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MODELLING NESTING HABITAT PREFERENCES OF EURASIAN GRIFFON VULTURE *GYPS FULVUS* IN EASTERN IBERIAN PENINSULA

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Summary.—*Modelling nesting habitat preferences of Eurasian Griffon Vulture* Gyps fulvus *in eastern Iberian Peninsula.*

Aims: To apply modern habitat modelling techniques using generalized linear models approach to generate not only explicative but also predictive habitat suitability models. Ecological factors that could affect the species' nesting habitat preferences at two spatial scales, one referred to the colony as a sampling unit and another trying to reflect the landscape level, had been underlined.

Location: Castellón province, eastern Iberian Peninsula.

Methods: Occupied and unoccupied cliffs and 10x10Km U.T.M. squares were compared using univariate tests. A generalized linear model, employing logistic regression, was applied to explain and predict the occurrence of Griffon Vultures at two spatial scales. In order to select the most parsimonious model amongst a set of logistic models built with different explanatory variables, the Akaike´s information criterion (AIC) was performed. With the aim of testing the predictive performance of the previously selected models, the threshold-independent Receiver Operating Characteristic (ROC) plot was computed.

Results: 19 of 29 variables analyzed presented significant differences between occupied and unoccupied cliffs and between occupied and unoccupied squares. Colony parameters, climate, disturbance and vegetation variables, showed a good model performance in accordance with ROC plots and AUC. Despite geomorphological variables being significant on logistic model, model assessment techniques applied in this study suggested that they could not discriminate Griffon Vulture probability of occurrence by themselves. Trophic variables were not selected as good predictors by any method.

Conclusions: Model selection is useful for making inferences from field data. When coupled with Geographic Information System (GIS), habitat models generated by logistic regression approach can aid to develop occurrence maps displaying suitable habitat for nesting. This new applied technique has a broad potential application in conservation biology and management. Future research will involve the development of GIS-based predictive models to a finer scale of description and management application.

Key words: Akaike´s information criterion (AIC), cliff-nesting raptor, generalized linear models (GLM), Geographic Information System (GIS), habitat preferences, habitat selection, information-theoretic approaches, ROC plots.

Resumen.—*Modelización de las preferencias de hábitat de nidificación del Buitre Leonado* Gyps fulvus *en el este de la península Ibérica.*

Objetivos: Aplicación de técnicas modernas para modelizar la selección de hábitat utilizando el Modelo Lineal General para generar modelos no sólo explicativos sino también predictivos. Se han destacado los factores ecológicos que podrían influir en las preferencias de hábitat de la especie a dos escalas espaciales: a nivel de colonia y a nivel de paisaje.

Localidad: La totalidad de la provincia de Castellón, en el Este de la península Ibérica.

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Métodos: Tanto los roquedos como las cuadrículas U.T.M. de 10x10km se han comparado utilizando estadísticos univariantes. Se han aplicado modelos de regresión logística para explicar y predecir la probabilidad de aparición del Buitre leonado en las dos escalas espaciales consideradas. Se ha aplicado el Criterio de Información de Akaike con objeto de seleccionar el modelo más parsimonioso entre la serie de modelos obtenidos, construidos con diferentes variables independientes. El poder predictivo de los modelos previamente seleccionados se testó mediante el cálculo del estadístico independiente ROC.
Resultados: 19 de las 29 variables utilizadas mostraron diferencias significativas tanto entre roquedos como entre cuadrículas ocupadas y no ocupadas. Los parámetros de la colonia, climáticos, molestias y las variables de vegetación mostraron un buen ajuste de acuerdo con las curvas ROC y el índice AUC. Pese a que las variables geomorfológicas fueron significativas en el modelo logístico, las técnicas de validación aplicadas en este estudio sugirieron que por si solas no podían discriminar la probabilidad de aparición de la especie. Las variables tróficas no fueron seleccionadas como buenos predictores por ningún método.
Conclusiones: La aplicación de modelos de selección es una herramienta útil para hacer inferencias con datos de campo. Cuando se conjugan con Sistemas de Información Geográfica, estos modelos generados mediante regresiones logísticas pueden servir para desarrollar mapas de aparición de la especie mostrando los lugares más adecuados para la nidificación. Esta nueva técnica aplicada presenta una elevada aplicabilidad en Biología de la Conservación y en la gestión. La investigación futura irá encaminada al desarrollo de modelo predictivos basados en SIGs cada vez a una escala más precisa de aplicación.

Palabras clave: aves de presa rupícolas, preferencias de hábitat, Criterio de Información de Akaike (AIC), curvas ROC, Modelo Lineal General (MLG), selección de hábitat, Sistemas de Información Geográfica (SIG), Teoría de la información.

INTRODUCTION

Several habitat selection studies have been done on birds of prey in recent years, mostly referring to rare or endangered species (González *et al.,* 1990; Donázar *et al.,* 1993; Penteriani & Faivre, 1997; Fargallo *et al.,* 1998; Ontiveros, 1999; Carrete *et al.,* 2001; Ontiveros & Pleguezuelos, 2003; Martínez *et al.,* 2003). The relationship established between the species and their habitat is determinant when designing proper strategies for territory use and management, most of all in places where human interests and the vital needs of birds of prey come into conflict. Nevertheless, there are few studies directly related to spatial distribution and the factors concerning the Griffon Vulture (*Gyps fulvus*) nesting habitat selection (Donázar *et al.,* 1989, 1993; Donázar, 1993; Parra & Tellería, 2004), most of the existing papers focusing just on population census and reproductive parameters within different study areas (Donázar, 1987; Donázar & Fernández, 1990; Sarrazin *et al.,* 1995; Fernández *et al.,* 1996; Martínez *et al.,* 1997; Del Moral & Martí, 2001).

The Griffon Vulture has experienced a notable increase in its population in the entire Iberian Peninsula (Errando *et al.,* 1981; Donázar, 1987; Arroyo *et al.,* 1990; Del Moral & Martí, 2001, Parra & Tellería, 2004) without increasing its known distribution area in an even manner (Arroyo *et al.,* 1990; Urios *et al.,* 1991; Donázar, 1993; Olea *et al.,* 1999; Del Moral & Martí, 2001). To a lesser extent, it has also increased in France but not in the rest of the European range where it has mostly decreased (Tucker & Heath, 1994). At present it is not catalogued as a threatened species in the National Catalogue of Endangered Species of Spain, and the Iberian Peninsula houses the highest percentage of the European population, with 22.455 pairs in 1999 (Donázar & Fernández, 1990; Del Hoyo *et al.,* 1994; Del Moral & Martí, 2001).

The Griffon Vulture is a colonial cliff-nesting raptor that feeds on carrion coming mainly from human livestock exploitations and, to a lesser extent from wild ungulates which have died in the field (Donázar, 1993). Coloniality shown by many raptor species is an evolutionary strategy selected in consequence of the unpredictable distribution of food (Newton, 1979; Solonen, 1993; Donázar, 1993). The Griffon Vulture is a good example of this kind of spatial distribution pattern. However, it is necessary to take into account that the ecological factors affecting the spatial distribution pattern act in a differential way according to the considered scale (Wiens, 1989; Orians & Wittenberg, 1991; Levin, 1992; Bevers & Flather, 1999). There is a spatial hierarchy in the choosing of suitable places for breeding (Manly *et al.*, 2002), and there is a need for studies which take into account these scales to model the studied population (Carrete *et al.,* 2002a).

The development of new information-theoretic approaches has considerably changed the modelling techniques in the last three years (Rushton *et al.,* 2004). Most past papers were based on the formal hypothesis-testing approach (Penteriani & Faivre, 1997; Ontiveros & Pleguezuelos, 2000). Nowadays, this technique is being substituted by new multimodel inference approaches (Cabeza *et al.,* 2004; Engler *et al.,* 2004; Frair *et al.,* 2004; Gibson *et al.,* 2004; Jeganathan *et al.,* 2004; Johnson *et al.,* 2004; Poirazidis *et al.,* 2004) showing a new philosophy of modelling (Johnson & Omland, 2004; Rushton *et al.,* 2004).

The aim of this work is to apply modern habitat modelling techniques using a generalized linear models approach to generate not only explicative but also predictive habitat suitability models. The intention is to stress those ecological factors that affect the species' nesting habitat preferences at two spatial scales, one referring to the colony as a sampling unit and another trying to reflect the landscape level.

MATERIAL AND METHODS

Study area

The Griffon Vulture population studied is located in the Castellón province, in eastern Iberian Peninsula (Area = 6670 km^2; 39º42´-40º47´N; 0º32´-0º51´W, rank = 0-1814 a.s.l.; Fig. 1). It is characterised geomorphologically by being at the confluence of two great mountain ranges: the Iberian System, oriented NW-SE on the one hand, and the ENE-NE-orientated structures of the Catalánides, parallel to the coastline, on the other hand. This adds up to a subtabular and much folded peak line with calcareous material, mostly sedimentary, which favours the existence of many cliffs and faces suitable for the nesting of the Griffon Vulture. Climatologically, it belongs to the Mediterranean area, with an annual average temperature varying between 17ºC in the coastal area and 8-9ºC in the inner highlands. The annual average precipitation range is 400-900mm, with maximum values during the autumn and minimum values in summer, characterised by the great interannual irregularity of the Mediterranean weather (Quereda *et al.,* 1999). The vegetation is mainly made up by *Pinus spp., Quercus ilex* and Mediterranean bush forests (Folch *et al.,* 1984; Costa, 1986; Rivas-Martínez, 1987). In the less sheer areas irrigated crops, mainly citric, prevail on the shoreline, and unirrigated ones, mainly cereals, inland. The livestock industry is mainly porcine (92%), followed in importance by the ovine (4%) and the bovine (2%). The equine and caprine livestock is almost null (CAPA, 1999). Most farming is intensive, although in northern areas there still remains traditional extensive farm working.

Landscape and breeding colonies characterisation

The Griffon Vulture colonies were located during the 2002 and 2003 breeding sessions, giving a total of 112 pairs and 16 colonies in 2002 and 151 breeding pairs and 17 colonies in 2003. All areas where breeding by griffons was known were explored, as were cliffs of more

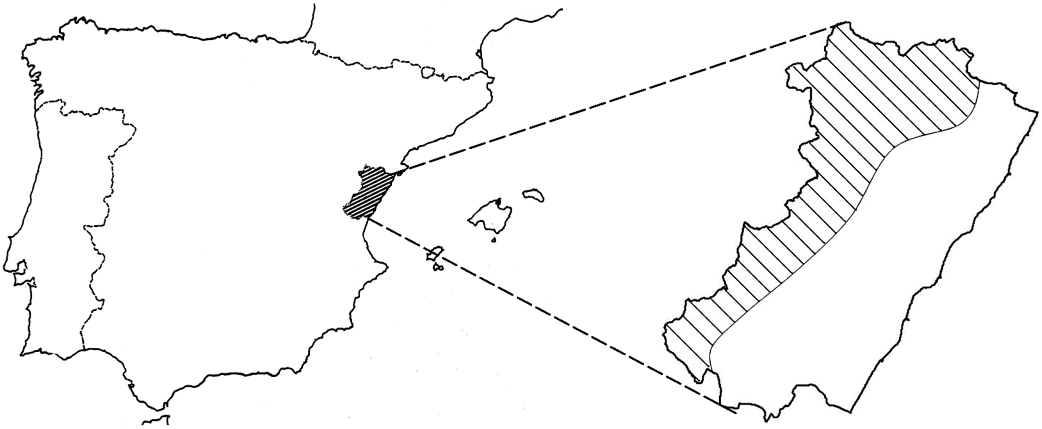

FIG. 1.—Left: Iberian Peninsula. Shaded area shows the study area. Right: Castellón province. Shaded area shows Griffon Vulture distribution area.
[Izquierda: península Ibérica. El área rayada muestra el área de estudio. Derecha: provincia de Castellón. El área rayada muestra el área de distribución del Buitre Leonado.]

than 40m height with suitable ledges that could be colonized by nesting vultures (Donázar, 1993). For the latter, 85% of the potential nesting cliffs were monitored, thus an occasional isolated reproductive pair may have been missed. Observations were made with a 20-60 × telescope during clear days at 300 m from nesting cliffs to avoid disturbance to vultures (Fernández *et al.,* 1996; Olea *et al.,* 1999). At least three visits were made to every reproductive colony. A preliminary search was made between 20 December and 10 January, in which nuptial flights and copulations were observed. The first visit was made between 15 February and 25 February, in which a sketch of the cliff that hosts the colonies was made, noting the locations of pairs and nests. The second visit was made between 20 March and 5 April to confirm the presence or absence of the previously detected pairs, the existence of new nests, and the newly-hatched chicks. The third visit took place between 20 April to 10 May to monitor the development of previously detected chicks and the presence of new hatchings. Finally, a fourth visit was made in the period between 20 May and 25 June. Those cliffs where the species was not detected during the first two visits were not visited subsequently (Martínez *et al,.* 1997, Del Moral & Martí, 2001).

A cliff was considered as a colony if it was occupied by at least two pairs and was at least 1000 m away from its closest neighbour, according to the methodology used in the species' 3rd Spanish National Census (Del Moral & Martí, 2001).

The province was divided into 89 U. T. M. 10x10 km squares, 13 of which contained at least one Griffon Vulture colony. In order to compare factors characterising breeding habitat preferences at landscape level, 13 unoccupied squares were randomly chosen. Since the Griffon Vulture is a species with a broad home range area (Donázar, 1993; Blanco *et al.,* 1996), the sampling unit was assigned to fit the U.T.M 10x10 km square to characterize the terrain. Besides, for a more detailed analysis on nest site selection, each of the breeding colonies ($n = 20$) was characterized. These colonies were used as a lower-level sampling unit by comparing with 20 unoccupied cliffs randomly selected.

In order to avoid overparametrization (Edwards, 1985; Hobson *et al.,* 2000; Kirk *et* *al.,* 2001) and processing problems in multivariate analyses (Boutin *et al.,* 1998; Hobson *et al.,* 2000; Grand & Cushman, 2003), a colinearity analysis was made to prevent from redundancy in variables (Leamer, 1973; Ontiveros & Pleguezuelos, 2003). Initially, a total of 49 variables were taken, divided into six subsets: colony variables, climate, disturbance, geomorphologic, trophic, and vegetation. These variables were tested for multi-colinearity based on the Variance Inflation Factor (VIF) analysis (Montgomery & Peck, 1982). This method holds that variables with a tolerance values less than 0.1 or a VIF larger than 10 are removed from the analysis (Bowerman & O´Connell, 1990). Therefore, only 29 variables were included in the analysis and are detailed in Table 1.

Preliminary statistical analysis

Preceding nest habitat modelling (colony-level variables and landscape-level ones), a Kolmogorov-Smirnov normality test (Sokal & Rholf, 1981) was applied. The variables “linear distance from side to side of the cliff hosting the colony” and “habitants in the four municipalities nearest to the colony” were normalized by natural logarithmic transformation (Edwards, 1985; StatSoft Inc., 1998). Occupied and unoccupied cliffs were compared (Table 2). Quantitative variable were compared with t-Test. Categorical variables were analyzed with χ^2 test. Likewise, landscape level parameters were also compared at Griffon Vulture occupied and unoccupied U.T.M. squares (Table 3).

Model development and model selection

Generalized linear modelling was applied to explain and predict the occurrence of Griffon Vulture at two spatial scales in the Castellón province. A GLM has three components: the linear predictor, a link function and an error structure. In species distribution modelling, logistic regression is considered to be the most appropriate approach for presence/absence field data and nowadays is a frequently employed method (Pearce & Ferrier, 2000). In logistic regression, the link function is logit and the error structure is assumed to be binomial (McCullagh & Nelder, 1989). Standard backward stepwise procedure was used, including at once all variables and removing non-significant ones stepwise by Wald´s test (Johnson, 1998; MacNally, 2000). If the Wald statistic was significant then the parameter was included in the model. In each step the criterion was $P = 0.05$ for entry and $P = 0.10$ for removal.

In order to select the most parsimonious model amongst a set of logistic models, the Akaike´s information criterion (AIC) was performed (Akaike, 1973). AIC is based on information-theoretic approaches to modelling (Gibson *et al.,* 2004), and it is considered a proper approach to select variables for inclusion or exclusion in models. It considers both fit and complexity, and allows multiple model comparisons simultaneously (Johnson & Amland, 2004), establishing a trade-off between predictive and explicative power. In our case, as the sample size divided by the number of variables is less than 40 (Burnham & Anderson, 2002; Johnson & Amland, 2004), a second-order Akaike´s information criterion corrected for small sample size (AIC_c) was computed for each model. To identify the best model inside each subset of variables (colony, climate, disturbance, geomorphologic, trophic and vegetation), the lower AIC_c value was considered, which includes the less number of significant variables (increasing predictive power without losing explicative power).

Model assessment

In order to test the predictive performance of the previously selected models, the Receiv-

TABLE 1

Variables used to characterise habitat and Griffon Vulture colonies.
[Variables empleadas para caracterizar el hábitat y las colonias de cría del Buitre Leonado]

Abbreviation	Variable description
Colony	
LCOL[d]	Linear distance in meters from side to side of the cliff hosting the colony [a]
AROQ	Height in meters of the cliff hosting the colony [a]
DMC	Linear distance in meters to the nearest cottage [a]
DNP	Linear distance in meters to the nearest urban centre [a]
DCOL	Linear distance in meters to the nearest Gyps fulvus colony [c]
DCAS	Linear distance in meters to the nearest paved road [a]
DCNA	Linear distance in meters to the nearest vehicle-allowing non-paved road [a]
SNM	Average altitude of the colony above sea level. [a]
Climate [b]	
TMAG	Average temperature in the hottest month (August)
TME	Average temperature in the coldest month (January)
TMA	Average annual temperature
PTA	Average Annual Rainfall (l/ m^2) (0: <400; 1: 400-500; 2: 500-600; 3: 600-700; 4: >700)
IH	Rain index (1: semi-arid; 2: dry; 3: sub-wet; 4: wet)
HAI	Annual sun hours (1 <2600; 2: 2600-2700; 3: >2700)
HIJ	Sun hours in July (1: >340; 2: 340-330; 3: 330-320; 4: <320)
HID	Sun hours in December (1: <140; 2: 141-145; 3: 146-150; 4: 151-155; 5>156)
Disturbance	
NKA	Paved kilometres in the sampling unit [c]
NKP	Non-paved, vehicle-allowing kilometres in the sampling unit [c]
DPH [d]	Habitants in the four municipalities nearest to the colony [e]
NNP	Population centres in the sampling unit [c]
LTE	Length in km of the high-voltage (>110Kv) and medium-voltage (>45Kv) electric wiring in the sampling unit [c]
Geomorphologic	
IA	Absolute steepness index [f]
AMC	Average altitude in the square (1: 0-400m.; 2: 400-800m.; 3: >800m.)[f]
CAR	One or more rivers or tributaries in the square (1: yes, 0: no)[c]
Trophic	
PGE	Presence of extensive livestock exploitations in the square (1: yes; 0: no)
ZAS	Presence of Supplementary Feeding Areas in the sampling unit (1: yes; 0: no)
Vegetation	
REG	Percentage of irrigated area (1: <10%; 2: 10-20%; 3: 20-30%; 4: >30%)[f]
CVEG	Percentage of forest vegetal coating (1: <10% square area; 2: 10-20%; 3: 20-30%; 4: >30%)[f]
INC	Percentage of burnt area between 1975 – 2000 (1: <10%; 2: 10-20%; 3: 20-30%; 4: >30%)[f]

[a] Valencian Cartographic Institute (Scale 1: 10 000). [b] Thematic Atlas of Valencian Region (Matarredona & Santos, 1991) [c] Military Cartographic Service of Spain (Scale 1: 50 000). [d] Variable normalized by natural logarithmically transformation because of not normal distribution. [e] Statistical National Institute (2002). [f] Ornithological Atlas of Valencian Region (Urios *et al.*, 1991) and own data.

[[a] Instituto Cartográfico Valenciano (Escala 1: 10 000). [b] Atlas Temático de la Comunidad Valenciana (Matarredona & Santos, 1991). [c] Servicio Cartográfico del Ejército (Escala 1: 50 000). [d] Variable normalizada tras la transformación por su logaritmo neperiano. [e] Instituto Nacional de Estadística (2002). [f] Atlas de las Aves Nidificantes de la Comunidad Valenciana (Urios et al.*, 1991) y datos propios.]*

TABLE 2

T-test comparison between parameters recorded at Griffon Vulture-occupied and unoccupied cliffs (both *n* = 20) in Castellón province.
*[Test t para la comparación de las variables obtenidas en los roquedos ocupados y no ocupados por el Buitre leonado en la provincia de Castellón (*n* = 20 en ambos casos)]*

	Occupied cliffs [Roquedos ocupados]		*Unoccupied cliffs [Roquedos no ocupados]*	
Variables [a]	*Mean [Media]*	*SD [Desviación típica]*	*Mean [Media]*	*SD [Desviación típica]*
LNLCOL ***	6.8	0.95	5.5	1.01
AROQ *	116.5	72.42	68.8	53.38
DMC **	737.5	402.06	1260.2	689.93
DNP $^{\text{n.s.}}$	3712.1	1772.29	3124.9	1517.01
DCOL **	7011.9	6171.39	14832.5	10061.37
DCAS $^{\text{n.s.}}$	1440.8	1490.60	1373.8	1029.83
DCNA $^{\text{n.s.}}$	374.6	328.63	386.3	371.79
SNM **	852.5	174.53	672.9	201.48

[a] Abbreviations defined in Table 1. **P* < 0. 05; ***P* <0.01; ****P* < 0.001; $^{\text{n.s}}$ Non-significant
[[a] Acrónimos definidos en la Tabla 11. *P *< 0. 05;* **P *<0.01;* ***P *< 0.001;* $^{\text{n.s}}$ *No significativo]*

er Operating Characteristic (ROC) plot was computed. This is a threshold-independent approach in the assessment of logistic regression models. The use of this method has increased extensively in recent years (Manel *et al.,* 1999; Pearce & Ferrier, 2000; Osborne *et al.,* 2001; Luck 2002b; Suárez-Seoane *et al.,* 2002; Gibson *et al.,* 2004). The ROC curve is a plot of true positive cases (sensitivity) against corresponding false positive cases (1 – specificity) across a range of threshold values (Fielding & Bell, 1997). The area under the ROC function (AUC) varies from 0.5 to 1, where the former corresponds with model discrimination not better than random, and the later for a model with perfect discriatory ability (Fielding & Bell, 1997; Pearce & Ferrier, 2000). In example, an AUC value of 0.7 means that 70% of the time the model will correctly distinguish between two cases. The AUC ± SE (standard error) was displayed, and it was based on a non-parametric assumption (Manel *et al.,* 2001).

All calculations were performed using SPSS version 11.5 for Windows (SPSS Inc., 1999).

RESULTS

Colony level

Except “LCOL”, all variables were normally distributed. Five of the eight variables were significantly different between cliffs occupied by Griffon Vultures and unoccupied ones (Table 2). The mean values of “DNP, DCAS and DCNA” did not differ. The variables related to colony size (“LNLCOL and AROQ”) were higher in occupied cliffs than in unoccupied ones. The “average altitude over sea level” was higher for occupied cliffs. The best logistic regression model identified “LNLCOL”, distance to the nearest cottage, distance to nearest colony, and average altitude over sea level as the most parsimonious predictive variables (χ^2 = 37.384; df = 4;

TABLE 3

Comparison between parameters recorded at Griffon Vulture-occupied and unoccupied U.T.M. squares (both $n = 13$) in Castellón province.

*[Comparación de los parámetros obtenidos en las cuadrículas U.T.M. ocupadas y no ocupadas por el Buitre leonado en la provincia de Castellón (*n *= 13 en ambos casos)]*

	Occupied squares [Cuadrículas ocupadas]		*Unoccupied squares [Cuadrículas no ocupadas]*	
	Mean [Media]	*SD [DT]*	*Mean [Media]*	*SD [DT]*
Climatic variables				
TMAG [a, n.s.]	20.7	2.62	22.1	2.99
TME [a, **]	4.5	1.20	7.2	2.34
TMA [a, ***]	11.9	1.36	14.5	2.23
PTA [b, **]	3.0	0.58	2.2	0.80
IH [b, **]	2.7	0.63	1.9	0.56
HAI [b, n.s.]	1.9	0.28	2.1	0.64
HIJ [b, n.s.]	1.7	0.75	2.2	0.80
HID [b, **]	1.7	0.86	3.2	1.54
Disturbance variables				
NKA [a, **]	23.1	12.52	38.9	12.82
NKP [a, ***]	58.2	27.28	150.4	59.02
LN_DPH [a, *]	5.3	2.52	7.5	1.54
NNP [a, n.s.]	2.4	1.56	2.6	1.19
LTE [a, n.s.]	3.0	4.20	9.3	10.76
Geomorphologic variables				
IA [a, **]	17.5	3.13	11.8	5.28
AMC [b, **]	2.8	0.60	1.7	0.86
CAR [b, n.s.]	0.5	0.52	0.3	0.48
Trophic variables				
PGE [b, n.s.]	0.7	0.48	0.5	0.52
ZAS [b, n.s.]	0.2	0.44	0.1	0.28
Vegetation variables				
REG [b, *]	1.0	0.00	1.5	0.88
CVEG [b, ***]	3.6	0.77	1.6	0.87
INC [b, *]	1.1	0.28	1.8	1.09

[a] *t*-Tests; [b] Chi-square; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; [n.s] Non-significant. Abbreviations defined in Table 1.

[[a] Tests de la t; [b] Ji-cuadrado; *P *< 0.05;* **P *<0.01;* ***P *< 0.001;* [n.s] *No significativo. Acrónimos definidos en la Tabla 1]*

P <0.001; Table 4). The ROC plot (Fig. 2a) indicated an AUC = 0.925 ± 0.049 (P < 0.001).

Landscape level

Climate variables

All variables followed the normal distribution. In the univariate comparison with random selected U.T.M. squares, five variables showed a significant difference (Table 3). The average temperature of the coldest month, the average annual temperature, the average annual rainfall, the rain index, and the sun hours in December were different between occupied and unoccupied squares. The variables selected by the final logistic regression model (χ^2 = 25.286; df = 5; P <0.001) were: "TMA, HAI, and HIJ" (Table 4). The respective ROC plot (Fig. 2b) showed an AUC = 0.923 ± 0.061 (P < 0.001) with a good model performance.

Disturbance variables

The "DPH" parameter was normally transformed. Three of the five variables show differences between occupied and unoccupied squares (Table 3). Kilometres of paved and non-paved roads were significantly lower in occupied squares as well as the number of human habitants in the surroundings. The only variable considered the best predictor for Griffon Vulture occurrence in the logistic regression (χ^2 = 17.616; df = 1; P <0.001) was the number of non-paved roads in the sampling unit, with an AUC = 0.846 ± 0.083 (P = 0.003; Fig. 2d).

Geomorphologic variables

All variables were normally distributed. The absolute steepness index and the average altitude in the square were significantly larger in occupied squares (Table 3). Despite the most parsimonious model (χ^2 = 17.133; df = 3; P <0.001) was significant including only the above-mentioned predictors, the AUC = 0.692 ± 0.107 (P = 0.096) was not significant (Fig. 2e), showing that discrimination ability was not higher than chance.

Trophic variables

The presence of livestock exploitations and the existence of vulture feeding stations did not show differences between occupied and unoccupied squares (Table 3). Both variables were normally distributed. No logistic regression model could be fitted for these subset of variables considered (χ^2 = 1.433; df = 1; P = 0.231).

Vegetation variables

The three parameters considered were normally distributed and displayed significant differences between occupied and unoccupied squares (Table 3). Occupied squares had less percentage of irrigated and burnt area, and larger forest coverage than unoccupied ones. The most parsimonious model included all the parameters considered (χ^2 = 33.271; df = 7; P < 0.001). The AUC was 0.962 ± 0.044 (P < 0.001; Fig. 2c).

DISCUSSION

Generally, the presence of large raptors relies mainly on the availability of suitable places for nesting, on the trophic availability and in the presence of other competitors (Newton 1979; Donázar 1993; Parra & Tellería, 2004). For a better understanding, an analysis of each subset of parameters separately at two spatial scales was considered.

TABLE 4

Results of small sample unbiased Akaike Information Criterion (AIC_c) model selection for the Griffon Vulture at each set of variables considered. Number of predictor variables (*K*), AIC_c differences (Δ_i).
*[Selección de modelos para el Buitre leonado según el Criterio de Información de Akaike para muestras pequeñas no sesgado, para cada subgrupo de variables considerado. Número de variables predictoras (*K*), diferencias* AIC_c *(*Δ_i*).]*

Nº	Model [Modelo]	-2log likelihood	K	AIC_c	Δ_i
	Cliff variables				
1	LNLCOL, AROQ, DMC, DNP, DCOL, DCAS, DCNA, SNM	15.351	9	39.351	9.518
2	LNLCOL, AROQ, DMC, DNP, DCOL, DCNA, SNM	15.377	8	36.022	6.189
3	LNLCOL, AROQ, DMC, DNP, DCOL, SNM	16.144	7	33.644	3.811
4	LNLCOL, AROQ, DMC, DCOL, SNM	17.253	6	31.798	1.966
5	LNLCOL, DMC, DCOL, SNM	18.068	5	29.833	0.000
6	LNLCOL, DMC, SNM	21.033	4	30.176	0.343
	Climatic variables				
1	TMAG, TME, TMA, PTA, IH, HAI, HIJ, HID	<0.001	9	29.251	8.588
2	TMAG, TME, TMA, PTA, IH, HAI, HIJ	<0.001	8	24.472	3.809
3	TMAG, TME, TMA, IH, HAI, HIJ	9.576	7	29.798	9.135
4	TMAG, TME, TMA, HAI, HIJ	9.856	6	26.277	5.614
5	TME, TMA, HAI, HIJ	10.195	5	23.195	2.532
6	TMA, HAI, HIJ	10.758	4	20.663	0.000
7	TMA, HAI	15.243	3	22.334	1.671
	Disturbance variables				
1	NKA, NKP, LNDPH, NNP, LTE	17.287	6	33.708	10.758
2	NKA, NKP, LNDPH, NNP	17.358	5	30.358	7.408
3	NKA, NKP, LNDPH	17.456	4	27.361	4.411
4	NKA, NKP	17.506	3	24.597	1.647
5	NKP	18.428	2	22.950	0.000
	Geomorphologic variables				
1	IA, AMC, CAR	17.533	4	27.438	1.437
2	IA, AMC	18.910	3	26.001	0.000
3	IA	25.619	2	30.141	4.140
	Vegetation variables				
1	REG, CVEG, INC	2.773	4	12.678	0.000
2	REG, INC	22.493	3	29.584	16.906
3	INC	30.012	2	34.534	21.856
4	CVEG	10.044	2	14.566	1.888

Models for trophic variables are not shown because of any model resulted significant in logistic regression analysis. Abbreviations defined in Table 1.
[No se muestra ningún modelo para las variables tróficas porque ninguno resultó significativo en el análisis de regresión logística. Acrónimos definidos en la Tabla 1].

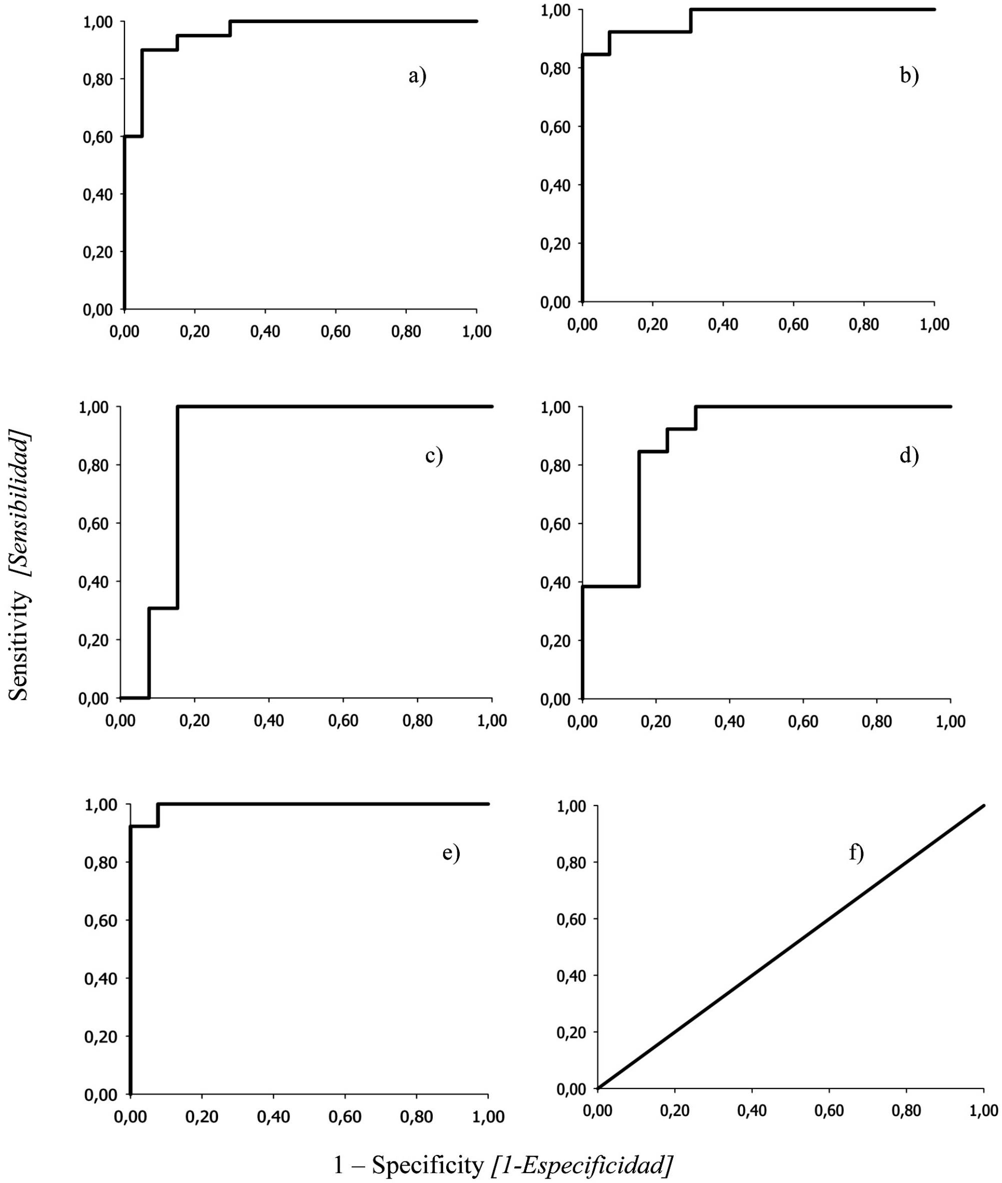

FIG. 2.—ROC plot for: a) Cliff model, b) Climate model, c) Disturbance model, d) Geomorphologic model, e) Vegetation model, f) Chance performance. Sensitivity: Number of positive sites correctly predicted/Total number of positive sites in sample. Specificity: Number of negative sites correctly predicted/Total number of negative sites in sample. For details see: Cumming (2000); Pearce & Ferrier (2000). *[Gráficos ROC para los modelos que incluyen variables: a) Roquedo, b) Climáticas, c) Molestias, d) Geomorfológicas, e) Vegetación, f) Probabilidad por azar. Sensibilidad: Número de casos positivos correctamente predichos /Número total de casos positivos en la muestra. Especificidad: Número de casos negativos correctamente predichos/Número total de casos negativos en la muestra. Para más detalles véase: Cumming (2000); Pearce & Ferrier (2000)].*

Colony level

At colony level, the probability of Griffon Vulture occurrence shows a positive relationship with variables related to cliff size, with the bigger the cliff, the greater the number of breeding pairs it can host for a colonial raptor. In addition, Griffon Vulture colonies are located at the highest altitudes over sea level which could be related with inner rough areas (Fig. 1). It is remarkable that the best logistic regression model involved the abovementioned parameters but not those related to direct human disturbance, such as the distance to the nearest urban centre and to the nearest paved and unpaved roads. It could indicate a relatively high tolerance to human presence on their settlements. In addition, the linear distance to the nearest cottage is significantly less in occupied than in unoccupied cliffs (Table 2). The good performance of the concluding model can be identified by the AUC value of 0.925 which implies a good discrimination power.

Landscape level

Climatic variables

Griffon Vultures seem to prefer coldest, wettest places with least sunshine in December when comparing with unoccupied squares. It is necessary to make clear that the study area is located in eastern Iberian Peninsula with a high Mediterranean influence. In the Castellón province, the coldest areas have an annual average temperature of almost 12ºC, not comparable with other inner peninsular areas where the species occupies more frosty places like the neighbouring province of Teruel with an 8-9ºC average. The most parsimonious logistic regression model also pointed to annual sunshine as a good predictor of Griffon Vulture occurrence. Despite the fact that the colinearity test was not significant for annual sunshine and annual temperature, climatic maps utilized to characterize the study showed that less sunny areas are related with coldest ones, which could be probably a possible explanation for this result. Since the Griffon Vulture begins its reproductive cycle in December (Donázar, 1993), it could be expected to show a preference for sunnier sites in spite of less sunny ones as multivariate comparisons showed.

Disturbance variables

Disturbance variables were taken as an antropic measure at landscape level. Univariate comparisons point out that human population density and kilometres of paved and non-paved roads displayed a negative relationship with Griffon Vulture occurrence. In the same way, the best logistic regression model chose kilometres of non-paved roads as the only significant predictor. Although *a priori* it could seem to be related with avoiding direct human influence that could be explained by the fact that inland countryside, where most Griffon Vulture colonies are located, have suffered an important human depopulation in the last 50 years with population densities of less than one inhabitant per square kilometre (Burriel & Salom, 2001).

Geomorphologic variables

The traditional technique of univariate comparisons revealed that the absolute steepness index and the average altitude in the square differed significantly between occupied and non-occupied squares. In the same way, the logistic regression model included these variables as the best predictors. However, model assessment techniques applied in this study suggested that they could not discriminate the probability of occurrence of Griffon Vultures by themselves. In the study area, Griffon Vulture occupies inner rough areas with an average altitude in the square over 800 metres, but there are still U.T.M. squares that remain unoccupied with similar geomorphologic characteristics. The availability of cliffs for nesting is held as the most relevant factor affecting the breeding density of the species (Donázar *et al.,* 1989; Donázar, 1993; Parra & Tellería, 2004). These results suggest that Castellón Griffon Vulture population might still have suitable habitat available for nesting.

Trophic variables

Univariate comparisons did not show significant differences between occupied and unoccupied squares along landscape level referred to trophic availability. In addition, no logistic regression model could be significantly fitted for the probability of occurrence of Griffon Vultures. In the study area, Griffon Vultures could take profit of trophic resources provided by man from the livestock industry (Urios *et al.,* 1991; Donázar, 1993) and vulture feeding stations (García-Ripollés *et al.,* 2004), but they also appear to search for food far from the breeding colonies.

Vegetation variables

The difference of percentage of forest cover between occupied and unoccupied squares was highly significant. In contrast, the percentage of irrigated and burnt areas was significantly higher in unoccupied areas. As mentioned above in disturbance variables, the greatest human depopulation suffered in inland Castellón province regions in the early 1950s also favoured an increase in the vegetable cover with the abandoning of the traditional farming practice. Hence, nowadays Griffon Vulture occurrence is associated with these less exploited depopulated areas of difficult access. The best logistic regression model included all three vegetation variables and the model performance was satisfactory when discriminating the probability of occurrence of Griffon Vulture.

Model evaluation and applicability

Knowing the ecological requirements of a species is an essential instrument when it comes to properly managing the lands where they survive, since appropriate knowledge will bring about their sustainable use and avoid unnecessary conflicts (Sánchez-Zapata & Calvo, 1999; Carrete *et al.,* 2002b; Rushton *et al.,* 2004). The most important aim of this study was to quantify the relationships between the Griffon Vulture occurrence and a subset of independent predictors. It was considered necessary to evaluate the predictive power of the models. This evaluation could be faced up by two main approaches: one considering an independent data set from other study area to evaluate, and another one by considering a single data set both to calibrate and to evaluate model predictions. The latter approach is generally tested by cross-validation, jack-knife, or bootstrap techniques (Guisan & Zimmermann, 2000).

This study area represents a small part of the global Griffon Vulture distribution area (Tucker & Heath, 1994; Ferguson-Lees & Christie, 2001). The relationships found in this study could not be extrapolated beyond the original rank of the variables considered. Hence, models should be tested in a wider range of situations allowing the definition of the range of applications for which model predictions are suitable (Guisan & Zimmermann, 2000).

Management implications

The Griffon Vulture's great geographic mobility is a major condition for the management and monitoring of its breedding places and has a buffer effect in the habitat selection procedures of the species (Donázar, 1993). Results obtained in this study could help wildlife managers to define important areas for vulture nesting. A GIS-based approach can aid in the development of occurrence maps displaying suitable habitat for nesting (Guisan & Zimmermann, 2000; Gibson *et al.,* 2004). This method permits the delimitation of protection or restoration areas where the occurrence of target species is more probable, and to point out places that still remain unoccupied but are suitable for nesting. Future research will involve such GIS-based predictive models development to a finer scale description and management application.

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