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DO DISTURBANCES IN SURROUNDING AREAS AFFECT A CORE POPULATION OF CANTABRIAN CAPERCAILLIE *TETRAO UROGALLUS* CANTABRICUS? THE CASE OF THE NATURAL RESERVE OF MUNIELLOS (ASTURIAS, NW SPAIN)

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SUMMARY.—*Do disturbances in surrounding areas affect a core population of Cantabrian Capercaillie* Tetrao urogallus cantabricus*? The case of the Natural Reserve of Muniellos (Asturias, NW Spain).*
Aims: The Cantabrian Capercaillie is an endemic subspecies which is declining over much of its range in the Cantabrian Mountains. The main aim of this paper is to test whether human disturbances in areas surrounding mature woodland patches affect more than habitat structure and composition a core population of this species in southwestern Asturias.
Locality: The Natural Reserve of Muniellos (Asturias, NW Spain).
Methods: In order to characterize currently occupied leks *vs*. random points and abandoned *vs*. occupied leks, we ran univariate (*U*-test) and multivariate (generalised additive models GAM) analyses, evaluating habitat features and human disturbances independently.
Results and Conclusions: GAM models based on disturbances were more discriminative than habitat pattern-composition models; similarly, models based on random points classified better the data than occupied *vs*. abandoned models. In all cases, models were highly accurate and relatively complex. Places selected by males as display areas were located at the core of larger patches of woodland exhibiting a higher relative richness of woodland types, at higher altitude and further from rivers than random points. These suitable areas supported less human disturbances, as they were sited farer from roads, paths, houses and recurrently burned areas than random points. Capercaillie disappeared from leks situated in rolling hills, at lower altitude, nearer to «pre-woodlands», under shrubs and pine forests. These sites were closer to houses, hunting sites and repeatedly burnt areas than occupied leks.
Key words: Breeding habitat selection, Cantabrian Mountains, Capercaillie, conservation, display areas, ecological modelling, fire, GAM, large scale.

RESUMEN.—*¿Afectan al Urogallo Cantábrico* Tetrao urogallus cantabricus *las molestias producidas por el hombre en el entorno de un núcleo bien conservado? El caso de la Reserva Natural de Muniellos (Asturias, NO España).*
Objetivos: El Urogallo Cantábrico es una subespecie endémica que está sufriendo una disminución en su área de distribución en las Montañas Cantábricas. El principal objetivo de este estudio era comprobar si las molestias producidas por el hombre en los alrededores de zonas de bosque maduro afectan por encima de la estructura del hábitat en la composición de un núcleo de esta subespecie en el suroeste asturiano.
Localidad: La Reserva Natural de Muniellos (Asturias, NO España).
Métodos: Para caracterizar los cantaderos (leks) ocupados por la especie *vs*. puntos al azar y los cantaderos abandonados *vs*. los ocupados, se realizaron análisis univariantes (prueba de la *U*) y multivariantes (GAM, modelos aditivos generalizados), evaluando las caracteristicas del hábitat y de las molestias humanas de forma independiente.

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Resultados y Conclusiones: Los modelos GAM basados en las molestias fueron más discriminates que los modelos basados en la composición del hábitat. De forma similar, los modelos basados en puntos al azar clasificaron mejor los datos que los modelos de cantaderos abandonados *vs.* ocupados. En todos los casos, los modelos fueron muy precisos y relativamente complejos. Los lugares selecionados por los machos para realizar sus cortejos estaban localizados en el corazón de grandes fragmentos de bosques y presentaban una mayor riqueza de tipos de especies de árboles, una mayor altitud y estaban más alejados de los ríos que los puntos al azar. Estas áreas propicias soportan una baja molestia por parte del hombre, al estar más alejadas de carreteras, pistas, casas y zonas recurrentemente quemadas que los puntos al azar. Los Urogallos desaparecen de cantaderos situados en colinas, a baja altitud, en las partes externas del fragmentos de bosque, en zonas de matorral y en bosques de pino. Estos sitios se situan más cerca de viviendas, de cotos de caza o de zonas repetidamente quemadas, con respecto a las arenas ocupadas.

Palabras clave: Selección del hábitat reproductor, Montañas Cantábricas, Urogallo, conservación, cantaderos, modelización ecológica, fuego, gran escala.

Introduction

The capercaillie *Tetrao urogallus* is a large grouse of western Paleartic boreal and montane forests. This bird has been declining over much of its range in central (Storch, 1995) and western Europe since the 1970s (Catt *et al.*, 1998; Moss, 2001), with a greater decline in females (Wilkinson *et al.*, 2002). In Spain, the breeding population has been estimated at 1878-1978 adults divided between two isolated subspecies, *Tetrao urogallus cantabricus,* living in the Cantabrian Mountains, and *T. urogallus aquitanicus*, living in the Pyrenees. Both are very demanding with respect to habitat quality: mostly selecting deciduous woodlands and pine forests, respectively (Canut *et al.*, 2003).

The Cantabrian Capercaillie *Tetrao urogallus cantabricus*, described by Castroviejo (1967), is an endemic subspecies, which is under special protection in Europe. The Regional Government of Asturias (NW Spain) has recently approved its Conservation Plan, which aims to avoid the main threats for the subspecies. However, measures adopted for its habitat conservation are not sufficient and the bird remains at risk of extinction. See Storch (2000) for a more detailed description of the species status.

In 1982, the number of male Capercaillies recorded in the Cantabrian Mountains was 574 (291 living in the province of Asturias; Del Campo & García-Gaona, 1983). During the last 20 years, this population has decreased dramatically by 60%. In the province of Asturias, the most recent counts, carried out by the regional Government in 2000 and 2001, showed a decline to 100 males, divided between two main nuclei (central-eastern and western Asturias). More recent studies point to the disappearance of the central population (Obeso & Bañuelos, 2003), which increases the isolation of the two remaining nuclei and the subsequent risk of extinction. The western nucleus is probably the best preserved and the most stable over the time (Obeso & Bañuelos, 2003). Habitat fragmentation, the recurrence of fire (probably the most severe environmental problem in the Cantabrian Mountains), hunting, cattle, predation, competition, tracks and mining are the main threats to the Cantabrian Capercaillie at population and local scales; loss of habitat (Obeso & Bañuelos, 2003; Canut *et al.,* 2003) and climate change (Moss *et al.*, 2001) appear to be the main risk factors at a global scale.

The Capercaillie is considered a good example of an «umbrella species», at least in terms of mountain avian biodiversity (richness and abundance; Suter *et al.*, 2002). In Muniellos, the core of our study area, Nores *et al.* (2003) recorded 73 bird species sharing the same habitat as the Capercaillie. Therefore, the conservation of this emblematic species may assure the preservation of all these other species.

The central aim of this paper is to test whether environmental disturbances (mainly caused by humans) in areas surrounding the well-preserved woodland patches of the study area affect the Capercaillie population. Conservation in 'islands' of suitable habitat is a very controversial but common policy. Some reserves represent an archipelago of surviving habitats, but they are often islands in a matrix of «developed» areas. This isolation can result in the risk of stochastic extinction (Farina, 1998). Antropogenic habitat deterioration and fragmentation not only leads to range contractions and extinctions, but may also have significant genetic and evolutionary consequences for surviving populations (Segelbacher *et al*., 2003). The study is focused in the core population of Muniellos, a natural integral reserve located in southwestern Asturias, where human activities are currently highly restricted (it was exploited for timber since the sixteen century until very recent times) and interaction with the surrounding area is unusual. This can be considered as a case of study of a population of Cantabrian Capercaillie living in a good quality habitat patch, where the bird status remains relatively stable. This patch is surrounded by a large disturbed area, especially affected by fire and mining, where other deciduous wood patches with a high conservation value still exist. Distance between fragments allows for dispersal movements (see Moss & Picozzi, 1994 for more information on forest patch management for maintaining Capercaillie populations). The aims of the manuscript are to (1) establish the environmental characteristics of the display areas (»leks») currently occupied by the species; (2) identify which variables explain why the birds abandoned display areas used in the past; (3) assess how disturbances and human activities (i.e. fire, cattle, mining, hunting) in neighbouring zones to the breeding areas can affect lek occupancy.

MATERIAL AND METHODS

Study area

The Integral Natural Reserve of Muniellos is located in southwestern Asturias (NW Spain, Fig. 1), among the municipalities of Ibias and Cangas del Narcea. The area under special protection since 1982 and has been recently been designated as a Biosphere Reserve. It covers an area of around 5500 ha. It contains one of the best preserved Atlantic deciduous woodlands in western Europe, the largest Iberian oak wood and the most important forest area in Asturias. Oak *Quercus petraea*, Birch *Fagus sylvatica* and White Birch *Betula pendula* are the dominant tree species. Other companion species include Yew *Taxus baccata,* Holly *Ilex aquifolium,* Filbert *Corylus avellana,* Rowan *Sorbus aucuparia* and Bilberry *Vaccinium myrtillus*. For a more detailed description of the study area see Díaz & Fernández-Prieto (1994), Fernández-Prieto & Bueno (1996), INDUROT (2000), and Nores *et al*. (2003).

Muniellos is a remote, undisturbed area, with few human infrastructures and has one of the lowest demographic densities in Asturias. The regime of visitors is restricted. All theses facts contribute to its preservation. However, Muniellos is affected by conservation problems due to its isolation within a disturbed matrix, where other deciduous wood patches with a high conservation value still exist, constituting the recently designated Natural Park of Fuentes del Narcea y del Ibias.

In order to investigate the effects of degradation in the surrounding areas on the breeding Capercaillie population, we selected a total area of about 50000 ha comprising the Reserve and its environs and distributed among the municipalities of Ibias, Cangas de Narcea and Degaña (Fig. 1).

Capercaillie display areas in the study area

In the Cantabrian Mountains, leks are mainly located at an average altitude of 1200-1450m (range 800-1600m), with north-northeasterly aspects, in oak or beech woods with 50-80% tree cover (Del Campo & García-Gaona, 1983). In order to characterize (both) the currently occupied and the abandoned leks in our study area, we gathered breeding data from the most recent census carried out by the Regional Government of Asturias during the years 2000 and 2001 (the study area was surveyed in 2000). This survey confirmed a total of 64 leks for this area (35 were occupied, 26 abandoned and 3 indeterminate). It is remarkable that 34.3% (n = 12) of these occupied leks occurred within the boundaries of the Reserve of Muniellos, which covers a tenth of the study area. However, it also contained 15.4% (n = 4) of the abandoned display areas.

Figure 2 shows the number of display areas/km^2 per hunting management category within the study area. As expected, we found significant differences (Chi= 23.95, df = 8, P < 0.001) in Capercaillie frequency for the four hunting categories: the greatest density of leks

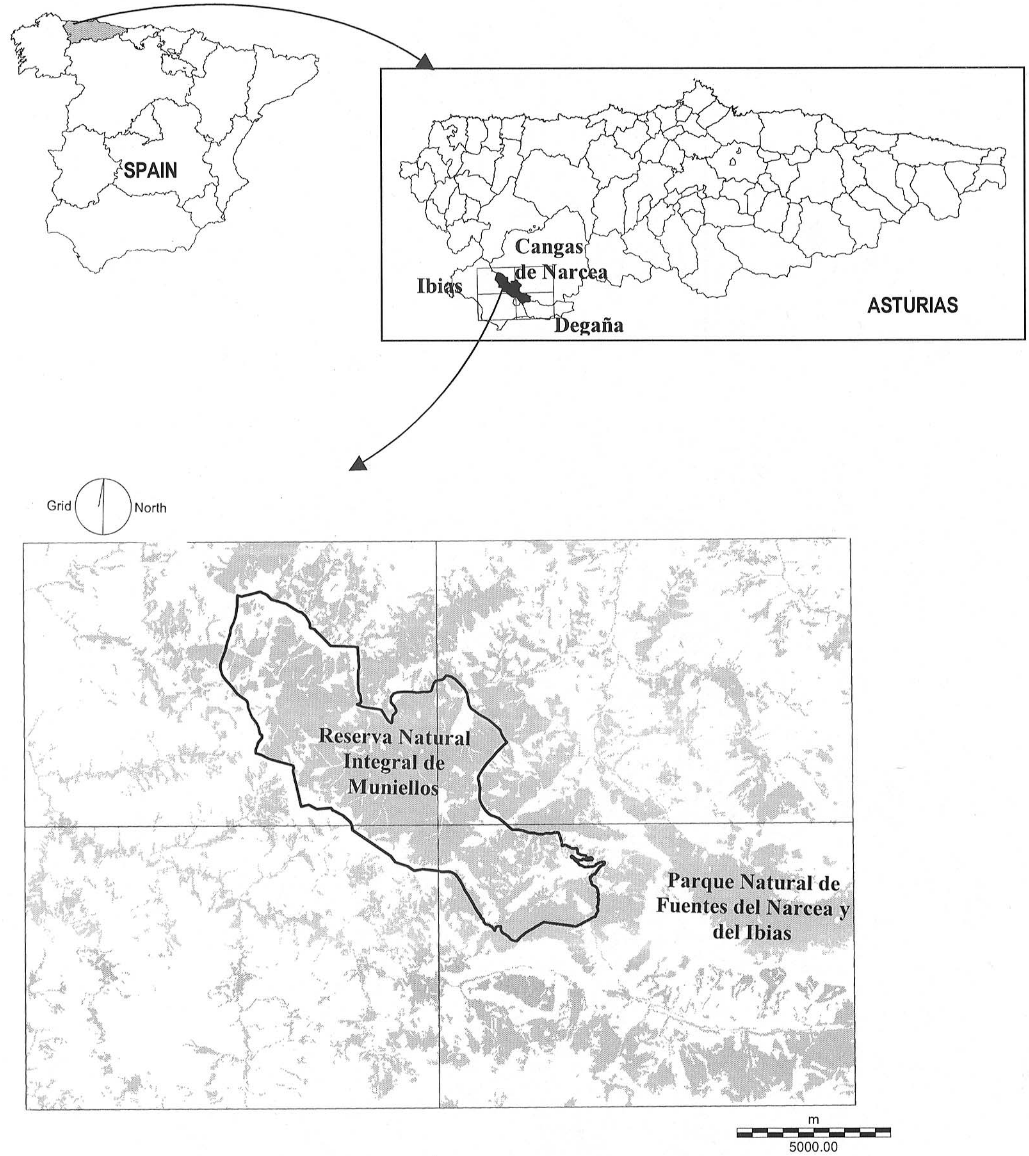

FIG 1.—Location of the study area. Grey patches represent deciduous forests.
[Localización del área de estudio. Las manchas grises representan bosques caducifolios.]

in use occurred in areas with more restricted hunting («Refugio de Caza»). All leks were abandoned in the more heavily exploited hunting category («Coto Regional de Caza»).

In the study area, lek sites were located in oligotrophic oak forests with birch (n = 15 and n = 10 for occupied and abandoned leks, respectively), oligotrophic beechwoods (n = 10 and n = 7), Orocantabrian altimontanous birch forests (n = 9 and n = 4) and oligotrophic tall shrub formations dominated by oak species (n = 1 and n = 1). Abandoned leks occurred also in heath formations (n = 4), which may have been affected by fire over the last two decades (see Díaz & Fernández Prieto, 1994; INDUROT, 2000).

For the subsequent analyses, we created three different data samples. (1) We used the occupied leks (n = 35) as «presences». (2) For «absences» we produced an equivalent random sample (n = 35) avoiding the areas in a radius of 200m around each UTM location for both occupied and abandoned leks. This is an estimation of the average size of the display areas in Muniellos, measured on 17 leks mapped by the Regional Government of Asturias in 1994 (the mean size was 12.45 ha, and the interval was 6.22-25.41). We also avoided non-forested and urban/altered areas (towns, mines, burnt zones, crops or meadows) because they are rejected by the species for breeding. (3) Finally, we analyzed the «abandoned» leks (n = 26). All data were overlapped on grids of 30 m resolution.

With the aim of validating the model, we collected a complementary sample of 17 locations within the boundaries of the Reserve of Muniellos, including both droppings and direct observations of males and females.

Environmental predictors

In order to identify the environmental variables which best explain the differences between (1) occupied *vs*. abandoned leks, and (2) occupied sites *vs*. random points, we measured 28 variables for each pixel of 30 m, relating to habitat composition and structure, and disturbances caused by human activities (Table 1). The majority of these data were transformed into quantitative variables: (1) as the distance from each site (occupied, abandoned or random) to the nearest habitat features; or, (2) as a context variable in a moving window of 7x7 pixels centred sequentially in each pixel (equivalent to 210x210 m, the lek average radius).

Vegetation was characterised using updated maps produced by INDUROT (Instituto de Recursos Naturales y Ordenación del Territorio, University of Oviedo) at a scale of 1:25000 (INDUROT, 2000). A digital terrain model was built at 30 m resolution for all topographic variables. Infrastructure data (roads and housing) were recorded at a scale of 1:10000 from the cartographic database of the Regional Government of Asturias. Mines were mapped using a combination of the 1:25000 thematic cartography from INDUROT updated using a LANDSAT TM image from 2001. Hunting management classes were obtained from a map of the Principado de Asturias at a scale of 1:400000. The multitemporal analysis carried out previously at INDUROT for detecting burnt areas in Asturias, using a series of Landsat-TM imagery (from 1984 to 2001), has allowed the analysis of the relevance of fire recurrence on the Capercaillie population since the last census at the beginning of the 1980s. These maps were constructed by applying the image difference method followed by a supervised classification of maximum likelihood. Fire detection models were validated using the perimeters of a sample of real fires obtained by GPS. The coincidence was always greater than 80%. The method is described in Recondo *et al.* (2003). Variables related to the density of cattle were obtained from a survey carried out in 1999 by the Office of Statistics of the Regional Government of Asturias (SADEI) at the scale of the parish (a land unit smaller than the municipality).

All the analyses were performed at 30 m resolution using IDRISI 32.2 (Eastman, 2000), Er-Mapper and ArcView GIS 3.2 (ESRI, 1999).

Statistical analysis

The variables involved in the analysis were checked for statistical normality using the Kolmogorov-Smirnov test. Mean values for variables discriminating between occupied leks *vs*. abandoned sites, and lek sites *vs*. random points were compared using the univariate non-parametric Mann-Whitney test (U-test) for independent groups. The single categorical variable considered (aspect) was analysed by means of a chi-square test.

In order to identify the environmental predictors which best discriminate between sites, we ran four different multivariate analyses using different sets of variables over a total pool of 27 quantitative predictors related to (both) habitat and human disturbances occurring in Muniellos and its surrounding area. We evaluated habitat and disturbances separately (1) to distinguish between occupied leks *vs*. random sites (models A1 and A2 respectively), and (2) to understand why leks have been aban-

TABLE 1

Twenty-eight variables analysed to typify habitat structure and composition, and human disturbances, to characterise the Capercaillie leks currently used *vs*. abandoned sites and random points
[Veintiocho variables analizadas para tipificar la estructura y composición del hábitat, así como las molestias humanas, para caracterizar los cantaderos utilizados por Urogallos actualmente vs. *sitios abandonados y sitios elegidos al azar.]*

Code	Variable
	Habitat structure and composition *[Estructura y composición del hábitat]*
DIVW7	Diversity of vegetation classes (H'= -Σ p ln (p); where p = proportion of each class in the 7x7 kernel, and ln = natural logarithm) (Turner, 1989). *[Diversidad de clases vegetación (H' = -Σ p ln (p); Turner, 1989)]*
WOODRICHW7	Relative richness of woodlands classes (R= n/n_{max} x 100; where n = number of different classes present in the 7x7 kernel, and n_{max} = maximum number of classes in entire image) (Turner, 1989). *[Riqueza relativa de clases de bosque (R= n/n_{max} x 100; Turner, 1989)]*
PATCHAREA	Patch area (ha). *[Área de la parcela (ha).]*
DECISHAP	Shape (area/perimeter; m) of each patch. Higher values indicate regular, round forms; lower values show irregular structures. *[Forma (área/perímetro; m) de la mancha. Valores altos indican regularidad o formas redondeadas y valores bajos indican estructuras irregulares.]*
EDGED	Distance to the woodland edge. *[Distancia al borde del bosque.]*
PREWOODD	Distance to the nearest «pre-woodland» (young forest previous to the climatic stage), where dominant tree species are *Betula pendula, Fraxinus excelsior, Ilex aquifolium, Sorbus aucuparia.* *[Distancia al pre-bosque más cercano, donde las especies dominantes son* Betula pendula, Fraxinus excelsior, Ilex aquifolium, Sorbus aucuparia.]
TALLBUSHD	Distance to the nearest tall shrub formation of *Quercus orocantabrica, Arbutus unedo, Salix* spp. *[Distancia a la formación más cercana de* Quercus orocantabrica, Arbutus unedo, Salix *spp.]*
BROOMD	Distance to the nearest broomland (*Cytisus* spp., *Genista florida* subsp. *polygaliiphylla*). *[Distancia a la formación de piornal y escobonal más cercana.]*
UNDSHRUBD	Distance to the nearest undershrub, mainly gorse, heath or furze (*Ulex europaeus, Erica* spp., *Genista hispanica* subsp. *occidentalis*., *Halimium umbellatum, Calluna vulgaris*). *[Distancia a la formación de brezal y/o tojal más cercana* (Ulex europaeus, Erica *spp.,* Genista hispanica *subsp.* occidentalis., Halimium umbellatum, Calluna vulgaris).*]*
MEADOWD	Distance to the nearest crop (cereal, fruit trees) and meadow. *[Distancia al campo de cultivo más cercano.]*
PASTD	Distance to the nearest pastureland. *[Distancia al pastizal más cercano.]*
PINED	Distance to the nearest pine forest. *[Distancia al pinar más cercano.]*
ROCKD	Distance to the nearest rocky. *[Distancia al roquedo más cercano.]*
RIVERD	Distance to the nearest river. *[Distancia al rio más cercano.]*
MDT	Altitude. *[Altitud.]*
SLOPE	Slope. *[Pendiente.]*
ASPECT	Aspect. Categorical variable: 1: N, 2: NE, 3: E, 4: SE, 5: S, 6: SW, 7: W, 8: NW. *[Orientación.Variable categórica: : 1: N, 2: NE, 3: E, 4: SE, 5: S, 6: SW, 7: W, 8: NW.]*
	Human activities and/or disturbances *[Actividad y/o molestias humanas]*
ROADD	Distance to the nearest asphalted and paved road. *[Distancia a la carretera más cercana.]*
UNMADED	Distance to the nearest unmade path. *[Distancia al camino más cercano.]*
HOUSED	Distance to the nearest town and isolated building. *[Distancia al pueblo o edificio aislado más cercano.]*
MINED	Distance to the nearest mining. *[Distancia a la mina más cercana]*
FIRE9899D	Distance to the nearest most recently (between 1998 and 1999) burnt area before the census. *[Distancia a la más reciente (1998-1999) área quemada antes del censo.]*
FIRE1D	Distance to the nearest burnt area 1 time during the period 1984-2000. *[Distancia al área más cercana quemada 1 vez entre 1984-2000.]*
FIRE2D	Distance to the nearest burnt area 2 times during the period 1984-2000. *[Distancia al área más cercana quemada 2 veces entre 1984-2000.]*
FIRE3D	Distance to the nearest burnt area 3 times during the period 1984-2000. *[Distancia al área más cercana quemada 3 veces entre 1984-2000.]*
FIRE45D	Distance to the nearest burnt area 4 or 5 times (1984-2000). *[Distancia al área más cercana quemada 4 o 5 veces entre 1984-2000.]*
HUNTD	Distance to the nearest hunting area. *[Distancia al coto de caza más cercano.]*
COWS100	Number of cows /ha (x 100). *[Número de vacas por ha (x 100).]*

doned during the last 20 years (models B1 and B2 respectively). We chose to run Generalised Additive Models GAMs (Hastie & Tibshirani, 1990) with binomial error structure and logit link, because this method provides a less restrictive modelling framework and better predictions than others as binary logistic regression (Pearce & Ferrier, 2000; Suárez-Seoane *et al.*, 2002) (see paragraph about model limitations in the Discussion). Including highly correlated variables in a model affects the robustness of the analysis. Therefore, multicolinearity among the predictors was avoided by calculating pairwise Spearman correlations. Variables showing correlations greater than 0.8 were excluded from the subsequent analysis, retaining the correspondent proxy variables. Data were not transformed, as this is not a requirement of this analysis. Cubic splines with four knots were fitted to each variable. Parsimonious models were generated using backwards selection with an F-value of 0.05 (Pearce & Ferrier, 2000) for the variable to remain in the equation. For each selected variable we tested whether the smoothed term was significant over a linear model and replaced non-significant smoothed terms with linear terms. Terms were then dropped one by one from the final equation and their contribution to the model assessed using a likelihood ratio test (Venables & Ripley, 1999). Outputs from the GAMs were produced using Idrisi 32.2 (Eastman, 2000) and consisted in a surface of probabilities (values 0 to 1) of presence/persistence (the method is described in Suárez-Seoane *et al.*, 2002).

We assessed the predictive performance of the final model through 10-fold crossvalidation. Data were divided into 10 groups drawn at random, then each group was dropped in turn and predictions were made for the excluded group based on the remaining 90% of data points (Verbyla & Litvaitis, 1989; Fielding & Bell, 1997). Both final and cross-validated models were assessed using the area under the curve (AUC) obtained by the receiver-operating characteristic plot method (ROC-plot; Beck & Shultz, 1986; Fielding & Bell, 1997), which is a convenient measure that does not require a threshold for presence and absence to be set (Zweig & Campbell, 1993) and mitigates artefactual effects (McPherson *et al.*, 2004). Finally, as a complementary method, the predictive performance of the models was estimated by external validation (*sensu* Harrell *et al.*, 2001), measuring the probabilities predicted by the models in a validation set of 17 field data recorded in the Reserve of Muniellos.

Data were analysed using SPLUS S-plus 2000 (Venables & Ripley, 1999) and its GRASP interface (Lehmann *et al.*, 2002, 2003), SPSS 11.5 (SPSS 2003) and IDRISI 32.2 (Eastman, 2000).

Results

Occupied leks vs. non-occupied (random) sites

According to the results of the *U*-test, occupied leks in Muniellos and the surrounding areas were located at the core of bigger and more regular patches of woodland, placed in more inaccessible areas (more inclined slopes at higher altitude), and further from open areas (as undershrubs or meadows), pines and rivers. These sites were farer from roads, unmade paths, hunting places and areas burnt once or twice during the last 20 years, than random points (Table 2). Differences in aspect (occupied leks were principally placed on northern sides: mode = 1, and random points had mainly northwestern orientation: mode=8) were significant for both samples ($\chi^2 = 18.6$, $df = 8$, $P = 0.02$).

The backwards-generalised additive method gave a picture of ideal sites for Cantabrian Capercaillie display during the breeding season, compared with random unoccupied places, as follows: core of larger patches of woodland exhibiting a higher relative richness of woodland types, at higher altitude and further from rivers than random points (model A1). Model A2 show that leks are located in undisturbed areas, farer from roads, paths, houses and recurrently burned areas, and closer to mines (this is obviously an artefact produced by the proximity of mines to the best preserved woodlands) than random points (Table 3).

Occupied leks vs. abandoned sites

The univariate analysis (*U*-test) showed that abandoned leks in the study area were situated at the border of smaller and more irregular fragments of forest, at lower altitude and closer to

TABLE 2

Comparison (means and standard deviations) between 27 quantitative variables measuring the habitat for display areas which are currently occupied, abandoned and random points. The table shows the significance of the Mann-Whitney test (U-test) for independent samples. See Table 1 for the meaning of the codes.

[Comparación (media y desviación típica) entre las 27 variables cuantitativas que miden el hábitat para cantaderos ocupados, abandonados o áreas al azar. La tabla muestra la significación de la prueba de Mann-Whitney (U-test) para muestras independientes.]

Code	Presence (*n*=35)		Random (*n*=35)		Abandoned (*n*=26)		*Occupied* vs. *random*	Occupied *vs*. abandoned
	X	*SD*	*X*	*SD*	*X*	*SD*	U-test	U-test
DIVW7	0.5	0.5	0.7	0.5	0.7	0.5	0.34	0.25
WOODRICHW7	1.2	0.9	0.9	1.1	1.1	0.9	0.10	0.65
PATCHAREA	9141.8	4803.3	4494.4	5112.4	5036.3	5520.1	**<0.001**	**<0.001**
DECISHAP	88.5	24.4	34.2	41.5	60.9	37.1	**<0.001**	**<0.001**
EDGED	153.1	114.6	31.7	43.0	79.7	83.0	**<0.001**	**0.01**
PREWOODD	2231.9	1263.2	2080.4	1402.3	1767.4	1538.9	0.32	**0.01**
TALLBUSHD	329.9	210.4	403.4	324.8	493.3	357.0	0.62	0.08
BROOMD	338.6	227.2	259.2	242.6	205.4	162.3	**0.05**	**0.01**
UNDSHRUBD	345.0	214.8	166.8	268.1	177.9	132.0	**<0.001**	**<0.001**
MEADOWD	1001.1	555.1	747.6	667.5	1071.1	552.3	**0.02**	0.58
PASTD	772.6	385.6	838.5	518.4	668.2	398.2	0.79	0.23
PINED	3747.3	2262.1	2465.6	1801.2	3208.8	2413.5	**0.01**	0.16
ROCKD	342.4	275.7	414.6	381.5	322.5	290.4	0.81	0.65
RIVERD	321.5	126.9	246.3	205.8	306.4	190.9	**0.01**	0.49
MDT	1373.1	118.7	1109.0	208.9	1270.4	139.1	**<0.001**	**0.01**
SLOPE	29.4	9.5	24.6	11.1	26.7	10.2	**0.04**	0.21
ROADD	1799.4	1053.0	1220.9	749.7	1304.8	1012.0	**0.01**	**0.01**
UNMADED	987.1	593.3	709.1	680.6	833.9	476.3	**0.02**	0.34
HOUSED	1194.0	630.1	977.4	649.1	911.0	338.4	0.23	0.12
MINED	3524.6	2078.3	4261.1	2828.7	4183.7	2967.6	0.39	0.52
FIRE9899D	2061.2	926.1	1693.8	1053.6	1538.2	943.9	0.07	**0.04**
FIRE1D	366.1	287.7	195.6	265.8	215.5	173.5	**<0.001**	**0.02**
FIRE2D	851.7	507.2	588.9	592.2	639.9	529.7	**0.02**	0.05
FIRE3D	1697.6	747.9	1328.6	1043.9	1378.4	990.2	0.06	**0.03**
FIRE45D	2631.9	908.8	2417.0	1275.6	2789.4	1211.9	0.32	0.49
HUNTD	4545.9	2383.8	2302.9	2871.0	3200.5	2524.7	**<0.001**	**0.01**
COWS100	11.7	8.4	4.4	4.2	14.1	11.0	0.18	0.34

«prewoodland», undershrubs and broom formations than occupied leks. On the other hand, deserted display areas were closer to roads, hunting and areas more affected by fire than currently occupied sites (Table 2). Differences in aspect were not significant between samples ((^{2}= 9.50, *df* = 7, *P* = 0.22) as both occupied and abandoned leks were located mainly on north-facing sides (mode = 1).

The multivariate analysis characterised the abandoned display areas, by comparison with those currently occupied, as follows: Capercaillie disappeared from leks situated in rolling hills, at lower altitude, nearer to «pre-woodlands», under shrubs and pine forests (model B1). Disturbances model (B2) showed that the closeness to houses, hunting sites and repeatedly burnt areas affected lek abandonment (Table 3).

A global comparison among the models

GAM models based on disturbances (models A2 and B2) were more discriminative than models focused on habitat pattern and composition (models A1 and B1). Similarly, models based on random points (models A1 and A2) classified better the data than occupied *vs.* abandoned models (models B1 and B2) (see AUC scores for final models; Table 3). In all cases the accuracy of the models was very high (AUC was always bigger than 0.88 and 10-cross validated AUC was equal or better than 0.80). However, the predictive power measured as the value of 10-cross validated AUC decreased more for disturbance models (A2 and B2) and less for habitat models (A1 and B1). Predicted probabilities for the complementary sample of 17 droppings and new observations were especially low for model A2.

Disturbance models were more complex, involved more variables (7 and 6 variables for A2 and B2, respectively), than habitat models (5 variables within each model A1 and A2). Comparing the two habitat-based models, the results showed that only one variable was present in both cases: the altitude. The number of common variables involved in both disturbance-based models, explaining simultaneously lek occupancy and abandonment, was three: proximity to houses, mines and areas affected for the highest fire recurrence noted for the study area. Most of the terms were significantly non-linear (Table 3).

Discussion

Habitat selection and the importance of disturbances

Capercaillie populations are declining throughout its distributional area. Several studies suggested forest fragmentation and human disturbances as the major reasons for this reduction (Rolstad & Wegge, 1987; Ménoni & Bougerol, 1993; Kurki *et al.*, 2000; Sachot *et al.*, 2003; Obeso & Bañuelos, 2003). However, there are other possible causes. For example, the Scottish population is diminishing due to a reduced reproductive rate associated with both climate change (but unrelated to habitat destruction, Moss *et al.*, 2001) and the increase in predation (Summers *et al.*, 2004; Baines, *et al.*, 2004), being now at risk of a second extinction (Moss, 2001). In the Cantabrian Mountains, Canut *et al.* (2001) pointed the possible extinction of Capercaillie in three decades as a consequence of a very low productivity (< 0.4 offspring by female and year). However, it is very difficult to predict the future of a vulnerable species, even when much demographic information is available (Kangas & Kurki, 2000). Some of the factors affecting the decline of the bird are out of our control, but by understanding the local problems facing different populations and developing precise habitat management plans for controlling specific risk activities we may reverse the situation (Moss *et al.,* 2001).

The present study indicates that disturbances due to human activities and infrastructures are particularly important, explaining better the occupancy and the persistence of the display areas (models A2 and B2) than habitat composition and pattern (models A1 and B1). Model A2 had the maximum AUC value, but probability values for the validation set were extraordinarily low. The cause could be the nature of this data set: a mixture of direct observations and droppings neither dated nor sexed, which could correspond to both males and females, and to either display or passing sites. It is important to highline that disturbance models were more discriminative (highest AUC values) than habitat models; however, its pre-

TABLE 3

Contribution of each selected variable in the Generalised Additive Models. Drop indicates the marginal contribution of each variable: values are obtained by dropping each explanatory variable from the model and then calculating the associated change in deviance. Model gives an indication of the contribution of the variable within the selected model. It is calculated by the range between maximum and minimum contribution of each variable in the linear predictor scale before transformation by the link function (from Lehmann *et al.*, 2003). L means a linear term. S means a smoothed term. The table includes AUC values for both final and cross validated models. See Table 1 for the meaning of the codes.
[Contribución de cada variable seleccionada en el Modelo Generalizado Aditivo. Drop indica la contribución marginal de cada variable: los valores se obtienen eliminando cada variable del modelo y calculando la pérdida en devianza. Model es una indicación de la contribución de cada variable en el modelo seleccionado. Se calcula por el rango entre la máxima y mínima contribución de cada variable en una escala predictora lineal antes de la transformación por la función «link» (Lehmann et al.*, 2003). La tabla incluye el valor AUC para los modelos final y de validación cruzada.]*

Habitat pattern and composition models						
	Model A1: Occupied vs. random			**Model B1: Occupied vs. abandoned**		
	Drop	Model	Term	Drop	Model	Term
DIVW7	0	0	-	0	0	-
WOODRICHW7	4.15	19.95	L	0	0	-
PATCHAREA	2.56	27.02	L	0	0	-
DECISHAP	0	0	-	0	0	-
EDGED	21.35	113.08	L	0	0	-
PREWOODD	0	0	-	15.89	8.39	S
TALLBUSHD	0	0	-	0	0	-
BROOMD	0	0	-	0	0	-
UNDSHRUBD	0	0	-	18.31	19.04	L
MEADOWD	0	0	-	0	0	-
PASTD	0	0	-	0	0	-
PINED	0	0	-	15.18	14.10	S
ROCKD	0	0	-	0	0	-
RIVERD	9.28	30.38	L	0	0	-
MDT	12.11	57.51	L	20.57	18.07	L
SLOPE	0	0	-	10.40	10.92	L
null.dev		97.04 (*df* = 69)		83.23 (*df* = 60)		
resid.dev		35.02 (*df* = 64)		24.85 (*df* = 49.32)		
AUC		0.95 (*SD* = 0.02)		0.88 (*SD* = 0.04)		
10-Cv AUC		0.94 (*SD* = 0.04)		0.84 (*SD* = 0.02)		
Probabilities for the validation set		Median = 0.97		Median = 1		
Disturbance models						
	Model A2: Occupied vs. random			**Model B2: Occupied vs. abandoned**		
	Drop	Model	Term	Drop	Model	Term
ROADD	14.10	16.46	S	0	0	-
UNMADED	2.72	5.86	S	0	0	-
HOUSED	3.38	6.12	L	11.25	9.62	L
MINED	9.80	6.96	S	8.57	5.89	S
FIRE9899D	0	0	-	7.79	5.48	L
FIRE1D	9.36	10.49	S	0	0	-
FIRE2D	0	0	-	5.29	4.36	L
FIRE3D	4.83	4.45	S	0	0	-
FIRE45D	0	5.13	S	10.28	11.45	S
HUNTD	0	0	-	15.16	7.29	S
COWS100	0	0	-	0	0	-
null.dev		97.04 (*df* = 69)		83.23 (*df* = 60)		
resid.dev		18.97 (*df* = 44.89)		44.22 (*df* = 45.28)		
AUC		0.99 (*SD* = 0.01)		0.92 (*SD* = 0.03)		
10-Cv AUC		0.83 (*SD* = 0.08)		0.80 (*SD* = 0.06)		
Probabilities for the validation set		Median = 0.42		Median = 0.81		

dictive power was worst (AUC values decreased more when we cross-validated the models and the probabilities for the validation set were lower). This could suggest that (1) complicated models, involving high number of variables, explain well the current situation but can not be easily extrapolated; or (2) disturbances explain better occupancy and persistence than habitat, but their effect is more unpredictable.

We found that the stability of Capercaillie breeding areas through time is mainly related to low fire recurrence in the surrounding area and few houses nearby (model B2). Our results (Fig. 2 and Table 3) show as well that hunting is still a relevant factor for the persistence of the species. However, in most parts of the study area, this has not been practised for 30 years at least, and is only focused on ungulates, which can disturb indirectly the species. This suggests that the effect of this activity could be a «relict» as a consequence of its intensity in the past, similar to referred bellow for fragmentation. Zones with more intensive hunting in the past are outside the currently protected areas and show the highest rates of disappearance.

The bird selects remote areas for displaying, which are located mainly on northern slopes, far from human presence, especially at altitudes within the range 1160-1600 meters (median = 1350) (abandoned leks: range= 1010-1490 m, median= 1245 m; random points: range= 647-1500 m, median= 1100 m). Other authors have recorded similar values over 1000 m: 1200-1450 m for the whole of the Cantabrian Mountains (Del Campo & García-Gaona, 1983), 1000-1300 m in the Bavarian Alps (Sachot *et al.*, 2003). Leks located on rolling hills (fewer slopes) were easily abandoned by the species, as they are more accessible and, therefore, more easily disturbed.

Our analysis also point out the relevance of woodland fragmentation as one of the main constraints on the lek occupancy by Capercaillie. Places located close to the borders of small and irregular mature forest patches were significantly less selected as display areas. These results are consistent to previous studies from authors as Rolstad & Wegge (1987), Storch (1991), Ims *et al.* (1993), Kurki (2000) or Obeso & Bañuelos (2003). There are evidences of Capercaillie distribution showing a metapopulation pattern associated with forest fragmentation. In the Alps, Segelbacher & Storch (2002) verified that edge populations are subject to limited gene flow and show genetic signs of a more severe population decline than core populations. The bird is constrained to move between the fragments, so increasing its exposure to predators, which are more numerous at the borders (Obeso & Bañuelos, 2003). On the other hand, some authors, such as Nagelkerke *et al.* (2002) proposed the hypothesis that the ex-

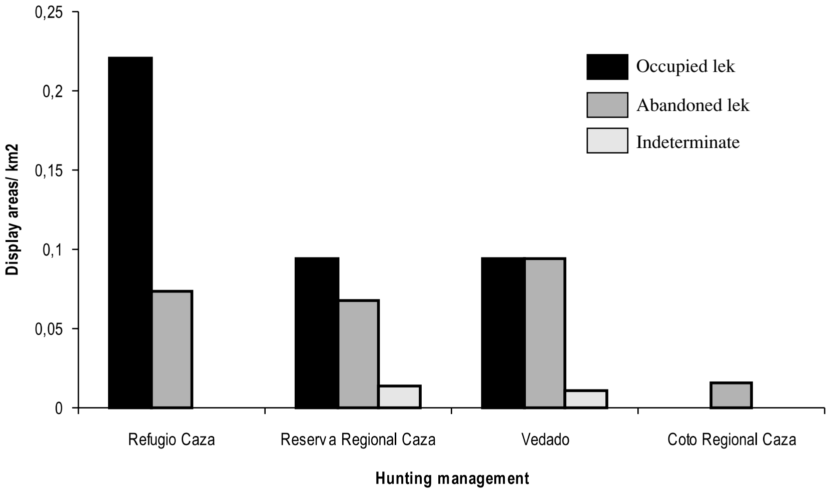

FIG. 2.—Lek densities in the study area by hunting management category
[Densidad de cantaderos en el área de estudio según las categorías de régimen cinegético.]

tinction of the bird is probably due to a retarded response to fragmentation produced during the 1950s-1960s. In any case, fires, roads, etc. contribute to the creation of more numerous and smaller forest patches affected by human disturbances.

The presence of occupied leks depends as well on the diversity of woodlands on the surrounding areas, probably according to availability of food. In the Cantabrian Mountains, Capercaillie eats mainly beech shoots, bilberries and ferns. In this particular area (*i.e.* Cangas de Narcea), annual diet consists mostly of beech, birch and holly. These last two species are especially important during the breeding season (Rodríguez & Obeso, 2000).

By contrast, the proximity to under shrub formations is avoided during the display season. In the western part of the Cantabrian Mountains, in common with northern Galaic-Asturian landscapes, there is a growing dominance of zones characterised by degraded soils covered with heath formations (Díaz & Fernández-Prieto, 1994). The cause is the recurrence of human-caused fires, which is probably the worst environmental problem in this area, causing erosion, fragmentation and lost of fertility. Most of the fires are produced during the winter season in order to create more pasturelands for cattle in spring and summer. An alternative, more environmentally sensitive technique, would involve clearing practises, avoiding cutting bilberry formations, essential for Capercaillie. Calvo *et al.* (2002) showed, for the Cantabrian Mountains, a predominance of perennial herbaceous species during the first five years of a secondary succession after burning. These species were gradually replaced by woody species from the sixth and seventh years. However, *Vaccinium myrtillus* increased after cutting and burning, exceeding its initial cover from the second year after the disturbances, which should be a food source for the bird. However, recurrently burnt areas are systematically avoided by the species, because they lose the natural capacity to regenerate and can not become suitable areas for Capercaillie use.

Model limitations

A possible criticism about this paper is the small sample size used for modelling the species distribution. This is precisely one of the main reasons why relatively few predictive models have been applied to endangered or rare species (Engler *et al.*, 2004). However, knowledge on what determines distribution is a necessary precursor for schemes to mitigate decline or to create new populations through reintroduction (Rushton *et al.*, 2004).

Sample sizes of species occurrence used to develop predictive models greatly affect the success rate of those models in predicting the occurrence of the species at a location, i.e. the accuracy (Stockwell & Peterson, 2002; McPherson *et al.*, 2004). Small data sets can lead to overfitting, which decrease with larger data sets (Stockwell & Peterson, 2002). Pearce & Ferrier (2000) estimated that for a multi-taxon evaluation of GAM and GLM approaches, sample sizes greater than 250 were needed to maximize accuracy. However, Stockwell & Peterson (2002) exploring sample sizes needed for accurate modelling for three predictive methods, including regression, founded that in all cases the most rapid improvement of model performance takes place bellow 20 data points. Analyses made using ten points gave an average accuracy of 64%, increasing this accuracy only to around 68% when 50 points were considered. They founded logistic regression (the alternative for our analyses) one of the least accurate method at lower sample sizes, showing lower rates of increase in accuracy with the increasing of the sample size, and reaching similar maximum accuracy with the other compared methods at 100 data points. This method was also sensitive to the nature of the environmental variables. For all these reasons, lek occupancy and persistence was modelled using a generalised additive model (GAM), a type of log-linear regression model that incorporates a smoothing function and provides a less restrictive modelling technique of GAM. It has been used at low sample size by authors as Fewster *et al.* (2000).

Another reason why there are few models for endangered species in the literature is that most of the data available for rare species consists of a set of presences without locations for absences. When working with rare species, choosing wrong absences (where the species could be present) could reduce significantly the quality of the model. In order to solve this problem, Engler *et al.* (2004) propose an approach consisting of generate multiple samples of pseudo-absences. In our case, we can assume that the census reflects correctly the real distribution of the species in the study area. As landscape is reasonably homogenous, we chose a random sample of absences avoiding non-suitable habitats or already occupied places, as is usual in these studies.

We founded some inconsistencies regarding both univariate and multivariate analyses. Some variables resulted significant for the univariate analysis but were not selected by the GAM analysis and viceversa. This fact suggests a correlation among the variables non-detected when we checked for the independence of the variables. Multivariate regression techniques evidence partial effects, which makes important differences when variables interact in the field. For this reason, they present a more synthetic view of habitat preferences (Sachot *et al.*, 2003).

Some of the variables showed misleading significances. This is the case for distances to mines and pines. For example, the proximity to mines is an obvious consequence of the immediacy of the Cerredo excavations to well preserved woodlands. Mature pine forest is the habitat most frequently used by Capercaillie in the boreal region; however, in the Cantabrian Mountains, the bird is not associated to this forest (though there are some exceptions, *e.g.* the lek located at the mature pine forest of Bedramón, Allande) because it is not a natural habitat. Pine forests are mostly young afforestations for timber exploitation. However, even if the bird does not use often this vegetation class, this does not account for its avoidance, as indicated by our results. The explanation could be that most of these forests are too young and *Pinus sylvestris*, the pine species preferred by Capercaillie, is scarce. In addition, these afforestations are attached to the presence of unmade roads.

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