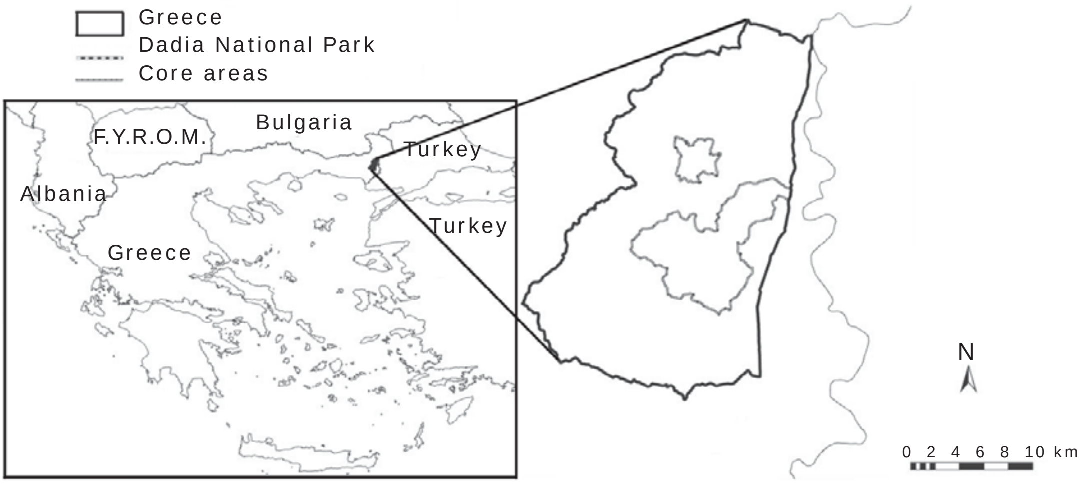

Fig. 1. Map of the study area.

Fig. 1. Mapa del área de estudio.

sion of the ArcGIS. Aspect was transformed into north/south and east/west components using cosine and sine, respectively. In the vertical dimension, variables describing nest–tree and stand structure were collected in the field at the end of the breeding season after the nestlings had fledged to avoid disturbance. All of these variables were measured in a circular area of 0.1 ha (radius 17.85 m) centered at each nest site (Selas, 1997). Tree diameter at breast height (DBH) was measured to the nearest cm using callipers, while tree and canopy heights were measured using Vertex III equipment (Haglof, Sweden). Mean canopy cover and height of the canopy were estimated visually by averaging the measurements of four canopy cover estimates (facing north, east, south and west) around the nest–sites.

Statistical analysis

Nesting site density was estimated using the nearest–neighbour distance method (NND) (Newton et al., 1977). The regularity in nesting site spacing was tested with the G–statistic, which was 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, where values close to 1 (> 0.65) indicate a uniform distribution of nests (Brown & Rothery, 1975). Ripley's K–function analysis was performed to analyze the nest pattern distribution.

Normality of the variables was tested using the Kolmogorov–Smirnov test. Subsequently, box–plots were checked for each habitat variable and for each raptor species for the effect of extreme values. All variables of distances and tree–numbers in all diameter classes were transformed into square roots. The variable "canopy cover", being a percentage, was arcsine–transformed. The variables "number of trees in diameter class 36–48 cm" and "number of trees in diameter class 48–80 cm" were normalized when combined in one category. To prevent multi–colinearity, the variables were tested with Variance Inflation Factor (VIF) Analysis (Quinn & Keough, 2002). Variables with a tolerance value < 0.1 or a VIF > 10 were removed from the analyses (Bowerman & O'Connell, 1990). In order to reduce the colinearity among the explanatory variables, a Pearson product–moment coefficient (r) was computed between all pairs of variables that remained from the VIF analysis and one variable was eliminated from pairs with r greater than 0.6 (Green, 1979). The decision as to which variable was to be retained was based on the results of a one–way ANOVA, and was that with the greatest among–group variance (McGarigal et al., 2000). In addition, a principal component analysis (PCA) of habitat variables was carried out to examine whether it was appropriate to substitute the original variables with a reduced set of component variables.

Univariate one–way ANOVA models were performed to check for significant differences ($p < 0.05$) in each of the remaining variables both in their linear and their quadratic format, followed by *Post–Hoc* tests to locate between–species differences. Further, the variables that were significant in the ANOVA were used in a multivariate analysis to test for inter–specific differences in the nesting habitat selection among species. MANOVA was used to check for significant differences in nesting habitats among the species and Discriminant Factor Analy-

Table 1. Nesting habitat variables measured at raptor nest sites.

Tabla 1. Variables del hábitat de nidificación, medidas en los lugares que anidan las rapaces.

Variable	Description
Horizontal level (Topographical–Landscape variables)	Estimated from GIS at the nest site
Geomorphological variables	
Elevation (m)	Elevation of the nest site (0.1 ha)
Slope (degrees)	Degrees Slope of the nest site (0.1 ha)
Aspect (sine)	Orientation of the nest site, expressed as deviation from the east
Aspect (cosine)	Orientation of the nest site, expressed as deviation from the north
Disturbance variables	
Distance from villages (m)	Distance to the nearest village
Distance from other settlements (m)	Distance to the nearest inhabited building
Distance from paved roads (m)	Distance to the nearest asphalted road
Distance from unpaved roads (m)	Distance to the nearest forest road
Distance from agriculture land (m)	Distance to the nearest farmland (extensively or intensively)
Ecological variables	
Distance from forest edge (m)	Distance to the nearest open habitat
Distance from main steams (m)	Distance to the nearest main stream
Distance from local steams (m)	Distance to the nearest local stream (included all the streams)
Distance from summer water ponds (m)	Distance to the nearest water body on July (measured in 2001)
Distance from rocky area (m)	Distance to the nearest rocky area
Vertical level (Tree–Stand variables)	Estimated in the field at the nest site
Nest–tree characteristics	
DBH (cm)	Diameter at breast height of the nest tree
Height of Tree (m)	Height of the nest tree
Nest Height (m)	Height of the nest above the ground
Stand structure characteristics (0.1 ha)	
Total number of trees (> 8 cm)	Total number of trees in the nest (0.1 ha)
Number of trees in diameter class 8–20 cm	Number of trees in diameter class 8–20 cm in the 0.1 ha plot
Number of trees in diameter class 22–34 cm	Number of trees in diameter class 22–34 cm in the 0.1 ha plot
Number of trees in diameter class 36–48 cm	Number of trees in diameter class 36–48 cm in the 0.1 ha plot
Number of trees in diameter class 50–80 cm	Number of trees in diameter class 50–80 cm in the 0.1 ha plot
Mean DBH in plot (cm)	Mean diameter at breast height in the 0.1 ha plot
Canopy height (m)	Mean height of the tree canopy in the 0.1 ha plot
Canopy cover	% of the ground in the 0.1 ha under the cover of the canopy

Table 2. Density and nearest neighbouring intraspecific and interspecific distances (mean values in m ± SD) of nesting places of the species studied. G–values in bold format and range of distance values are given in parenthesis.The mean nearest heterospecific distance of one species to another must be read below the species' name at column headings at the row representing the crossing point with the species of interest: [a] Number of active territories; [b] Territorial pairs / 100 km^2.

Tabla 2. Densidad y distancias intraespecíficas e interespecíficas del vecino más próximo (valores medios en m ± DE) de los lugares de nidificación de las especies estudiadas. Los valores G se expresan en negrita y el rango de los valores de las distancias entre paréntesis. La media de la distancia heteroespecífica más próxima de una especie a la otra debe leerse debajo del nombre de la especie en los encabezamientos de las columnas en la hilera que representa el punto en que se cruza con la especie de interés: [a] Número de territorios activos; [b] Parejas territoriales / 100 km^2.

	Black vulture (n[a] = 25)	Lesser spotted eagle (n = 19)	Booted eagle (n = 20)	Goshwak (n = 25)
Black vulture N[b] = 5.8	646 ± 464 **0.48** (279–2,460)	4,617 ± 2,319 **0.63** (1,566–10,985)	3,387 ± 2,531 **0.37** (489–10,481)	3,449 ± 2,154 **0.48** (182–10,085)
Lesser spotted eagle N = 4.4	3,162 ± 969 **0.83** (1,566–4,608)	2,285 ± 1,646 **0.45** (648–7,056)	2,525 ± 2,032 **0.34** (583–6,179)	2,800 ± 2,103 **0.32** (48–6,173)
Booted eagle N = 4.6	1,773 ± 682 **0.75** (489–3,189)	1,598 ± 1,000 **0.54** (524–4,471)	3,416 ± 1,257 **0.78** (2,043–6,632)	1,645 ± 1,151 **0.33** (122–4,213)
Goshwak N = 5.8	2,166 ± 834 **0.71** (452–3,409)	1,428 ± 908 **0.48** (121–4,348)	1,329 ± 988 **0.31** (122–3,769)	3,061 ± 1,088 **0.79** (1,739–5,134)

Table 3. Results of one–way ANOVA's (*F values*) testing for significant differences of habitat variables among the four species studied: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Test were performed on the trasformed variables as described in Methods. Only significant variables are shown for conciseness of presentation; full table available on request from the corresponding author.

*Tabla 3. Resultados del test del ANOVA unidireccional (*valores F*) para las diferencias significativas de las variables del hábitat entre las cuatro especies estudiadas: * *p* < 0,05; ** *p* < 0,01; *** *p* < 0,001. Los test se realizaron sobre las variables transformadas como se describe en el apartado Métodos. Para una presentación más concisa sólo se muestran las variables significativas; la tabla completa puede solicitarse a los autores.*

Variables	
Geomorphological variables	
Elevation (m)	29.845***
Slope (degrees)	4.788**
Aspect (north)	2.837*
Distance variables	
Distance from human infrastructure (m)	8.140***
Distance from unpaved road (m)	9.555***
Distance from forest edge (m)	9.970***
Distance from local steam (m)	4.663**
Distance from rocky area (m)	5.669**
Nest–tree characteristics and stand structure characteristics (0.1 ha)	
Height of tree (m)	6.832***
Total number of trees (> 8 cm)	3.706*
Number of trees in diameter class 22–34 cm	5.441**
Number of trees in diameter class 36–80 cm	10.964***

ses (DFA) was used to evaluate a possible differentiation of species along axes and the contribution of variables to species segregation.

In order to fit a parsimonious model (using as few variables as possible) and to deal with the problem of small samples in relation to the available predictors (Williams & Titus, 1988), the data were subdivided into three homogeneous sets (geomorphology, distances from elements and nest tree–forest structure) so as to determine the smallest subset of predictors per set. Since in any multivariate method, the use of automatic stepwise procedures has been criticized (James & McCulloch, 1990; Quinn & Keough, 2002) in our study all possible combinations of predictors were fitted, selecting the best one based on the smallest value of Akaike information criterion (AICc) (Burnham & Anderson, 2002). The selected variables per model were consequentially combined in the final DFA (full model).

A common problem in ecology when working with rare animal species such as raptors is the small sample size as it does not allow for the use of an independent set of data to evaluate the final model. Therefore, a cross–validated approach was used, where each case was classified by the functions derived from all cases other than that particular case. Statistical analyses were performed using SPSS 11. All means are given ± 1 SE, all tests were two–tailed and the significance level was set at $p < 0.05$.

Results

Breeding density and spatial distribution of nesting sites

A total of 89 different active territories were surveyed in 2001. The breeding density of the four species studied varied between 4.4 and 5.8 pairs/ 100 km^2 (table 2). Mean nearest– neighbour distances were shorter for the Black vulture than for the other species (table 2). Two groups of two species were distinguished by the G–test results. The first group included the Goshawk (G = 0.79) and the Booted eagle (G = 0.78) (with a regular nest distribution at all distances); whereas the second group included the Black vulture (G = 0.48) and the Lesser–spotted eagle (G = 0.45). Spacing distribution for the Black vulture showed a clear clustering pattern due to colonial behaviour but solitary nesting was also observed (fig. 2). Although a clumped nest distribution in the Lesser–spotted eagle was indicated on the larger scales by the G test, the nesting pattern showed a regular pattern on the smaller scales (Ripley *L(d)* < 600 m). The Black vulture nested at distances generally greater than other raptors between conspecifics. For the remaining three species, the nearest–nest site distances between heterospecifics were always shorter than those between conspecifics with a mean interspecific nesting distance greater than 1,300 m (table 2).

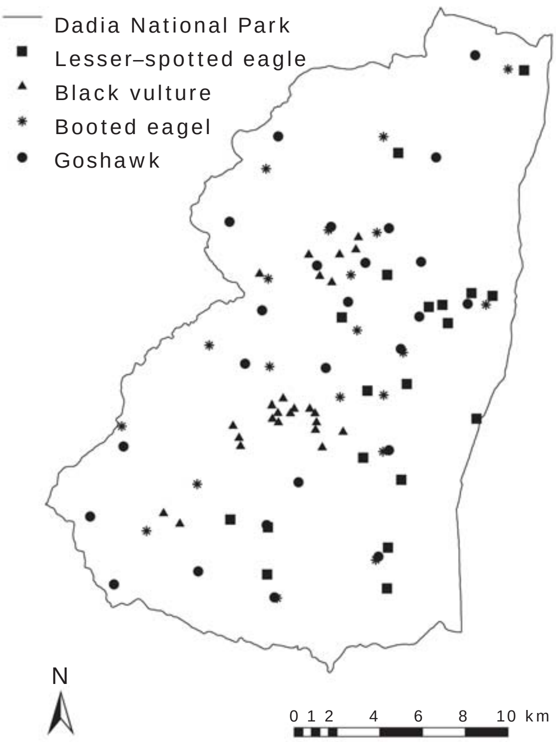

Fig. 2. Nest site distribution of the four raptor species studied in Dadia National Park.

Fig. 2. Distribución de los lugares de nidificación de las cuatro especies de rapaces estudiadas en el Dadia National Park.

Differentiation in nest–site selection among species

The initial 24 variables were used since PCA analysis could not reduce them to fewer component axes and the quadratic term of the variables was not incorporated for the improvement of the models. Two of the 24 variables as indicated by the VIF analysis and another four with a Pearson *r* value > 0.6 were removed from the sequential analysis.

From a dataset of 18 variables, twelve were significant in the ANOVA (table 3) (data of the *Post–Hoc* tests not included). The mean values (± 1 SE) for these variables plus the variable "distance from agricultural land" are shown in figures 3 and 4. With regard to the geomorphologic variables, Black vulture nests were situated at higher altitudes with steeper slopes, the Lesser–spotted eagle and the Goshawk nested in the lowlands and the Booted eagle in the intermediate areas. Black vulture nesting sites were father from the urban infrastructure and unpaved forest roads than the other species. The Lesser–spotted eagle nested in areas closer to forest openings and agricultural land compared with the other species. Regarding "distance from local streams",

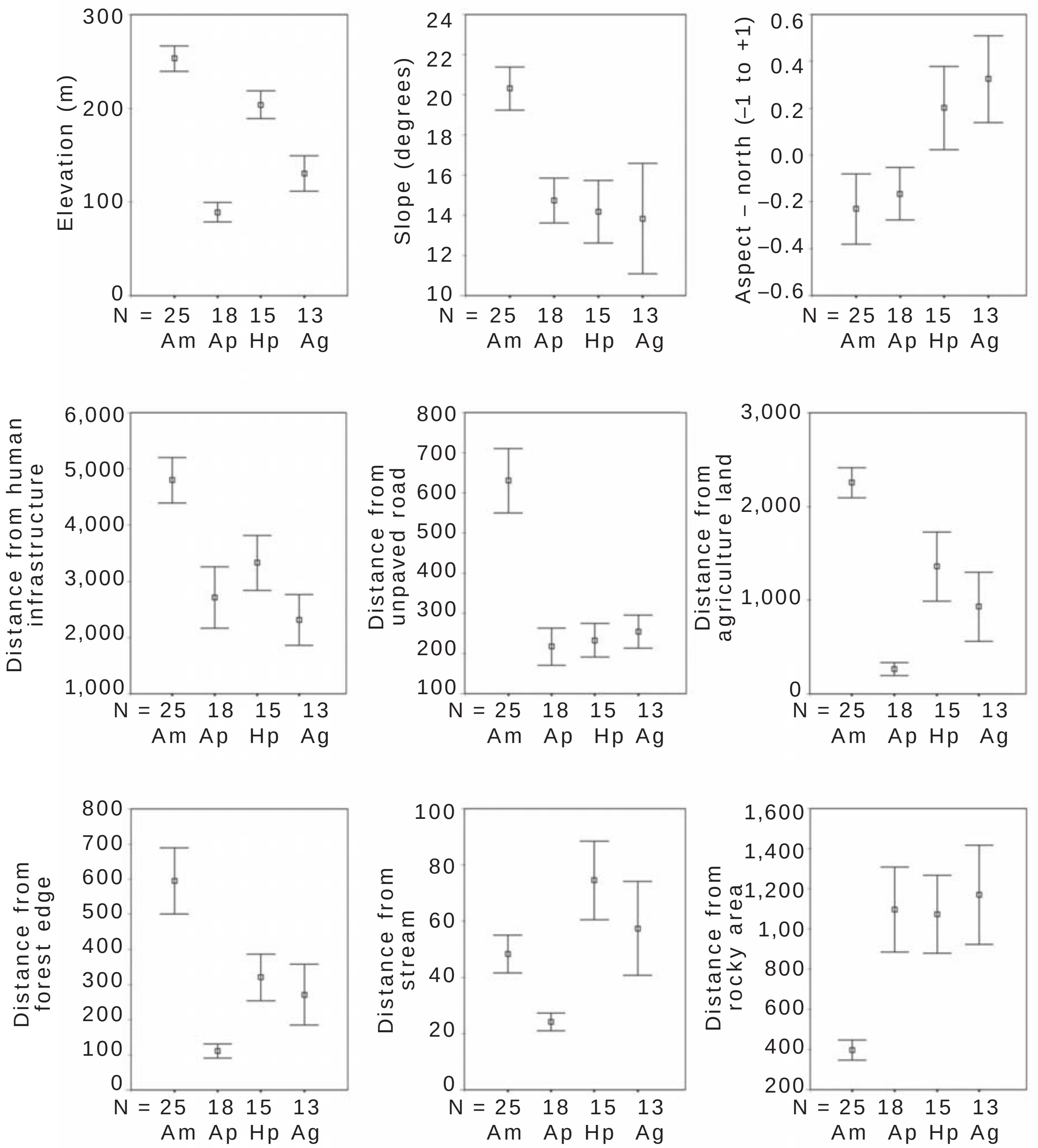

Fig. 3. Topographical–landscape habitat characteristics (mean values ± 1 SE) of the four raptor species in Dadia National Park: Am. *Aegypius monachus*; Ap. *Aquila pomarina*; Hp. *Hieraaetus pennatus*; Ag. *Accipiter gentilis.*

Fig. 3. Características topográfico–paisajísticas del hábitat (valores medios ± 1 EE) de las cuatro especies de rapaces en el Dadia National Park: Am. Aegypius monachus*; Ap.* Aquila pomarina*; Hp.* Hieraaetus pennatus*; Ag.* Accipiter gentilis.

a significant difference was detected only between the Lesser–spotted eagle and the Booted eagle, while "distance to rocky areas" differentiated the Black vulture from the Booted eagle and the Lesser–spotted eagle. The Goshawk and the Booted eagle nested in areas with more trees in the diameter classes 22–34 cm and 36–80 cm than the other two species. Finally, the Booted eagle and the Goshawk nested in taller trees than the Black vulture.

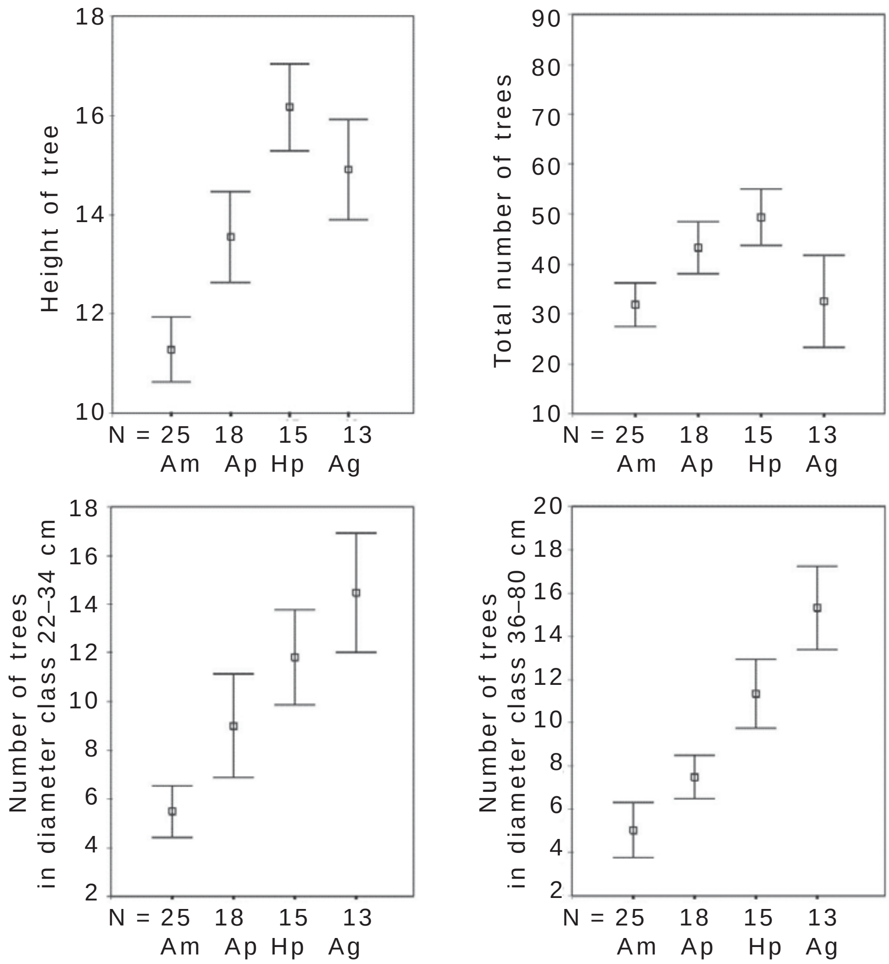

Fig. 4. Vegetation characteristics (mean values ± 1 SE) of the four raptor species in Dadia National Park. (For abbreviations see fig. 2.)

Fig. 4. Características de la vegetación (valores medios ± 1 EE) de las cuatro especies de rapaces en el Dadia National Park. (Para las abreviaturas ver la fig. 2.)

Discriminant function analysis

The overall difference in nest–site selection characteristics among raptors was highly significant (MANOVA, Wilks' lambda = 0.099, F = 4.957, $p < 0.001$). According to Akaike Information Criterion (AICc), seven variables were selected from the three homogeneous datasets and were included in the final DFA full model. The analysis of multi–colinearity showed that no variable had a VIF value of more than 1.9. This model created three significant discriminant functions that explained the differentiations among the species (table 4).

The first axis contributed to 67.5% of the total variance explained. The variables "elevation" and "number of trees in diameter class 36–80 cm" received the greatest relative weight on raptors' differentiation. This axis represents the transition from lower altitude areas with many old trees (chosen by the Lesser–spotted eagle and the Goshawk) to areas of higher altitudes with fewer old trees (chosen by the the Black vulture). The Booted eagles' scores overlapped considerably with the other species (fig. 5). These two variables also had the maximum F–value in the univariate analysis, being thus of primary importance in the differentiation of the four raptor species in Dadia NP (table 3). On the second axis (23.1% of the explained variance), the "number of trees in diameter class 36–80 cm" and "distance from local streams" were the most important variables. This axis represents a transition from forest areas with many old trees to forest areas with fewer old trees surrounding local streams. On this axis, all species overlapped considerably and differentiation was only found between the Booted eagle and the

Table 4. Results of the discriminant function analysis according to the overall full model of the nesting habitat

Tabla 4. Resultados del análisis de función discriminante, según el modelo global total del hábitat de nidificación.

	Function 1	Function 2	Function 3
Eigenvalue	2.291	0.784	0.321
Percentage of eigenvalue associated with the function (%)	67.50	23.10	9.50
Cumulative variance (%)	67.50	90.50	100.00
Canonical correlation	0.834	0.663	0.493
Wilks' Lambda	0.129	0.424	0.757
Chi–square statistic	125.978	52.723	17.118
Significance (degrees of freedom)	$P < 0.001$ (21)	$P < 0.001$ (12)	$P < 0.01$ (5)
Standardized canonical discriminant function coefficients			
Elevation	0.723	0.452	0.182
Aspect (north)	–0.254	0.104	–0.241
Distance from forest edge	0.278	0.036	–0.407
Distance from local stream	–0.005	0.576	0.161
Total number of trees	–0.029	0.219	0.928
Number of trees in diameter class 36–80 cm	–0.538	0.577	–0.279
Height of tree	–0.036	0.298	0.527

Lesser–spotted eagle (fig. 5). Finally, the third axis explained only 9.5% of the total variance with the most important variable being the "total number of trees" representing a transition from sparse to denser forest areas. On this axis all species overlapped considerably and most nests were situated in the centre of the axis (fig. 6).

The overall classification rate was 82.4% in the model. The most accurate classifications were found for the Black vulture, the Lesser–spotted eagle and the Booted eagle (91.7%, 88.9% and 78.6%, respectively), while a medium classification was found for the Goshawk (58.3%). In the evaluation model, the Lesser–spotted eagle and the Black vulture were reclassified correctly as in the original model but a misclassification occurred for the Booted eagle and the Goshawk, decreasing the overall rate to 77.9%.

Discussion

Spatial distribution of nests

Clumped raptor dispersions may arise due to the diminished suitability of breeding sites (Solonen, 1993) but also as a result of species sociality (e.g. colonial species such as the Black vulture). The Lesser–spotted eagle is known as being solitary and strictly territorial in other European sites, nesting 7–10 km apart, though nest distances of only 300–400 m do occur (Cramp & Simmons, 1980). In Dadia NP nest spacing of the Lesser–spotted eagle has quite possibly been defined by the proximity of foraging habitats such as mosaic habitats, arable fields and streams (Xirouchakis, 1999; Poirazidis et al., 1996) resulting in a closer proximity of nest sites. Territorial behaviour may have influenced nest spacing of the Booted eagle and the Goshawk in Dadia NP, as suggested also by the results of Booted eagles in Spain (Martinez et al., 2006) or of the near perfect nest spacing reported for Goshawks in Italy, France, Finland and Germany (Kostrzewa, 1991; Solonen, 1993; Penteriani & Faivre, 1997; Penteriani et al., 2001).

Species–specific habitat use is considered to be a basic prerequisite for the coexistence of different species of sympatric raptors (Newton, 1979; Bechard et al., 1990). In Dadia NP, in addition to different food habits, the raptors studied use open foraging areas through a temporal rotation (Xirouchakis, 1999; Vasilakis et al., in press), possibly minimizing conflicts among species in this way. Where nearest–nest site distances between heterospecifics were found to be shorter than those between conspecifics, interspecific competition for nesting habitat selection

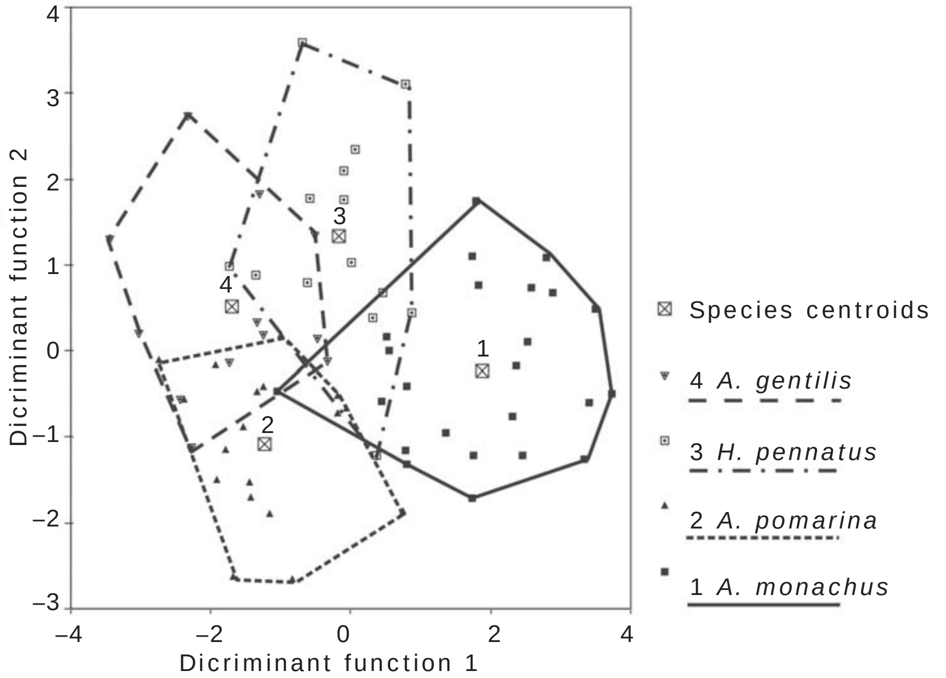

Fig. 5. Discriminant function analysis of nesting habitat characteristics of raptors in Dadia National Park (first and second axes).

Fig. 5. Análisis de función discriminante de las características del hábitat de nidificación de las rapaces en el Dadia National Park (primer y segundo ejes).

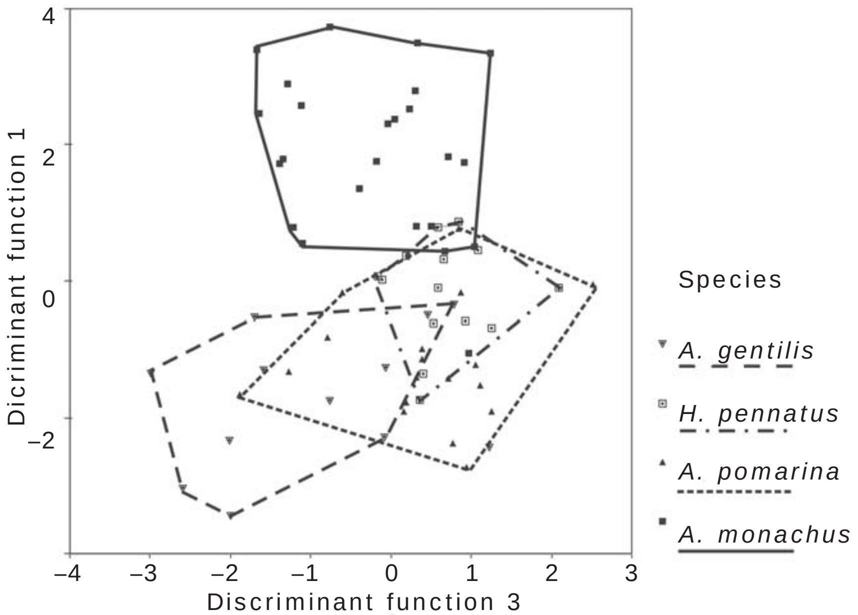

Fig. 6. Discriminant function analysis of nesting habitat characteristics of raptors in Dadia National Park (first and third axes).

Fig. 6. Análisis de la función discriminante de las características del hábitat de nidificación de las rapaces en el Dadia National Park (primer y tercer ejes)

may have had weak effects on their distribution. Studies of raptor assemblages in Kazakhstan (Katzner et al., 2003) and in Finland (Solonen, 1993) led to similar conclusions. The high interspecific G–values found in the Black vulture population were related more to the particularities of the bird's nesting habitat (higher altitudes, steep slopes) than to interaction with the other species. The Lesser–spotted eagle and the Goshawk avoided nesting at higher altitudes, possibly be due to the absence of favoured foraging habitats in these areas (Poirazidis et al., 2006).

Species differentiation

Sympatric raptors show a varying level of differentiation in nest–site characteristics (e.g. Titus & Mosher 1981; Janes, 1985; Kostrzewa, 1989; Bechard et al., 1990). Geomorphologic habitat characteristics seem to be the most important factors for a variety of animal species, especially in areas with heterogeneous landscape features (Pereira & Itami, 1991). The DFA analysis indicated that altitude was the primary variable distinguishing the Black vulture from the other species. The preference for slopes, as shown by the Black vulture at Dadia NP (see also Poirazidis et al., 2004), has also been reported in Spain and is generally interpreted as a response to the existence of slope winds that enhance flight energy during foraging (Donázar et al., 2002). The three remaining species were not markedly differentiated by slope since many of their nests were located either at middle altitudes or in the lowlands, which have fewer steep areas (Poirazidis, 2003a). Other studies of sympatric forest raptors have likewise reported that relatively few species select steep slopes for nesting purposes (Titus & Mosher, 1981; Speicer & Bosakowski, 1988; Selas, 1997).

Landscape heterogeneity greatly contributes to both the diversity and abundance of raptors (Sanchez–Zapata & Calvo, 1999; Anderson, 2001). Although a considerable level of overlapping was observed among species in the multivariate analysis, the Lesser–spotted eagle was partly differentiated from the other species, reflecting its choice for nesting in mosaic habitats dominated by forest edges, small portions of mature forests and local streams (Väli et al., 2004). There was a marked relocation in the altitudes where the Lesser–spotted eagles placed their nest platforms; for instance, while only 50% of the pairs bred below 100 m in the 1980s (Hallmann, 1979) in this study the number rose to 67%. This lowering in height could be the result of a trend showing a definite reduction in the availability of open and semi–open habitats, as has been recorded in the study area since the 1950s and which is largely due to land use changes (Triantakonstantis et al., 2006). These changes have occurred for socio–economic reasons and involve land abandonment as well as the decline of free–range livestock (Adamakopoulos et al., 1995), subsequently affecting the availability of the raptors' prey (Baker & Brooks, 1981; Preston, 1990). Such reduction in forest heterogeneity has most likely resulted in a decrease in the density of reptiles, an important food source for the Lesser–spotted eagle in our study area (Vlachos & Papageorgiou, 1996).

The Goshawks' choice for nesting at low altitudes (54% of nests below 130 m) —like the Lesser–spotted eagle— is probably also related to higher densities of prey available in the lowlands (Poirazidis et al., 2006). An association between breeding density and main prey distribution has also been reported in Italy, where a higher nest density of Goshawks at lower elevations rather than in the mountain zone was found (Penteriani, 1997), in Sweden where results showed that food was the main factor determining Goshawks' habitat use (Kenward & Widen, 1989), and in Spain for the Booted eagle where nesting sites were placed close to marshland with abundance of prey (Suarez et al., 2000).

The importance of the mature forest as a vital parameter in raptors' nesting habitat is suggested by the fact that the variable "number of trees in diameter class 36–80 cm" had the highest loading in the first and second axes of the DFA. Compared to the other species, the Black vulture nesting areas were characterized by the occurrence of large trees on steep slopes, emphasising the bird's most basic nest–site requirements. This is previously known from other studies (Donázar et al., 2002; Poirazidis et al., 2004). The Goshawks' preference for mature forest stands has also been reported elsewhere (e.g. Reynolds et al., 1982; Block et al., 1994; Kenward, 1996) and explains the importance of the nest stand structure as a proximate factor in the selection of nesting place (Penteriani et al., 2001). Mature forest stands offer many tall trees with open space around the trunks, favouring breeding and foraging activities of the Goshawk (Titus & Mosher, 1981; Kenward et al., 1993; Moorman & Chapman, 1996; Penteriani et al., 2001) and the Booted eagle (Suarez et al., 2000).

Anthropogenic disturbance did not seem to be an important factor in nest site selection of the raptors under study. It appears that many raptors can tolerate a low intensity and short duration of human disturbance near their nests when related to food availability but avoid areas of intensive activity (e.g. Andrew & Mosher, 1982; Anthony & Isaaks, 1989). Non–intensive cultivation and grasslands within the forests of Dadia NP comprise the raptors' foraging grounds and are vital elements for their conservation (Bakaloudis et al., 1998; Xirouchakis, 1999). Over the last 20 years the Lesser–spotted eagle has lost most of its traditional forest territories in the highlands, largely due to human activities of low intensity, and it is nowadays forced to nest in the lowlands where a mosaic of habitats prevails. An increase in the Lesser–spotted eagle's tolerance to the proximity of humans has also been observed in Estonia (Väli et al., 2004); and a similar situation with the

Booted eagles has been noted in Donãna, Spain (Suarez et al., 2000). In addition, the results of other studies clearly show that the distribution of Buzzards (*Buteo buteo*) and Goshawks (Speiser & Bosakowski, 1987; Kostrzewa, 1989; Penteriani & Faivre, 1997; Sergio et al., 2002) has been affected by intense persecution. Historically, the raptors in Dadia NP have not suffered persecution and they have been able to coexist with humans.

Differentiations in the conditions of the raptors' nesting habitat as presented in this work suggest that their division was partly due to different species–specific nest–characteristic demands. Habitat selection proceeds in a stepwise fashion where the various selection criteria are hierarchically ordered (Penteriani et al., 2001). The bird species studied were initially differentiated by geomorphology and distance to foraging areas. Once these criteria were determined breeding areas were subject to forest structure.

Management implications

A varied plan should be implemented to preserve the remarkable diversity of raptors in Dadia NP and certain management measures should be enforced. Conservation action must be directed primarily to the preservation of the mature forest stands in the area. Landscape heterogeneity could be preserved by the creation and/or restoration of small forest openings in areas of dense forest with controlled logging and perhaps with the reintroduction of herd grazing. Promotion of traditional land uses such as extensive agriculture and low–intensity livestock grazing would preserve a mosaic of habitats. This is particularly important for raptor species such as the Lesser–spotted eagle, priority targets for conservation (Meyburg et al., 2001). Such actions would also contribute positively to the biodiversity of other taxa in Dadia NP (Kati et al., 2004). For the Black vulture, apart from the preservation of tall trees on steep mountain slopes, advanced planning is needed to prevent the construction of forest roads near existing nest sites. Furthermore, any forestry activity should be strictly avoided in the vicinity of the Black vulture' nesting sites, especially during the breeding period (Morán–López et al., 2006). Nest–site protection measures should be applied throughout the whole area of the Dadia NP from the lowlands to the uplands, in both the cores and the intensively managed zones.

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