

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

The decline of Cantabrian capercaillie: How much does habitat configuration matter?

Mario Quevedo*, María José Bañuelos, José Ramón Obeso

Department of Biology of Organisms and Systems, Ecology Unit, Oviedo University, Catedrático Rodrigo Uría s/n, 33071 Oviedo (Asturias), Spain

ARTICLE INFO

Article history:

Received 24 January 2005

Received in revised form 22 July 2005

Accepted 29 July 2005

Available online 21 September 2005

Keywords:

Forest fragmentation

Grouse

Logistic model

Tetrao urogallus

Spatial scale

Population decline

ABSTRACT

The endangered Cantabrian capercaillie (*Tetrao urogallus cantabricus*) has undergone a severe decline during recent decades. Capercaillies require large tracts of mature forest, and are thus sensitive to landscape-level habitat alteration. The high degree of fragmentation and anthropogenic disturbances in the habitat of Cantabrian capercaillie suggested that habitat patterns may be related to the population decline. To evaluate this we developed predictive habitat suitability models. We used a geographic information system (GIS) to integrate environmental variables and spatial context into two logistic models, comparing (a) presence vs. pseudo-absence habitat units (General model) and (b) presence vs. abandoned habitat units (Decline model). We obtained low overall habitat suitability and poor connectivity between high-suitability areas. We found evidence that habitat suitability is indirectly related to the process of population decline, and that the relationship between capercaillie presence and habitat configuration goes beyond the local spatial scale and the average size of forest fragments. We suggest that the combination of these two modelling procedures provides a deeper insight into the decline process, differentiating overall optimal and suboptimal areas (General model) and predicting the direction of eventual local extinctions (Decline model).

© 2005 Elsevier Ltd. All rights reserved.

1. Introduction

The analysis of wildlife-habitat relationships is a major feature in conservation strategies. Ideally, conservation planning should be based on in-depth knowledge of the population dynamics and responses to spatially structured habitats, and how environmental changes affect them (Collinge, 2001). This task is particularly challenging when dealing with highly mobile, rare, shy or inaccessible species. In such cases, occurrence data may constitute the only available or reliable information (Bellamy et al., 1998; Jansson and Angelstam, 1999; Radford and Bennett, 2004), and the analysis of the relationship between habitat variables and species occurrence

has become a much appreciated tool in conservation planning. Combining spatial information of species occurrence with multivariate statistics and geographic information systems (GIS), it is possible to shed light on the spatial patterns of habitat suitability for the species of concern, defined as the probability of the species occurrence in space (Guisan and Zimmermann, 2000). In the case of specialist species, habitat modelling is particularly useful, since it may provide an accurate prediction of the presence of a species and its spatial distribution. One of the key aspects of habitat modelling is the spatial scale at which environmental variables influence the focal species. This may differ among species (Andrén, 1994; Keitt, 1997), but also among environmental

* Corresponding author. Tel.: +34 985 104831; fax: +34 985 104866.

E-mail address: mario.quevedo@mariecurie.org (M. Quevedo).
0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2005.07.019

variables for the same species. However, few habitat models have been reported that explore species response to environmental factors at different spatial scales (Graf et al., in press; Schadt et al., 2002; Thompson and McGarigal, 2002), despite its relevance in understanding habitat use patterns that may only become apparent at certain scales.

Capercaillie is a forest species that requires large tracts of mature, pristine forest habitat (Gjerde and Wegge, 1989; Swenson and Angelstam, 1993). Hence, it is not surprising that capercaillies are quite sensitive to landscape-level habitat alteration (Storch, 1995). Capercaillie populations have declined throughout most of the species range, and the species is accordingly listed in the National Red Data Books in 17 countries (Storch, 2000a). We studied the capercaillie population living in the mature forests of the Cantabrian Mountains, NW Spain, i.e., *Tetrao urogallus cantabricus* (Storch, 2000a). This population has declined severely in the last 20–30 years, leaving an adult population estimated at 500 birds (Obeso and Bañuelos, 2003), constrained to an area of occupancy of less than 2000 km² (Fig. 1). Its geographical location, isolated from its nearest neighbours in the Pyrenees by more than 300 km, makes its situation even more delicate, and as a consequence it has been designated the most threatened population at present (Storch, 2000a). However, interest in the species lies beyond its endangered status, as the Cantabrian capercaillie occupies the SW edge of the grouse family distribution in Eurasia and presents numerous ecological peculiarities. Populations at the edge of the distribution range are of special interest because they help in our understanding of aspects such as ecological niches and threshold responses to environmental change (Brown et al., 1996; Holt et al., 2005). In this sense, this peripheral population differs from most of its conifer-specialists conspecifics (Picozzi et al., 1992; Rolstad and Wegge, 1987) in that it inhabits deciduous forests of beech *Fagus sylvatica*, sessile oak *Quercus petraea*, and birch *Betula pubescens* along the steep slopes of the Cantabrian Mountains (Quevedo et al., 2006). Furthermore, in terms of applied conservation, knowl-

edge acquired in other parts of species range is not readily applicable to distribution edges, where populations often show ecological peculiarities, such as small size and density, and use ecologically marginal habitats (Brown, 1984; Lawton, 1993).

Species-habitat relationships are often complex and scale-dependent. The use of rather simple data on species occurrence and habitat variables, and a large-scale approach, may include the main factors operating at home range scales and above (see for instance Carroll et al., 1999). Large-scale assessment of the spatial pattern of suitable habitats for endangered species or populations is a prerequisite for sound conservation and management strategies (Storch, 2000a; Twedt and Loesch, 1999). However, this does not neglect the existence of local processes that perhaps dominate at smaller scales, or the importance of matrix habitat both in general (Fahrig, 2001; Ricketts, 2001) and for this particular capercaillie population (Quevedo et al., 2006). The acute decline of the population has led to an explicit and urgent need for the development of quantitative habitat suitability maps in order to identify critical areas for capercaillie in the Cantabrian mountains (Obeso and Bañuelos, 2003), a species that may be an indicator for the overall conservation of mountain birds (Suter et al., 2002). Previous information suggests that habitat availability is low in these populated mountains, where the results of anthropogenic landscape alteration and habitat fragmentation are evident. Only 23% of the montane landscape is presently covered by forests, a low value compared with the 30–50% in other areas of temperate or boreal forests in Europe and North America (Löfman and Kouki, 2001; Mladenoff et al., 1993), and it is highly fragmented (García et al., 2005). Theory predicts that below this percentage of habitat cover not only habitat loss but also the spatial arrangement of remaining habitat patches and their quality are relevant for dispersal success and population persistence (Andrén, 1994; King and With, 2002).

The aim of this study was to develop predictive habitat suitability models for the Cantabrian capercaillie along a continuous range of scales. Our specific objectives were:

1. To identify natural and anthropogenic landscape variables defining habitat units as suitable for the Cantabrian capercaillie.
2. To generate habitat suitability maps for the Cantabrian capercaillie, as a tool to identify (a) high-suitability areas where protection should be boosted and (b) high-risk areas where measures to prevent local extinctions should be taken.
3. To detect the critical scale at which different landscape variables influence capercaillie occurrence.
4. To evaluate whether habitat modelling can detect a relationship between the ongoing decline process and habitat patterns.

2. Methods

2.1. Area of study

We studied an area of 5900 km² of montane landscape (above 600 m a.s.l.) in the northern slope of the Cantabrian

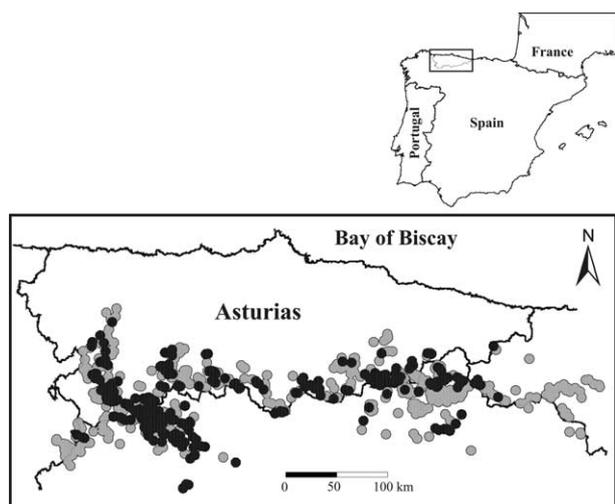


Fig. 1 – Approximate area of occupancy (see Storch, 2000b for criteria) of Cantabrian capercaillie in the early 1980s (grey) and in 1997–2001 (black), mapped by plotting buffer areas of 2 km radius around display grounds.

Mountains, Asturias, NW Spain (Fig. 1). The Cantabrian Mountains are an ecotonal zone at the SW edge of the Euro-iberian biogeographic region, and the forests in the area are included within the “cool temperate moist forest” ecological zone (Iremonger et al., 1997). These are deciduous semi-natural forests with a long history of human use (Tucker and Evans, 1997). Most of the alteration perceived nowadays in the forested landscape is due to logging and extensive cattle herding, although several areas have been acutely disturbed due to coal mining. Forests are dominated by beech *F. sylvatica*, sessile oak *Q. petraea*, and birch *B. pubescens*, which account for 63%, 21%, and 5% of the forest cover, respectively. There are also some areas covered by conifer plantations at lower elevations, mostly Scots pine *Pinus sylvestris*, which account for about 5% of the forest cover (García et al., 2005; Quevedo et al., 2006).

2.2. Capercaillie presence

We used capercaillie display areas as the unit of analysis of capercaillie presence. Display areas and the surrounding habitat are central to capercaillie conservation because they sustain high capercaillie activity throughout the year (Picozzi et al., 1992; Storch, 1995). These areas include the display ground itself, defined as the sites at which one or more cocks consistently display for females (Picozzi et al., 1992), plus the nearest surrounding habitat in the forest. For simplicity we will hereafter use the term display ground, with the broader meaning outlined above.

Data on the location of display grounds were provided by the Asturian environmental agency (Consejería de Medio Ambiente del Principado de Asturias). We used data from the 352 known display areas in Asturias. These display areas were occupied until the early 1980s, according to an extensive survey carried out in spring 1982 and information on capercaillie territories from forest wardens and hunters (capercaillie

lie was hunted legally in the region until the early 1970s). Display areas were repeatedly surveyed during the period 1997–2001, always in spring (April–May) to coincide with the gathering and displaying of the males. Every display ground was visited at least twice, both at night and during the day-time. For night surveys, observers (2–3 per display area) went to the area close to the centre of activity before dawn, and remained there until the display finished, or until well past dawn when no capercaillies were seen or heard. Later in the day the observers returned to sites where no direct sightings were made, to look for signs such as feathers, fresh droppings or footprints. The size of area surveyed varied according to the accessibility and the size of the forest fragment, but was usually up to 1 km². When poor weather or disturbance had prevented observations, return visits were made 2–3 days later to confirm whether or not a display ground should be considered as empty. A display ground was considered as occupied whenever signs of presence (direct sightings, feathers, fresh droppings, tracks) were recorded in at least one of the surveys performed. The display grounds were located on digital maps (scale 1:10,000), using a GPS. The lowest display area of the Cantabrian capercaillie is located at 775 m a.s.l., and this was the basis for the altitudinal limit of the study area mentioned above. See Quevedo et al. (2006) for analyses of patterns in display ground occupancy. The 1997–2001 survey yielded 152 occupied and 201 unoccupied display grounds, i.e., a decline of more than 55% during the last two decades (Fig. 1).

2.3. Habitat database

The basic unit for the habitat models was a 500 × 500 m cell grid (25 ha), which we overlaid with maps of capercaillie occupancy and environmental variables. We chose a priori explanatory variables to maximize the balance between clarity and ecological meaning (Table 1).

Table 1 – Description of a priori explanatory variables considered to model capercaillie presence

Abbreviation	Description
forest _{local}	Forest cover (%) in the local 25 ha habitat unit
forest _{n(1–10)}	Mean forest cover (%) in scaling neighbourhoods from 1 to 10 km (1 km radius), excluding the value of the local habitat unit
slope	Mean slope (%) in the local 25 ha habitat unit
elevation	Mean elevation (m a.s.l.) in the local 25 ha habitat unit
aspect	Percentage of north-oriented terrain in the local 25 ha habitat unit
track _{local}	Length (m) of roads, surfaced tracks and 4WD tracks in each habitat unit
track _{n(1–10)}	Mean length (m) of roads, surfaced tracks and 4WD tracks in scaling neighbourhoods from 1 to 10 km (1 km radius), excluding the value of the local habitat unit
urban _{local}	Urbanized area (%) in the local 25 ha habitat unit
urban _{n(1–10)}	Mean urbanized area (%) in scaling neighbourhoods from 1 to 10 km (1 km radius), excluding the value of the local habitat unit
settlement _{local}	Number of human settlements (>1 ha) in the local 25 ha habitat unit
settlement _{n(1–10)}	Mean number of human settlements (>1 ha) in scaling neighbourhoods from 1 to 10 km (1 km radius), excluding the value of the local habitat unit
pop _{local}	Population density (inhabitants × km ⁻²) in the local 25 ha habitat unit
pop _{n(1–10)}	Mean population density (inhabitants × km ⁻²) in scaling neighbourhoods from 1 to 10 km (1 km radius), excluding the value of the local habitat unit
Spatial terms	3rd degree polynomial of the standardized UTM coordinates: $X + Y + XY + X^2 + Y^2 + X^2Y + XY^2 + X^3 + Y^3$

We extracted information on a priori explanatory variables from a high-resolution GIS database (Consejería de Medio Ambiente, Principado de Asturias), except for the data on human population density, extracted from the 1999 national population census. The GIS database is a thematic cartography composed of Arc-Info vectorial layers and based on the Spanish National Topographic Map 1:25,000. Most of it is derived from orthophotos (1994–1996, scale 1:25,000), completed with aerial pictures at scales ranging from 1:18,000 to 1:50,000, and fine-tuned with field observations. The original vegetation layer distinguished 138 vegetation classes at a resolution of 25×25 m, including 26 types of mature forest and 8 types of young, secondary growth forest. We summarized them into major habitat types from the dominant species in the forest patch, and overlaid them with the habitat grid, in order to calculate the forest cover in each habitat unit. See [García et al. \(2005\)](#) for further details on the database and forest composition.

To obtain the topographic information for our habitat models we built a digital elevation model (DEM) with a cell size of 100 m from digital elevation contours (50 m elevation interval), i.e., we obtained 25 topography data points for each cell of the grid (hereafter habitat unit). We derived slope and aspect from the DEM, and calculated the average values of elevation and slope, and the percentage of terrain with a northern exposure for each habitat unit.

We used two types of explanatory variables in the model, depending on their spatial definition:

1. Local variables that are defined for each 25 ha habitat unit by assigning the corresponding values of each variable to the habitat unit.
2. Landscape variables that incorporate the spatial scale information. To construct these variables we performed neighbourhood statistics on the original local habitat units. We used the moving window technique to assign to each habitat unit the mean value of its neighbours, excluding its own value (doughnut-shaped moving window with a 500 m diameter gap), thus, overcoming to some degree the arbitrary election of grid size as habitat unit. We used a scaling radius of 1000 m, from 1 to 10 km from the local habitat unit. We defined the proportion of forest cover and the anthropogenic variables as landscape variables ([Table 1](#)). The former represents the spatial variation in the main, irreplaceable habitat requirement of capercaillie, and the latter seek to identify the scale of anthropogenic disturbance, whose influence probably spreads across spatial scales.

2.4. Habitat models

Probability maps that represent the likelihood of species occurrence are often referred to as habitat suitability models. This is because the probability of the presence of a species in the units of the modelled habitat is interpreted as an index of habitat suitability ([Guisan and Zimmermann, 2000](#)). We fitted different generalized linear models (GLM, logit link and binomial error distribution) to our data, in order to obtain an index of habitat suitability for capercaillie in the Cantabrian range. Our habitat models include large-scale habitat variables as explanatory variables and capercaillie presence as the binary-dependent variable.

To assess the relationship between environmental variables and capercaillie presence in the habitat units, we used two modelling approaches. Firstly, we explored the connection between the decline of the population and habitat patterns. This model, hereafter called Decline model, was used to compare habitat units from the grid that contained a currently occupied display area ($n = 152$) with those including a display area occupied until the 1980s, but currently unoccupied ($n = 201$). Secondly, we modelled overall habitat associations comparing presence habitat units with random pseudo-absences ($n = 150$). Pseudo-absences are defined as random habitat units with a suitability < 0.30 according to a preliminary Ecological Niche Factor Analysis (ENFA) habitat suitability map ([Engler et al., 2004](#); [Hirzel et al., 2002](#)). We used freeware Biomapper 3.1 to calculate ENFA ([Hirzel et al., 2004](#)). We will hereafter refer to this procedure as General model.

Our landscape explanatory variables are correlated by construction and we therefore chose only one landscape variable for each local variable, to avoid non-independence. Landscape variables were selected as a priori explanatory variables if they matched the following selection criteria: (1) significant relationship with capercaillie presence ($p < 0.1$) in univariate logistic regressions; (2) not too strong correlation with the corresponding local variable (Pearson correlation coefficient $r < 0.6$).

To build the minimal adequate model, we first fitted univariate models that were retained with a significance level of $p < 0.1$, i.e., a less restrictive procedure than the classical 0.05 alpha level due to its exploratory nature. From these initial univariate models, we retained that with the lowest Akaike information criterion (AIC, [Burnham and Anderson, 1998](#)). We then continued to test bivariate models, always retaining the one with the lowest absolute AIC. The process ended when addition of new variables did not further reduce the AIC. Thereafter, we tested for non-linearity and interaction effects by adding quadratic and product terms to that minimal adequate model. We used a Trend Surface Analysis to control for linear and complex spatial structure and neighbourhood effects ([Guisan and Zimmermann, 2000](#); [Legendre and Legendre, 1998](#)). This involves adding spatial terms to the minimal models as the 3rd degree polynomial of standardized UTM coordinates, and checking whether these spatial terms are retained in the model. The minimal models plus the spatial terms retained at $p < 0.05$ composed the final models.

We evaluated the models with the same dataset via bootstrap re-sampling with replacement ([Efron and Gong, 1983](#); [Guisan and Zimmermann, 2000](#)), which approximates the population values of the statistic of interest. The method provides the bias, or optimism, of the coefficients estimated in the model. The bias is subtracted from the initial apparent measure to obtain a bias-corrected estimate of model coefficients, which is the difference between the coefficient estimated from the sample and the population value ([Guisan and Zimmermann, 2000](#)). This difference gives idea of the stability of the models, and their 'overfitting optimism' ([Efron and Gong, 1983](#)). If the difference is large, the adequacy of the models should be questioned. To perform the bootstrap re-sampling (10,000 iterations) we used the *boot* package for R Statistical Environment (R Development Core Team, 2005).

We chose the probability cut-off level that maximized Cohen's kappa coefficient of prediction agreement (Guisan and Zimmermann, 2000), while providing a better prediction of occupancy because absences cannot be considered to be as certain as presences (Gu and Swihart, 2004). Cohen's kappa values range from -1 to 1 , where 1 indicates a perfect agreement, whereas values <0 indicate a performance no better than random. We followed Landis and Koch's (1977) classification of Cohen's kappa strength of agreement. We also used receiver operating characteristic (ROC) plot analysis as an independent, reliable measure of model accuracy (Guisan and Zimmermann, 2000; McPherson et al., 2004). The area under the ROC curve (AUC) was used to test if the model performs better than guessing, considering $AUC_{critical} = 0.5$, where values between 0.7 and 0.9 indicate a reasonable discrimination ability of the model.

We used R statistical environment (R Development Core Team, 2005) for all the statistical analyses.

3. Results

The procedure of variable selection yielded 10 explanatory variables with a significant relationship with capercaillie presence in either the Decline or the General modelling approaches (Table 2). The proportion of forest cover is the variable that best explains capercaillie presence in univariate logistic regressions, in either the local habitat unit or the 4 km radius. Overall, the General procedure showed a better fit of the explanatory variables to the data, and identified more variables related to anthropogenic disturbance as candidates for the minimal models. Details on the univariate relationships and the correlation coefficients of the different radii with their respective local variables are provided in the online Electronic Appendix 1.

The step-up model selection procedure based on the AIC, and the resulting minimal models are shown in Table 3. The minimal model fitted to the Decline dataset explained 11% of the deviance in the presence vs. absence habitat units. The minimal model fitted to the General dataset explained 66% of the deviance in the occupied vs. random pseudo-absence habitat units. The strongest variable in the Decline

Table 3 – Summary of the step-up model selection procedure based on Akaike Information Criterion (AIC)

	RD	D ²	AIC
<i>Decline</i>			
Null model	481		
forest ₄	453.7	5.8	457.7
forest ₄ + aspect	444.2	7.7	450.2
forest ₄ + aspect + forest _{local}	440.4	8.5	448.4
forest ₄ + aspect + forest _{local} + settlement ₃	437.5	9.1	447.5
forest ₄ + aspect + forest _{local} + settlement ₃ + X	428.5	11.0	440.9
<i>General</i>			
Null model	415.7		
forest _{local}	196.9	52.6	200.9
forest _{local} + elevation	170.9	58.8	176.9
forest _{local} + elevation + X + Y + X ² Y	141.3	66.0	153.3
Spatial terms retained into the minimal models after the Trend Surface Analysis (TSA). RD = residual deviance. D ² = % explained deviance (Guisan and Zimmermann, 2000).			

model was the proportion of forest cover in a radius of 4 km from the local habitat unit (forest₄), whereas the main variable in the General model was the proportion of forest cover in the local habitat unit (forest_{local}), without including landscape-scale variables (Table 3). The coefficients and the significance of the explanatory variables in both modelling procedures are shown in Table 4. Both minimal models showed small bias from the sample estimated coefficients to the population values obtained from the bootstrap (Table 4; see Electronic Appendix 1 for the density distribution of coefficients).

The habitat suitability indices, i.e., the probability of occupancy of habitat units, can be calculated for both approaches as

$$P = \frac{1}{1 + e^{-\text{logit}(P)}}$$

where $\text{logit}(P)$ is the linear combination of the factors shown in Table 4.

The predictive power of the modelling procedures, assessed via ROC curves (Electronic Appendix 1), showed a

Table 2 – Coefficients (± 1 SE) and significance in univariate logistic regressions of the explanatory variables considered for either the Decline or the General models

Factor	Decline model			General model		
	Coefficient	Wald z	p	Coefficient	Wald z	p
forest _{local}	2.11 \pm 0.44	4.7	<0.001	6.70 \pm 0.66	10.1	<0.001
forest ₄	4.30 \pm 0.85	5.0	<0.001	–	–	–
elevation	0.002 \pm 0.001	3.5	<0.001	0.005 \pm 0.001	8.8	<0.001
slope	–	–	–	0.13 \pm 0.02	5.5	<0.001
aspect	0.012 \pm 0.005	2.7	0.007	0.030 \pm 0.004	6.0	<0.001
settlement ₃	–19.40 \pm 6.24	–3.1	0.002	–	–	–
pop ₁	–	–	–	–0.15 \pm 0.04	–4.0	<0.001
urban ₄	–	–	–	–83.4 \pm 19.9	–4.2	<0.001
tracks _{local}	–0.03 \pm 0.01	–2.6	0.010	–0.08 \pm 0.01	–5.8	<0.001
tracks ₅	–	–	–	–0.13 \pm 0.02	–5.7	<0.001

Selection results from removing those strongly correlated to each other ($r > 0.6$) and those that did not show significant univariate relationship with capercaillie occupancy.

Table 4 – Coefficients ($\pm 1SE$) and significance for the explanatory variables and spatial terms (TSA, Legendre and Legendre, 1998) entering the minimal models Decline and General

Factors	Decline					General				
	Coefficient	Z	p	Bootstrap coefficient	Bias	Coefficient	Z	p	Bootstrap coefficient	Bias
(intercept)	-3.02 ± 0.59	-5.1	<0.001	-3.10 ± 0.56	0.08	-10.44 ± 1.51	-6.9	<0.001	-11.01 ± 1.61	0.57
forest _{local}	1.20 ± 0.54	2.2	0.027	1.27 ± 0.55	-0.07	7.42 ± 0.96	7.7	<0.001	7.76 ± 0.99	-0.34
forest ₄	3.46 ± 1.10	3.1	0.001	3.51 ± 1.10	-0.05	-	-	-	-	-
elevation	-	-	-	-	-	0.007 ± 0.001	5.8	<0.001	0.007 ± 0.001	0.00
aspect	0.013 ± 0.005	2.6	0.010	0.014 ± 0.005	-0.001	-	-	-	-	-
settlement ₃	-15.89 ± 7.20	-2.2	0.027	-16.12 ± 7.10	0.23	-	-	-	-	-
Spatial terms										
X	-0.44 ± 0.15	-2.9	0.004	-0.44 ± 0.15	0.00	-1.33 ± 0.33	-4.1	<0.001	-1.38 ± 0.33	0.05
Y	-	-	-	-	-	2.03 ± 0.53	3.8	<0.001	2.14 ± 0.56	-0.11
X ² Y	-	-	-	-	-	-1.39 ± 0.46	-3.0	0.003	-1.46 ± 0.48	0.07

Bootstrap coefficients are the mean ($\pm 1SE$) of a bootstrap resampling procedure (10,000 iterations). Bias indicates the difference between the coefficient estimate and the true population value, the bootstrap coefficient. Selection results from removing those strongly correlated to each other ($r > 0.6$) and those that did not show significant univariate relationship with capercaillie occupancy.

low AUC value of 0.72 for Decline and very good value of 0.97 for General. The p cut-off values for the models discriminating between occupied and unoccupied sites were $p = 0.40$ for Decline with fair value of Cohen's kappa $\kappa_c = 0.31$ ($p < 0.0001$), and 0.50 for General with a good $\kappa_c = 0.80$ ($p < 0.0001$). The Decline modelling procedure correctly predicted 72% of the occupied sites and 60% of the abandoned, whereas General predicted correctly 90% of both occupancies and pseudo-absences.

The different modelling procedures assigned different suitability indices to habitat units. The mean (± 1 SD) habitat suitability index for the studied area according to the Decline procedure was 0.14 ± 0.14 , with a maximum value of 0.90. Mean (± 1 SD) index value was 0.18 ± 0.27 with a maximum value of 0.99 for General. The Decline procedure showed lower overall suitability values, but differences in performance were not limited to this. Suitability values for Decline were more

gradually spread among all habitat units (Fig. 2(a)). The suitability values assigned by both procedures to the habitat units with known capercaillie presence/absence are shown in Fig. 2(b); values of the General procedure were more extreme, clumped towards the high-suitability end of the plot. We carried out cross-comparison of the respective predictive ability of models on each other's datasets. Decline model performed well predicting presence/random pseudo-absence habitat units, and showed a high AUC value of 0.95, whereas General predicting presence/absence habitat units showed a poor predictive ability with an AUC of 0.68. The discrimination ability of Decline for presence/pseudo-absence habitat units showed a good $\kappa_c = 0.65$ ($p < 0.0001$), predicting correctly 71% of presences and 95% of the pseudo-absence units. The discrimination ability of General on presence/absence habitat units showed a low $\kappa_c = 0.12$ ($p = 0.0070$), correctly predicting 90% of the presences and 23% of the absences.

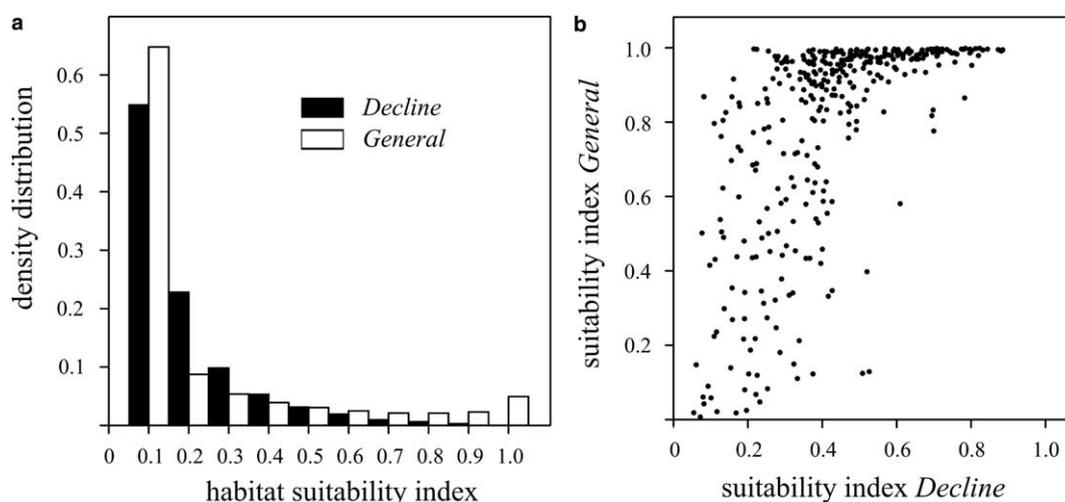


Fig. 2 – Comparison of model outcomes. (a) Distribution of the values of habitat suitability indexes in the study area, according to the Decline and General models (N habitat units = 23,663). (b) Relationship between the habitat suitability indexes derived from the Decline and the General models for the habitat units containing display grounds ($N = 352$).

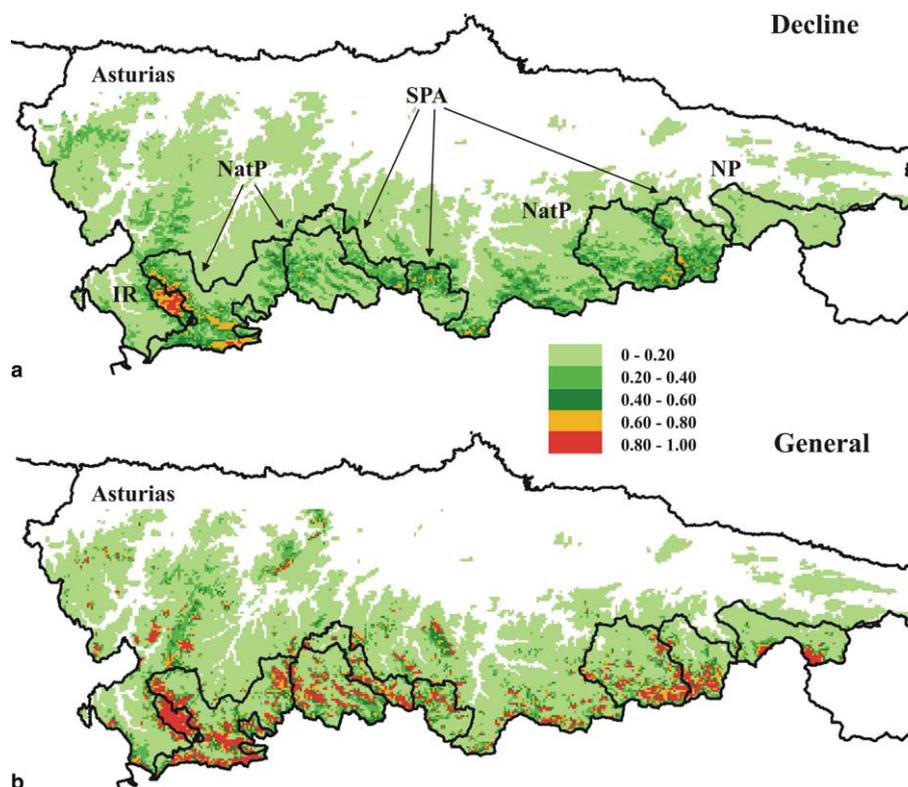


Fig. 3 – Habitat suitability maps for Cantabrian capercaillie in the study area: (a) Decline model, occupied vs. abandoned habitat units; (b) General model, occupied vs. random pseudo-absence habitat units. Habitat unit size = 500 × 500 m, N = 23,663. Boundaries of the protected areas within the study area are marked in black: IR, Integral Reserve of Muniellos; NatP; Nature Park (from west to east, Fuentes del Narcea, Somiedo and Redes); NP, National Park of Picos de Europa; SPA Special Protection Areas for Birds (from west to east, La Mesa, Ubiñas and Ponga).

Both modelling procedures identified very small amounts of habitat with reasonable suitability for Cantabrian capercaillie. The habitat area with suitability values over the cut-off of the models was 7% for Decline and 14% for General (Fig. 2(a) and Fig. 3). See [Electronic Appendix 2](#) for mean habitat suitability index of the different types of forest and the protected areas that hold (or until recently held) capercaillies.

4. Discussion

In this study, we provide evidence that large-scale habitat suitability for Cantabrian capercaillie is very low within its main stronghold in the province of Asturias (NW Spain). We also show that habitat configuration plays a role, probably indirect, in the current process of population decline, and that the influence of habitat configuration on capercaillie occurrence takes place beyond the local spatial scale, and beyond the average size of forest fragment in the range.

4.1. What did we model?

Our findings stem from two different modelling procedures that differed a priori in the use of information on capercaillie absences, and that resulted in marked differences in their sta-

tistical accuracy. Such differences must be considered prior to discussing the outcomes with any confidence, because of the existing debate on the appropriate approach to model species occurrence and the reliability of absence data. Confirmed absences of rare and endangered species, which are more complicated to obtain, often lack from databases. There are specific methods, such as Ecological Niche Factor Analysis (ENFA, [Hirzel et al., 2002](#)), that can be used to analyse presence-only data. However, these methods tend to predict the species at too many locations because they lack reliable absences to restrict the predictions in environmentally inappropriate locations ([Engler et al., 2004](#)). Another approach is to generate ‘pseudo-absences’ at random over the study area and weigh them against the results of a previous suitability map derived from ENFA ([Engler et al., 2004](#)). This is our approach in the General procedure, but this method may exaggerate differences between habitat units with presences and absences beyond species ecology. However, there is a special situation where other types of absences can be detected, i.e., local extinctions. Comparing sampling sites where the species is present with those once but no longer occupied, the approach used in the Decline model, avoids assuming specific occupancy of random points ([Carroll et al., 1999](#)), and provides information about the spatial pattern of the decline process. Although this also runs the risk of generating

“false absences” due to failures in detection (Gu and Swihart, 2004), repeated surveys can help to minimize this error (MacKenzie et al., 2002). In our particular case, we cannot say that absence indicates that no capercaillie is there at all, and that the habitat is not used in other seasons. However, we consider that absences in 1997–2001 reflect a robust indication of change in the distribution of capercaillie during mating and early breeding season.

Nevertheless our aim was not to compare modelling approaches, but to evaluate different aspects of the habitat associations of Cantabrian capercaillies. There are assumptions, advantages and constraints associated with both modelling procedures, which can be considered as complementary (Carroll et al., 1999). General aims to maximize the generality of the habitat associations, and provides insight into overall habitat availability, whereas Decline takes into account a change in the distribution of the population in the recent decades, and may predict the direction of eventual local extinctions. To the best of our knowledge, this combination of information has not been used so far in habitat modelling.

Given the much better performance of General, at least with its own dataset, one may consider discarding the Decline procedure. However, the ecological meaning must also be taken into consideration in model selection and discussion (Keitt et al., 2002), as it is usually required in the process of selecting explanatory variables. The question arises as to why Decline only provides a fair fit to the data. Among other reasons, all the training points used for Decline come from either extant or historical capercaillie territories, i.e., of overall higher suitability than the pseudo-absence habitat units. Therefore, these training points comprised a smaller range of values of the environmental variables, which decreases statistical power per se, and we feel this may be a common and overlooked problem in habitat modelling (but see Andrén, 1996; Luck, 2002). In other words, Decline deals with finer, more complex processes. General modelling procedure bears higher statistical power, but is also more naive, because it does not consider the ongoing process of population decline. When comparing the predictive ability of models on each other's data sets, we found that Decline performed much better at predicting presence vs. pseudo-absence habitat units than General at predicting presence vs. known absences. Furthermore, Decline provided a smoother classification of habitat units, whereas General accurately predicted presences but showed higher variances in the suitability indexes and a drastic change from high to low suitability with few intermediate values (Fig. 3 and Electronic Appendix 2). Therefore incorporating information on population status provides a more dynamic view of the habitat, and both modelling procedures should be discussed together.

4.2. Conservation implications

The Decline model showed that the response of capercaillie to habitat configuration takes place beyond the local spatial scale (Table 4). Any particular habitat unit would require very high proportions of forest cover both at the local scale and at landscape levels, to reach a suitability index above 0.9. The proportion of forested habitat in a radius of 4 km seems to

ultimately determine the suitability of the habitat, and its positive influence was almost 3 times higher than the proportion of forest cover in the local habitat unit (Table 4). However, we do not claim that our modelling procedure identified the precise scale of capercaillie response to landscape configuration, but that it extends much farther than the forest close to displaying areas. This result is consistent with recent findings showing that coarse-grained habitat models perform better for capercaillie in the Swiss Alps (Graf et al., in press). Although the information we have on the home range of Cantabrian capercaillie is very scarce, the figures for Central European birds range between 132 and 1200 ha, varying with seasonal shifts in activity patterns (Storch, 1997a). Together with our results, these values clearly suggest that both the home range and the effects of habitat spatial configuration extend far beyond the average patch size of suitable habitat in the Cantabrian range, where 55% of the forest fragments are smaller than 1 ha and only 1.4% are bigger than 100 ha (García et al., 2005).

By contrast, although also identifying small amounts of suitable habitat, the General model requires a more relaxed combination of local proportion of forest cover to classify a habitat unit as highly suitable, irrespective of how much forest remains in the neighbourhood (Table 4). This may indicate that the overall availability of suitable habitat is acceptable, but that other factors related to habitat configuration are affecting population decline. Therefore, we cannot conclude that habitat loss or spatial configurations are the most important causes of the population decline, but that they may be playing an indirect role since capercaillie has disappeared from areas with certain habitat characteristics. Predation and resource competition with other herbivores have been cited as potentially important causes of decline in other capercaillie populations (Baines et al., 2004; Storch, 2000a), factors ultimately related to, and modulated by, landscape spatial pattern (Kareiva, 1987; Kurki et al., 2000).

Both modelling procedures identified similar zones as highly suitable, regardless of the absolute values of the index. Moreover, both habitat maps (Fig. 3) picture fairly large gaps in the central part of the region, suggesting a low connectivity of subpopulations. Indeed, the central part of the southern slope of the Cantabrian Mountains is mostly deforested along the southern edge of the mountain range (Electronic Appendix 2), thus, it cannot alleviate an eventual connectivity problem. Should further habitat or connectivity loss occur, the Cantabrian capercaillie population may end up disaggregated into a few isolated subpopulations too small to ensure their own long-term persistence (Grimm and Storch, 2000), more isolated than maximum juvenile dispersal distances known from other populations (Storch, 1997b). Furthermore, capercaillies still remain in habitat units that show habitat suitability indexes below the cut-off values of Decline and General models (30% and 10% of the habitat units, respectively), which may indicate a high risk of local extinction. The variable selection of our models indicates that facilitation of gradual forest recolonization, aided by reforestations with native trees, may substantially improve the habitat suitability. This would be of particular interest in those areas connecting the few remaining highly suitable habitat patches where

capercaillie presence seems safer, thereby providing better suitability of dispersal habitats.

Capercaillie presence appears safer higher up and facing north. Both modelling procedures showed similar effects for the topographic variables, both in univariate logistic regressions (Table 2) and in the minimal models (Table 4). General minimal model positively selected elevation, a variable that also showed a positive relationship in the univariate logistic regressions of the Decline model. This may be related to the overall higher availability of less-disturbed forest at higher altitudes, and to better climatic conditions for the development of forest masses of beech and oak in cooler environments (García et al., 2005), backed up by the inclusion of aspect, as percentage of northern exposure, as a positive factor in the Decline minimal model. This implies a shrinkage of the range towards higher elevations that may reflect synergic negative effects of habitat loss and climate alteration (Travis, 2003). Furthermore, the pattern fits the predicted negative effects of the latter combination on local populations along distribution edges, lower latitudes, isolated mountain tops or forest fragments (Beever et al., 2003; Diamond, 1984; Walther et al., 2002).

In the present study, display grounds were the basic units providing information on capercaillie presence. Even though display grounds sustain high capercaillie activity throughout the year (Picozzi et al., 1992; Storch, 1995), these are basically sites where one or more cocks display for hens in spring. Therefore, cocks attend display grounds in spring for reasons other than mere suitability of habitat, and thus may continue to attract displaying males long after the habitat has lost substantial suitability. This probably adds noise to the modelling capability under the Decline scheme, but it also leads to an interesting (though speculative) insight that merits further investigation: both modelling procedures showed that capercaillie presence is negatively related to variables reflecting anthropogenic disturbance both at the local and the diffusive level (Table 3). This combination of display ground attractiveness plus anthropogenic disturbance suggests that some capercaillie display grounds may act as ecological (or behavioural) traps (Battin, 2004; Kristan and William, 2003). Indeed, it has been found that anthropogenic variables determine areas of higher mortality for another endangered “flagship” in the Cantabrian Mountains, the brown bear *Ursus arctos* (Naves et al., 2003). Capercaillie display grounds are often very well known to local human populations, probably the best known of capercaillie habitats, mainly due to the recent history of legal hunting on grouse populations (Storch, 2000b). Hence, an special effort should be made to preserve highly suitable spots and their surroundings from anthropogenic disturbance, to minimize the occurrence of ecological traps that may attract dispersing animals, thereby accelerating the decline process even further (Delibes et al., 2001).

4.3. Final remarks

We have built predictive models that portray the suitability of the habitat for capercaillie in the northern slope of the Cantabrian Range. We propose these models as tools for the management of this capercaillie population, since “habitat improvement” is one of the first actions that wildlife author-

ities tend to implement. We are well aware, however, that habitat models like ours cannot provide answers to all aspects of the populations modelled, particularly involving demographic parameters (Fahrig, 2001; Tyre et al., 2001). Therefore, there is an urgent need for accurate data about reproductive parameters that could identify source and sink areas, to complement present habitat models.

The amount of extant suitable habitat for Cantabrian capercaillie is very low. Every small patch should be protected against development, and connectivity should be favoured. However, there is no indication that a decline in habitat availability has occurred concurrently with the acute decline in this capercaillie population (Manuel et al., 2003). Hence, we suggest that indirect effects associated with habitat suitability and configuration, such as nest predation and competition with wild and domestic ungulates, should be considered as priority factors in research and management.

Acknowledgements

We thank Javier Naves and Thorsten Wiegand for advice on the process of model building, GIS, and moving window pitfalls. We acknowledge the comments from 4 anonymous reviewers, which greatly improved the statistical procedure and depth of focus. The project was funded by grants to JRO from the Spanish Ministry of Science and Technology (MCYT-BOS-2001-2391-C02-02) and the Asturian Environmental Agency (Consejería de Medio Ambiente). During the writing phase, MQ was funded by an EU Marie Curie IHP Fellowship and MJB by a post-doctoral fellowship from Spanish Ministry of Education. Christine Francis improved the English style.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2005.07.019](https://doi.org/10.1016/j.biocon.2005.07.019).

REFERENCES

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366.
- Andrén, H., 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. *Oikos* 76, 235–242.
- Baines, D., Moss, R., Dugan, D., 2004. Capercaillie breeding success in relation to forest habitat and predator abundance. *Journal of Applied Ecology* 41, 59–71.
- Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* 18, 1482–1491.
- Beever, E.A., Brussard, P.F., Berger, J., 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *Journal of Mammalogy* 84, 37–54.
- Bellamy, P.E., Brown, N.J., Enoksson, B., Firbank, L.G., Fuller, R.J., Hinsley, S.A., Schotman, A.G.M., 1998. The influences of habitat, landscape structure and climate on local distribution

- patterns of the nuthatch (*Sitta europaea* L.). *Oecologia* 115, 127–136.
- Brown, J.H., 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124, 255–279.
- Brown, J.H., Stevens, G.C., Kaufman, D.M., 1996. The geographic range: size, shape, boundaries and internal structure. *Annual Review of Ecology and Systematics* 27, 597–623.
- Burnham, K.P., Anderson, D.R., 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.
- Carroll, C., Zielinski, W.J., Noss, R.F., 1999. Using presence-absence data to build and test spatial habitat models for the fisher in the Klamath Region, USA. *Conservation Biology* 13, 1344–1359.
- Collinge, S.K., 2001. Spatial ecology and biological conservation. *Biological Conservation* 100, 1–2.
- Delibes, M., Ferreras, P., Gaona, P., 2001. Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters* 4, 401–403.
- Diamond, J., 1984. “Normal” extinctions of isolated populations. In: Nitecki, M.H. (Ed.), *Extinctions*. University of Chicago Press, Chicago, IL, pp. 191–246.
- Efron, B., Gong, G., 1983. A Leisurely look at the bootstrap, the jackknife, and cross-validation. *American Statistician* 37, 36–48.
- Engler, R., Guisan, A., Rechsteiner, L., 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology* 41, 263–274.
- Fahrig, L., 2001. How much habitat is enough? *Biological Conservation* 100, 65–74.
- García, D., Quevedo, M., Obeso, J., Abajo, A., 2005. Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain). *Forest Ecology and Management* 208, 29–43.
- Gjerde, I., Wegge, P., 1989. Spacing pattern, habitat use and survival of Capercaillie in a fragmented winter habitat. *Ornis Scandinavia* 20, 219–225.
- Graf, R., Bollmann, K., Suter, W., Bugmann, H., in press. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. *Landscape Ecology*, doi:10.1007/s10980-005-0063-7.
- Grimm, V., Storch, I., 2000. Minimum viable population size of capercaillie *Tetrao urogallus*: results from a stochastic model. *Wildlife Biology* 6, 219–225.
- Gu, W., Swihart, R.K., 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* 116, 195–203.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135, 147–186.
- Hirzel, A., Hausser, J., Perrin, N., 2004. *Biomapper 3.1*. Division of Conservation Biology, University of Bern., Bern. URL: <http://www.unil.ch/biomapper>.
- Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology* 83, 2027–2036.
- Holt, R.D., Keitt, T.H., Lewis, M.A., Maurer, B.A., Taper, M.L., 2005. Theoretical models of species’ borders: single species approaches. *Oikos* 108, 18–27.
- Iremonger, S., Ravilious, C., Quinton, T., 1997. A statistical analysis of global forest conservation. In: Iremonger, S., Ravilious, C., Quinton, T. (Eds.), *A Global Overview of Forest Conservation*. Centre for International Forestry Research and World Conservation Monitoring Centre, Cambridge, UK.
- Jansson, G., Angelstam, P., 1999. Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. *Landscape Ecology* 14, 283–290.
- Kareiva, P., 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature* 326, 388–390.
- Keitt, T.H., 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1, 4.
- Keitt, T.H., Bjornstad, O.N., Dixon, P.M., Citron-Pousty, S., 2002. Accounting for spatial pattern when modelling organism-environment interactions. *Ecography* 25, 616–625.
- King, A.W., With, K.A., 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147, 23–29.
- Kristan, I., William, B., 2003. The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos* 103, 457–468.
- Kurki, S., Nikula, A., Helle, P., Lindén, H., 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* 81, 1985–1997.
- Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. *Biometrics* 33, 159–174.
- Lawton, J.H., 1993. Range, population abundance and conservation. *Trends in Ecology and Evolution* 8, 409–413.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier Science BV, Amsterdam.
- Löfman, S., Kouki, J., 2001. Fifty years of landscape transformation in managed forests of Southern Finland. *Scandinavian Journal of Forest Research* 16, 44–53.
- Luck, G.W., 2002. The habitat requirements of the rufous treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. *Biological Conservation* 105, 383–394.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.L., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- Manuel, C., Díaz-Fernández, P., Gil, L., 2003. La transformación histórica del paisaje forestal de Asturias. Tercer Inventario Forestal Nacional (1997–2006), Madrid (in Spanish).
- McPherson, J.M., Jetz, W., Rogers, D.J., 2004. The effects of species’ range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology* 41, 811–823.
- Mladenoff, D.J., White, M.A., Pastor, J., Crow, T.R., 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3, 294–306.
- Naves, J., Wiegand, T., Revilla, E., Delibes, M., 2003. Endangered species constrained by natural and human factors: the case of brown bears (*Ursus arctos*) in Northern Spain. *Conservation Biology* 17, 1276–1289.
- Obeso, J.R., Bañuelos, M.J., 2003. El urogallo (*Tetrao urogallus cantabricus*) en la Cordillera Cantábrica. Parques Nacionales, Ministerio de Medio Ambiente, Madrid (in Spanish).
- Picozzi, N., Catt, D., Moss, R., 1992. Evaluation of capercaillie habitat. *Journal of Applied Ecology* 29, 751–762.
- Quevedo, M., Bañuelos, M.J., Sáez, O., Obeso, J.R., 2006. Habitat selection by Cantabrian capercaillie at the edge of the species distribution. *Wildlife Biology* 12(3), in press.
- R Development Core Team 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.r-project.org/>.
- Radford, J.Q., Bennett, A.F., 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. *Biological Conservation* 117, 375–391.
- Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158, 87–99.

- Rolstad, J., Wegge, P., 1987. Distribution and size of capercaillie leks in relation to old forest fragmentation. *Oecologia* 72, 389–394.
- Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Cerveny, J., Koubek, P., Huber, T., Stanisa, C., Trepl, L., 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology* 39, 189–203.
- Storch, I., 1995. Annual home ranges and spacing patterns of capercaillie in central Europe. *Journal of Wildlife Management* 59, 392–400.
- Storch, I., 1997a. Male territoriality, female range use, and spatial organisation of capercaillie *Tetrao urogallus* leks. *Wildlife Biology* 3, 149–161.
- Storch, I., 1997b. The role of the metapopulation concept in conservation of European woodland grouse. *Wildlife Biology* 3, 272.
- Storch, I., 2000a. Conservation status and threats to grouse worldwide: an overview. *Wildlife Biology* 6, 195–204.
- Storch, I. (compiler), 2000b. Status survey and conservation action plan 2000–2004: Grouse. WPA/BirdLife/SSC Grouse Specialist Group. IUCN, Glan, Switzerland and Cambridge, UK, and the World Pheasant Association, Reading, UK.
- Suter, W., Graf, R.F., Hess, R., 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology* 16, 778–788.
- Swenson, J.E., Angelstam, P., 1993. Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. *Canadian Journal of Zoology* 71, 1303–1310.
- Thompson, C.M., McGarigal, K., 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). *Landscape Ecology* 17, 569–586.
- Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London, Series B* 270, 467–473.
- Tucker, G.E., Evans, M.I., 1997. Habitats for birds in Europe – A Conservation Strategy for the Wider Environment. BirdLife International, Cambridge, UK.
- Twedt, D.J., Loesch, C.R., 1999. Forest area and distribution in the Mississippi alluvial valley: implications for breeding bird conservation. *Journal of Biogeography* 26, 1215–1224.
- Tyre, A.J., Possingham, H.P., Lindenmayer, D.B., 2001. Inferring process from pattern: Can territory occupancy provide information about life history parameters? *Ecological Applications* 11, 1722–1737.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.