UNIVERSIDAD DE OVIEDO
Dpto. de Biología de Organismos y Sistemas

Modelos espaciales de hábitat y análisis de viabilidad de la población de urogallo en la Cordillera Cantábrica

Adán C. Abajo Chic

2007

UNIVERSIDAD DE OVIEDO
Departamento de Biología de Organismos y Sistemas

TESIS DOCTORAL

MODELOS ESPACIALES DE HÁBITAT Y ANÁLISIS DE VIABILIDAD DE LA POBLACIÓN DE UROGALLO EN LA CORDILLERA CANTÁBRICA

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D. **Tomás Emilio Díaz González**, Director del Departamento de Biología de Organismos y Sistemas de la Universidad de Oviedo

AUTORIZA la presentación ante la Comisión de Doctorado de la Memoria titulada **MODELOS ESPACIALES DE HÁBITAT Y ANÁLISIS DE VIABILIDAD DE LA POBLACIÓN DE UROGALLO EN LA CORDILLERA CANTÁBRICA**, presentada por el Licenciado **Adán César Abajo Chic** para optar al grado de Doctor por la Universidad de Oviedo y realizada bajo la dirección de los Doctores D. José Ramón Obeso y D. Thorsten Wiegand, considerando que ésta representa trabajo de Tesis.

Y para que así conste, expido el presente certificado.

Oviedo, 13 de febrero de 2007

Fdo.: Tomás Emilio Díaz González

UNIVERSIDAD DE OVIEDO
Departamento de Biología de Organismos y Sistemas

D. **José Ramón Obeso Suárez**, Catedrático de Ecología de la Universidad de Oviedo, y D. **Thorsten Wiegand**, Doctor del Departamento de Modelado Ecológico del UFZ Centre for Environmental Research de Leipzig

HACEN CONSTAR que la presente Memoria, titulada "**MODELOS ESPACIALES DE HÁBITAT Y ANÁLISIS DE VIABILIDAD DE LA POBLACIÓN DE UROGALLO EN LA CORDILLERA CANTÁBRICA**", ha sido realizada bajo su dirección en el Departamento de Biología de Organismos y Sistemas de la Universidad de Oviedo por el Licenciado **Adán César Abajo Chic**, y reúne las condiciones necesarias para que su autor pueda optar al grado de Doctor por la Universidad de Oviedo, considerando que ésta representa trabajo de Tesis.

Oviedo, 13 de febrero de 2007

Dr. José Ramón Obeso Suárez Dr. Thorsten Wiegand

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AGRADECIMIENTOS

Llegado este momento, me gustaría dar las gracias a todos aquellos que, de una u otra forma, han contribuido a hacer posible esta tesis. No obstante, no me gustaría extenderme con un listado de sus nombres, pues si así hiciera seguro que alguien quedaría en el tintero. A todo aquel que, por poco que sea, se sienta partícipe de este trabajo, y también a algunos que quizá ni sepan que lo han sido, mi más sincero agradecimiento.

Muy especialmente, quiero agradecer a mi director Moncho Obeso y a Javier Naves por reunirse conmigo, un perfecto desconocido, aquella víspera de San Mateo de hace algo más de cinco años, y por ofrecerme su confianza desde entonces para embarcarme en esta empresa.

Alberto Fernández realizó la mitad del trabajo de campo que sirvió de base para la elaboración del Capítulo 3. Él y el resto de la gente del grupo de ecología terrestre donde aterricé me acogieron tan bien como cabría esperar después de conocerles. Aparte de trabajo, Mariajo, Mario, Javier, Alberto, Isa, Dani, Moncho, “and families” han compartido conmigo algunos muy buenos momentos en lo personal. Gracias a todos.

El departamento-área de ecología está plagado de buena gente así que, aunque no soy un bicho muy sociable, la convivencia con todos ha sido muy agradable, lo cual es de agradecer. Me gustaría agradecer especialmente a Jorge Sostres su permanente disponibilidad para ayudar y su energía positiva.

Gracias también a la gente de carnívoros de Doñana con la que traté durante mi estancia allí, desde el primero al último, sobre todo a Eloy Revilla por el trabajo compartido.

Thorsten Wiegand me recibió en sucesivas estancias en el OESA de Leipzig y acabó convirtiéndose ni más ni menos que en codirector de esta tesis. Le agradezco mucho su cercanía humana y su disposición a implicarse en mi trabajo. De forma indirecta también es el responsable de que haya conocido Alemania, y de forma muy directa el codillo con chucrut.

Finalmente en lo que al trabajo se refiere, quién me iba a decir cuando empecé con esto que mi hermano Norber iba a acabar metido aquí. Gracias a él aprendí a programar y a divertirme haciéndolo.

Y por último, ya que nombro a la familia, gracias a mis padres Norberto e Isabel, por estar ahí cuando lo he necesitado y porque sé que estarán orgullosos. Y gracias a Auxi, por soportarme en todos los sentidos y por alegrarme la vida.

El trabajo de esta tesis ha sido financiado principalmente por el Ministerio de Ciencia y Tecnología mediante el proyecto titulado “Metapoblaciones de vertebrados amenazados en paisajes fragmentados de la Cordillera Cantábrica” (MCYT-01-BOS-2391-CO2-02), así como por diversos líneas de financiación anuales de la Consejería de Medio Ambiente del Principado de Asturias.

Por mi parte, he disfrutado durante su realización de una beca de Formación de Profesorado Universitario del Ministerio de Educación y Ciencia, que incluyó la financiación de las mencionadas estancias en la Estación Biológica de Doñana y en el OESA de Leipzig, y posteriormente de una Ayuda para la Finalización de Tesis Doctoral proporcionada por la Universidad de Oviedo.

CAPÍTULO 1. Introducción general

El tamaño y estructura de las poblaciones varía de forma natural a lo largo del tiempo, ya que el balance entre la ganancia de individuos por reclutamiento o inmigración y la pérdida por emigración o muerte muy raramente se halla en equilibrio (Begon et al. 1990). Sin embargo, debido al incremento paulatino de la actividad humana, la pérdida y fragmentación del hábitat de las especies se ha convertido en un potente factor de desequilibrio de dicho balance. La fragmentación del hábitat trae consigo una estructuración espacial de las poblaciones afectadas, que en caso de ser suficientemente acusada puede producir la división de la población original en pequeñas subpoblaciones conectadas únicamente por puntuales eventos de inmigración-emigración a través de una matriz de hábitat desfavorable (Levins 1969, 1970; Hanski & Gilpin 1991). Estos aportes de individuos entre subpoblaciones se convierten en elemento clave para mantener la estabilidad de la "metapoblación", que de otro modo se verá abocada al declive (Rolstad 1991; Harrison 1994; Harrison & Fahrig 1995; Doncaster et al. 1997; Hanski & Simberloff 1997).

La fragmentación de los paisajes naturales inducida directa o indirectamente por el hombre es así uno de los factores que contribuyen de forma más importante a la pérdida de diversidad biológica (Wilcox & Murphy 1985; véase no obstante Fahrig 2003). Sólo recientemente, tras la constatación de esta pérdida, la conservación de la biodiversidad se ha convertido en un verdadero objeto de investigación científica. Nuevas disciplinas biológicas como la Biología de la Conservación y la Ecología del Paisaje, se han desarrollado desde entonces con el objetivo de proporcionar marcos conceptuales adecuados para el estudio de la distribución espacial de las poblaciones y de los procesos que las amenazan (Turner 1989; Caughley 1994; Meffe & Carroll 1994, 1997; Bissonette 1997; Mace & Balmford 2000; Gutzwiller 2002).

Ecología del Paisaje

La ecología del paisaje es una disciplina común a la ecología y la geografía, cuyo objetivo es estudiar las causas y consecuencias de la heterogeneidad espacial (Forman 1995). De un modo más concreto, se ocupa de estudiar cómo la estructura espacial del paisaje afecta a la abundancia y distribución de los organismos. Desde un punto de vista aplicado, la ecología del paisaje estudia el papel del impacto humano sobre la estructura y función del paisaje, proponiendo mecanismos para su restauración.

Probablemente el concepto fundamental de la ecología del paisaje, que se desprende de su propia definición, es el de la heterogeneidad espacial. A diferencia de la ecología tradicional, que asume que los sistemas son espacialmente homogéneos, el paisaje pasa a estar compuesto por "parches", que difieren entre sí en cuanto a su composición, estructura y calidad. Las relaciones entre los componentes del paisaje se consideran también muy especialmente. Si bien el límite entre los distintos parches del paisaje puede ser más o menos definido (Sanderson & Harris 2000), en la zona próxima al límite entre parches adyacentes se produce el denominado "efecto de borde". Éste consiste en una diferencia ambiental entre el interior del parche y su borde debida a las influencias de los parches adyacentes, que puede determinar una diferente composición o abundancia de especies entre ambas partes.

Otro concepto fundamental en ecología del paisaje es el de "escala", que se define como las dimensiones espaciales o temporales del sistema de estudio (Turner & Gardner 1991). La escala tiene dos componentes: el grano, entendido como el nivel más fino de resolución espacial, y la extensión, entendida como el tamaño del área de estudio (Turner et al. 1989).

Gracias a su origen como disciplina de síntesis biológico-geográfica, la ecología del paisaje tiene la ventaja de utilizar poderosas herramientas geográficas. Una de las más importantes para su aplicación en biología de la conservación son los Sistemas de

Información Geográfica (GIS, por sus siglas en inglés). Los GIS son sistemas para crear, almacenar, analizar y manejar datos espaciales, que permiten relacionar información de diferentes fuentes y convertirla en datos discretos y manejables. Aunque su aplicación va lógicamente más allá de las disciplinas puramente biológicas, su empleo en ecología proporciona un marco donde analizar las interacciones entre los patrones espaciales y la distribución y dinámica de las poblaciones.

Desde el aspecto teórico la ecología del paisaje establece el principio de estabilidad del paisaje, que acentúa la importancia de la heterogeneidad estructural del paisaje en la resistencia y recuperación a los impactos y en la estabilidad total del sistema (Forman & Godron 1986). Este principio es una contribución importante a las teorías ecológicas generales, que destaca la importancia de las relaciones entre los componentes del paisaje. La integridad de los componentes del paisaje ayuda a mantener la resistencia ante las amenazas exteriores, incluyendo la introducción de especies invasoras o el desarrollo y la transformación de la tierra por la actividad humana (Turner et al. 2001).

Análisis de Viabilidad de Poblaciones

El análisis de viabilidad de poblaciones (PVA por sus siglas en inglés) es un método de evaluación de riesgo usado cada vez con mayor frecuencia en biología de la conservación, que se podría definir como el proceso que determina la probabilidad de que una población se extinga dentro de un tiempo determinado (Shaffer 1990; Boyce 1992).

Un PVA consiste básicamente en la construcción de un modelo matemático que evalúa los factores que pueden tener influencia sobre el declive de una determinada población o especie. Si bien es obvio que la realidad es demasiado compleja y que dicho modelo no es más que una simplificación de la misma, sus aplicaciones resultan muy útiles en el campo de la conservación. Aparte de la propia evaluación de los factores que provocan el declive, un PVA proporciona información sobre cómo el manejo de los recursos puede invertir la tendencia negativa de la población actuando sobre los factores que la provocan. Su potencialidad como herramienta de evaluación ha permitido que la Unión Internacional para la Conservación de la Naturaleza (IUCN) los reconozca como criterios valiosos para evaluar de modo eficiente el riesgo de extinción y las opciones adecuadas de manejo de las poblaciones (IUCN 1994). Es importante destacar que cada PVA se desarrolla individualmente para una población concreta y, por lo tanto, cada PVA es único.

De la inclusión de los PVA en el marco conceptual establecido por la ecología del paisaje surgen los modelos de población espacialmente explícitos (SEPMs en inglés). Estos modelos se valen normalmente de un GIS para construir mapas de calidad del hábitat, de forma que el modelo simula el efecto de la estructura espacial del paisaje en la dinámica de la población (Pulliam et al. 1992; Dunning et al. 1995; Wiegand et al. 1999, 2004).

Recientemente, los modelos basados en el individuo han permitido la inclusión de reglas de comportamiento que describen la respuesta de los individuos al paisaje, pudiendo así relacionar el uso del espacio por los individuos (dispersión y selección de hábitat) con los fenómenos a escala de la metapoblación de una manera explícita (Pulliam & Dunning 1995; Wiegand et al. 1999). Sin embargo, una crítica importante en el uso de estos modelos es la incertidumbre en la determinación de los parámetros, debido a la dificultad intrínseca para obtener información sobre el comportamiento de los individuos así como a la carencia de validación de los modelos (Wiegand et el al. 2004). Los posibles errores en los parámetros demográficos pueden propagarse dando lugar a errores mayores en las predicciones del modelo (Wennergren et al. 1995; Wiegand et al. 2003, 2004), habiéndose incluso argumentado la imposibilidad práctica de tener acceso a suficientes datos de campo como para estimar los parámetros demográficos y de dispersión con la suficiente exactitud para evitar la propagación de los errores (Ruckelshaus et al. 1999).

Más recientemente aún, el modelado orientado por patrones se ha propuesto como respuesta a los mencionados problemas de incertidumbre (Grimm et al. 2005; Wiegand et al. 2003, 2004). Aunque nuestro conocimiento del comportamiento individual siga siendo escaso, esta nueva aproximación ayuda a resolver este problema accediendo a fuentes adicionales de datos para una estimación indirecta de los parámetros del modelo. Estos datos adicionales provienen de un nivel de organización más alto que el individual, como por ejemplo tendencias poblacionales (Wiegand et al. 1998, 2004) o datos de presencia-ausencia en poblaciones espacial estructuradas (Hanski 1994). Los datos sobre la dinámica y estructura de la población pueden así ser utilizados como valiosas fuentes de datos que reflejan los procesos ecológicos subyacentes.

El urogallo cantábrico

El urogallo (*Tetrao urogallus*) es un ave forestal de distribución paleártica, con una extensa distribución que comprende desde el este de Siberia hasta el suroeste de Europa. Pertenece a la subfamilia de las tetraónidas, siendo la de mayor tamaño entre las especies de dicho grupo y una de las mayores aves forestales del Paleártico. Presenta un acusado dimorfismo sexual, siendo el tamaño de los machos, que pueden alcanzar los 5 Kg., aproximadamente el doble que el de las hembras (Castroviejo 1975; Cramp & Simmons 1980).

El hábitat primario del urogallo es el bosque climácico boreal, dominado por bosques maduros. Se caracteriza por la presencia de coníferas, con estructura forestal abierta y coberturas de copas moderadas que permiten el desarrollo de un sotobosque de arándano (*Vaccinium myrtillus*) (Rolstad & Wegge 1987; Picozzi et al. 1992; Storch 1993). El urogallo es un folívoro típico del bosque boreal paleártico. Durante el invierno, la base de su alimentación la constituyen las acículas de coníferas, preferentemente *Pinus sylvestris*. En verano, incorpora a su dieta brotes, hojas, flores y frutos de varias herbáceas y matorrales, especialmente de arándano. En esta época, los pollos y juveniles dependen en gran medida de los insectos, en especial de las orugas que viven sobre *Vaccinium myrtillus* (Seiskari 1962; Jacob 1987; Storch et al. 1991; Storch 1993; Summers et al. 2004; Wegge et al. 2005).

El proceso de fragmentación comentado anteriormente supone no sólo el aislamiento de parches de hábitat sino la pérdida de superficie de hábitat respecto al paisaje continuo original, por lo que afecta particularmente a especies que precisan grandes territorios y tienen requerimientos de hábitat estrictos (Rolstad 1991). El área de campeo del urogallo es muy amplia, variando entre 100 y 1000 hectáreas (Gjerde & Wegge 1989; Storch 1995) dependiendo de las condiciones locales. Este hecho, unido a su sensibilidad a la perturbación humana, convierten al urogallo en una especie de las denominadas "paraguas", así como indicadora de la salud de los ecosistemas donde habita (Boag & Rolstad 1991; Suter et al. 2002; Pakkala et al. 2003).

La subespecie cantábrica (*Tetrao urogallus cantabricus*, Castroviejo 1967) ocupa un rango de aproximadamente 5000 Km^2 en la Cordillera Cantábrica, lo que constituye el borde suroeste del área de distribución de la especie. Su categorización como subespecie ofrece cierta controversia, no siendo reconocida como tal por Cramp & Simmons (1980), aunque sí posteriormente por Potapov & Flint (1989) y del Hoyo et al. (1994). Se trata de una población relicta completamente aislada de las poblaciones pirenaicas más cercanas, lo que la ha llevado a configurar una Unidad Evolutivamente Significativa (Rodríguez-Muñoz et al. 2006; Storch et al. 2006). La subespecie se adapta a la categoría de "amenazada" de acuerdo a los criterios de la IUCN (Storch et al. 2006), debido principalmente a la fragmentación de los bosques y a la presión humana, siendo la población de urogallo más amenazada del mundo (Storch 2000). En los últimos 25 años, el porcentaje de ocupación de las áreas de exhibición ha descendido más del 65% (datos propios), estimándose ya en 2001 un tamaño de población de no más de 500 adultos (Obeso & Bañuelos 2003).

Pinus sylvestris está prácticamente ausente de la Cordillera Cantábrica, donde la dieta invernal del urogallo se fundamenta en brotes de hayas, hojas de helechos y hojas de acebo (Castroviejo 1975; Martínez 1993; Rodríguez & Obeso 2000). El hábitat típico del urogallo en la Cordillera Cantábrica es el hayedo maduro (*Fagus sylvatica*), tanto en masas puras como mezclado con *Quercus petraea*, *Betula alba* o *Ilex aquifolium*, aunque en algunas zonas estas últimas especies pueden llegar a ser dominantes.

Área de estudio

La Cordillera Cantábrica es una cadena montañosa que se extiende en paralelo a la costa cantábrica de este a oeste a lo largo de aproximadamente 300 Km. Presenta una compleja historia geológica, lo que, unido a la proximidad al mar por la vertiente norte, le confiere un relieve muy acusado; el gradiente es lógicamente más acusado en la vertiente norte, con una pendiente media del 34%, mientras que en la cara sur ésta es del 21%. La altitud máxima es 2648 metros, aunque son numerosas las cimas que sobrepasan los 2000 m.

El clima es húmedo y templado debido a la influencia del mar al norte, con precipitaciones distribuidas a lo largo de todo el año. Los suelos son eminentemente calcáreos en las zonas central y oriental, mientras que en la occidental aparecen con mayor frecuencia suelos silíceos. Los bosques son caducifolios, dominados por el haya y el roble albar, pero su composición no es homogénea a lo largo de la cordillera. El haya domina claramente sobre el resto de especies en las zonas central y oriental, mientras que en el oeste, coincidiendo con los suelos silíceos, la abundancia del roble, acompañado por el abedul, aumenta notablemente. Escobas (*Cytisus* sp., *Genista* sp.), brezos (*Erica* sp.), brecina (*Calluna vulgaris*) y arándano (*Vaccinium myrtillus*) son las principales especies de matorral. Todas ellas aparecen en toda el área, aunque sus abundancias relativas, así como su localización en relación con el bosque, difieren entre los mencionados dominios calcáreo y silíceo. Por encima de 1700 m. de altitud las condiciones climáticas impiden el desarrollo del bosque, predominando la vegetación subalpina (Díaz & Fernández 1987).

Aunque el grado de manejo es actualmente bajo, los bosques cantábricos han sido utilizados por el hombre desde antiguo y están hoy muy fragmentados (véase Capítulo 2 - García et al. 2005), soportando actualmente una elevada presión de herbivoría por parte de ungulados tanto domésticos como salvajes. Los bosques actuales son maduros o semi-maduros, aunque los bosques secundarios también son abundantes en determinadas zonas debido a los fuegos o el abandono de pastos. De modo general, el paisaje de la Cordillera Cantábrica consiste en fragmentos forestales embebidos en una matriz no forestal compuesta por pastos, zonas de matorral y pequeñas aldeas (Mapa Forestal de España 2000; García et al. 2005).

OBJETIVOS Y ORGANIZACIÓN DE LA TESIS

Esta Tesis constituye una aproximación multiescalar a la ecología y la dinámica de la metapoblación de urogallo cantábrico. Su objetivo general es estudiar las relaciones entre el urogallo y su hábitat, y determinar la viabilidad de la metapoblación en un paisaje forestal altamente fragmentado. Con este fin se construyeron modelos de selección de hábitat a distintas escalas, así como un modelo de población espacialmente explícito que simula el comportamiento de los individuos en relación con su hábitat. Esperamos que estos modelos permitan, por un lado, entender la dinámica de la población y las causas de su declive, y por otro, predecir correctamente la distribución espacial de la especie.

El cuerpo de la tesis se compone de 5 capítulos, que a modo de esquema podríamos dividir en tres partes:

- En la primera parte (Capítulo 2), se describen los patrones de fragmentación forestal de la Cordillera Cantábrica. Mediante cartografía digital con ayuda de un GIS, se analizaron la composición y la configuración forestal del paisaje para determinar cómo las diferentes comunidades se ven afectadas actualmente por procesos de fragmentación. Siendo el bosque el hábitat primordial del urogallo, el estudio de la fragmentación forestal no es sino el estudio de la estructura espacial del hábitat del urogallo a escala de paisaje.

- En la segunda parte de la tesis (Capítulos 3 y 4) se llevan a cabo análisis de uso de hábitat a distintas escalas, mediante los cuales tratamos de identificar las características del hábitat que mejor predicen la presencia de la especie. La selección de hábitat es un proceso que posee una jerarquía espacial, de forma que los procesos que la determinan son diferentes en diferentes escalas (Wiens 1989; Levin 1992; Graf et al. 2005):

Análisis de selección del microhábitat (Capítulo 3). Aunque tradicionalmente se ha considerado el área de exhibición o cantadero como el hábitat del urogallo, éste varía según la época del año abarcando una extensión mucho mayor. Mediante muestreos bimensuales en dos áreas independientes de la cordillera con la extensión suficiente para incluir el área de campeo anual de los individuos, se llevó a cabo la localización de indicios de presencia de la especie. De esta forma, tomando diversas variables ambientales de estructura y composición vegetal se caracterizó el hábitat empleado por el urogallo a lo largo del ciclo anual. Con ello desarrollamos un modelo predictivo de presencia de la especie a escala de microhábitat.

Análisis de la calidad del hábitat a escala de paisaje (Capítulo 4). El paisaje montano de la cordillera se filtró con una malla dividida en celdas de 25 ha en las que se sintetizaron variables relacionadas con la vegetación, el grado de humanización y la topografía del terreno. Partiendo de datos de presencia-ausencia en los cantaderos en la época de celo se obtuvo, mediante regresiones logísticas múltiples, la probabilidad de presencia de la especie en cada unidad de hábitat como indicador de su calidad. Se llevó a cabo una aproximación bidimensional, desarrollando por separado modelos de calidad natural del hábitat (se asumió relacionada con la reproducción) y modelos de calidad humana del hábitat (relacionada con mortalidad de los individuos). Con la combinación de ambos modelos se construyó un mapa que permite categorizar funcionalmente el hábitat del urogallo, y que funciona como modelo predictivo de distribución de la especie.

- Finalmente, la tercera parte de la tesis (Capítulos 5 y 6) versa sobre los modelos de población espacialmente explícitos, que simulan el comportamiento de los individuos en su propio hábitat y evalúan el riesgo de extinción de la subespecie. El componente espacial del modelo de población consiste precisamente en los mapas de calidad de hábitat construidos en el Capítulo 4, que funcionan como representación del paisaje donde la población se desarrolla.

El modelo espacialmente explícito de dispersión (Capítulo 5) se construyó mediante un modelo informático que simula el movimiento de los individuos durante el proceso de dispersión. Los objetivos de este modelo fueron, por un lado, la obtención de unas reglas de dispersión que pudieran ser utilizadas en el modelo de población, y por otro, el estudio de la influencia del proceso de dispersión sobre la dinámica de desocupación de cantaderos observada en toda la cordillera.

Finalmente, se construyó un modelo global de población (Capítulo 6) que, incluyendo al anterior, reproduce el comportamiento de la población mediante la simulación del comportamiento de cada individuo durante el ciclo anual en relación con el resto de individuos y su hábitat. Los parámetros del modelo fueron ajustados de forma que se reprodujeran los patrones de distribución y extinción observados en la historia reciente de la población. El modelo permite determinar la influencia de cada parámetro demográfico sobre la probabilidad de extinción, así como generar distintos escenarios futuros para averiguar los puntos clave en la gestión de la población.

Los resultados de esta tesis suponen un importante avance en el conocimiento de los requerimientos de hábitat por parte del urogallo cantábrico y las causas demográficas de su declive. Asimismo, proporcionan herramientas valiosas para una más adecuada gestión de la población y manejo de su hábitat. En el Capítulo 7 se discuten estos y otros aspectos y se detallan las conclusiones de la tesis.

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CAPÍTULO 2. Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain)

Patrones de fragmentación y protección del bosque montano en la Cordillera Cantábrica

Daniel García, Mario Quevedo, J. Ramón Obeso, Adán Abajo. 2005. Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain). Forest Ecology and Management 208: 29-43

2.1. INTRODUCTION

The negative consequences of habitat loss and the concomitant fragmentation are evident in both recently and historically managed forests of temperate regions (Whitcomb et al. 1981; Harris 1984; Wilcove et al. 1986; Santos et al. 1999, 2002; Lindermayer and Franklin 2002). Among processes driven by fragmentation, the population declines of forest species, the alteration of species interactions (e.g. predation, pollination), and the disruption of key ecological functions are major causes of forest biodiversity change (Harrison and Bruna 1999; Davies et al. 2001; Lindermayer and Franklin 2002). In this context, a growing theoretical and empirical framework links these processes with the landscape configuration and composition of fragmented forests (Noss 1990; Fahrig and Merriam 1994; Harrison and Bruna 1999). In fact, it is known that landscape properties such as the proportion of forest habitat in the landscape (Andrén 1994; Cooper and Walters 2002; Fahrig 2002), the size distribution of fragments (Wilcove et al. 1986; Andrén 1994; Laurance et al. 2002), the fragment shape (Andrén 1995; Murcia 1995; Hill and Caswell 1999) and the degree of fragment isolation (Verboom et al. 1991; Andrén 1994; Laurance et al. 2002) underpin the impoverishment of forest biodiversity.

The explicit relationship between fragmentation and biodiversity makes essential the analysis of landscape patterns for forest conservation and management purposes (Turner et al. 2001; Guztwiller 2002, and references therein). For example, forest reserve design has frequently taken into account fragmentation patterns to preserve larger and less isolated forest fragments (Harris 1984; Ranta et al. 1998; Lambeck and Hobbs 2002), and to establish priorities for the protection of species sensitive to fragmentation by preserving their habitats (Arnold 1995; Rebane et al. 1997, and references therein). More recently, the inclusion of small fragments in protection networks has been emphasized, since these small reserves might represent high-quality remnants, especially in chronically fragmented landscapes where large reserves include higher proportion of degraded land (Schwartz 1999; Götmark and Thorell 2003). Complementary to these fragmentation concerns, the study of landscape composition might be applied to conservation goals such as the protection of rare landscape elements and the establishment of reserve networks efficiently representing forest heterogeneity, and thus biological diversity, at regional scale (Caicco et al. 1995; Scott et al. 2001; Lambeck & Hobbs 2002). The degree of biodiversity representativeness achieved by a reserve network will depend on its comprehensiveness, i.e. its ability to contain the full range of forest habitat types, but also on its adequacy, that is, the amount of each habitat type represented (Pressey et al. 1993; Lambeck & Hobbs 2002). In this sense, international commissions have called for the near-protection of a target percentage (≥10%) of the total land area of each ecosystem or habitat type, to maintain ecological processes and biological phenomena at the regional scale (Soulé & Sanjayan 1998; and references therein). Despite that this target coverage is considered far from adequate (Soulé & Sanjayan 1998), it can be still a useful tool for documenting a serious lack of representativeness in reserve networks (e.g. Caicco et al. 1995; Scott et al. 2001; Reyers et al. 2001).

The overall goal of the present study is to evaluate the fragmentation patterns and the protection status of the historically managed montane forest in the Cantabrian range (NW Spain). This mountain range contains the largest portion of the remnant Atlantic deciduous forests on the Iberian Peninsula. It represents the southernmost boundary of this system in Western Europe and is still sheltering high plant and animal species richness, because it is an ecotonal zone between the Eurosiberian and the Mediterranean regions in Europe (Polunin and Walters 1985; Díaz and Fernández 1987; Rebane et al., 1997). Our specific goals are:

1) To describe the composition and configuration of fragmented forest communities, by considering different forest types as particular components of the regional landscape

2) To evaluate the ability of the current reserve network to cope with fragmentation as well as to represent the heterogeneity of the Cantabrian forests at the landscape level.

2.2. METHODS

2.2.1. Study area

This study considers the montane area of the Cantabrian range in the Asturias region (NW Spain), i.e. roughly covering the northern exposure of the range. The study area spans from ca. 42.8° to 43.5 N, and 4.5° to 7.1 W (Fig 1). The landscape of study was arbitrarily established as the area above 700 m.a.s.l. up to the highest peak at 2,648 m.a.s.l., comprising 416,491 Ha. We considered as potential forest area the surface comprised between 700 and 1700 m.a.s.l. (montane lower limit and tree-line, respectively, Díaz and Fernández 1987), accounting then for 389,379 Ha. We considered this potential forest area to approximately fit to the surface of original, once unfragmented forests. The climate of the region is Atlantic, with precipitation distributed throughout the year. Annual average temperature is ca. 8.2ºC and total precipitation is ca. 1,250 mm. Originally covered by Atlantic deciduous forests, the Cantabrian range has a long history of deforestation by human causes. Indeed, Holocene pollen analysis reveals major decreases in forest cover associated to anthropogenic activity by 3000 BP (Muñoz et al. 1997). Historically, traditional cattle raising and selective logging transformed large patches of natural forests to pasturelands. More recently, other factors such as road construction, surface mining, increased fire frequency by human-induced causes, and timber exploitation in plantations have accounted for additional losses of natural forest habitat. Most of the forests in this area might be considered as mature forest with some degree of management, but some second-growth forests have developed during the last century after pasture abandonment. Thus, the current regional landscape contains remnant forest fragments standing out from a non-forest matrix mainly composed of pastures, heathlands in abandoned meadows and areas of shallow soil, and scattered small villages.

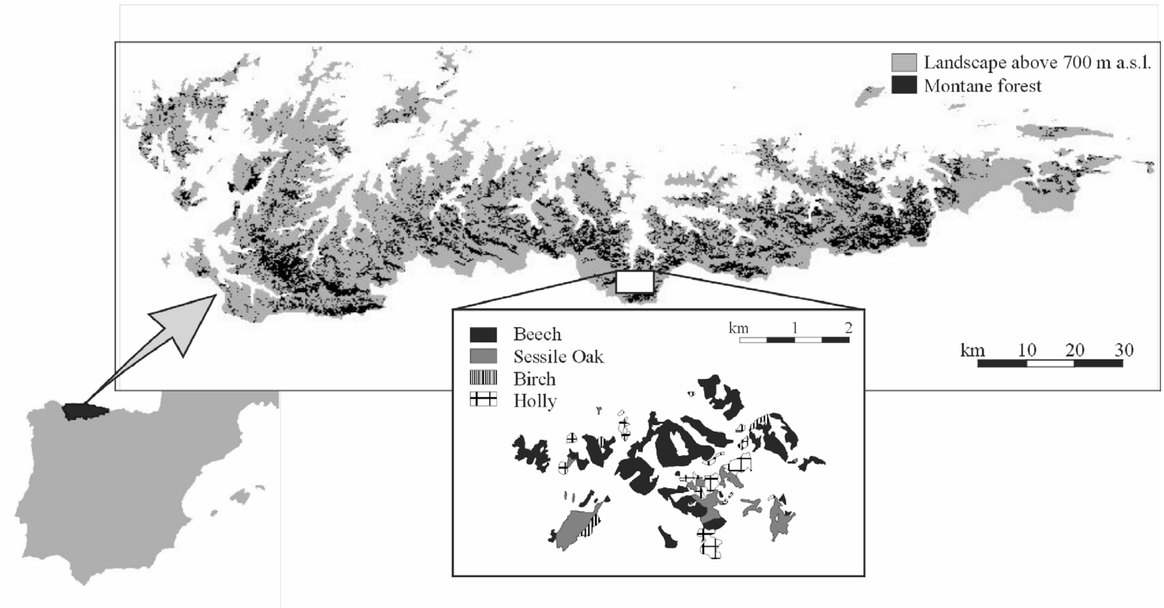

Figure 1. Map of the study area representing the geographical location, the sampled landscape in the Cantabrian range and the composition of forest fragments.

2.2.2. The GIS database

Vegetation and topographic information was derived from the geographic information system (GIS) of the regional environmental agency (Consejería de Medio Ambiente, Principado de Asturias), which represents the actual (not potential) vegetation cover and was generated in 1994. To obtain the vegetation layer, we merged together 37 single 1:25,000-scale sheets, each covering ca. 126 km2. The available vegetation data of forest vegetation, in the form of vectorial polygons, was classified into eight main different types, depending on dominant canopy species: 1- beech *Fagus sylvatica* L. (Fagaceae), 2- Pyrenean oak *Quercus pyrenaica* Willd. (Fagaceae), 3- sessile oak *Quercus petraea* Liebl. (Fagaceae), 4- ash-maple *Fraxinus excelsior* L. (Oleaceae) – *Acer pseudoplanatus* L. – *Acer platanoides* L. (Aceraceae), 5- white birch *Betula alba* L. (Betulaceae), 6- holly *Ilex aquifolium* L. (Aquifoliaceae), 7- rowan *Sorbus aucuparia* L. (Rosaceae), and 8- conifer plantations [mainly reforestations of *Pinus sylvestris* L. and *Pinus radiata* D. Don (Pinaceae)].

We considered a monospecific forest patch, in the aforementioned terms, as a forest fragment whenever isolated in a non-forest matrix. Sometimes, forest classes appeared in patches adjacent to each other (Fig. 1). In such cases, we considered that the adjacent forest classes formed a unique forest fragment surrounded by non-forest habitats. Then we calculated the area of the whole fragment, and the area occupied by each habitat type, and assigned each fragment to one of the eight forest classes outlined above, depending on the identity of the dominant class (in terms of coverage) among the patches within the fragment. The digital map of forests resulting from the aforementioned procedure was rasterized to a cell size of 15 m, a patch being defined as any collection of pixels that touch either at sides or corners, i.e. 8-neighbour clumping method. However, we retained the vectorial vegetation map in order to perform several database-related calculations.

2.2.3. Topographic data

To form the topographic base of the vegetation information, we built a digital elevation model (DEM) with a cell size of 100 m from 1:200,000 digital elevation contours (50 m elevation interval). We used the DEM raster file to derive slope and aspect information for each 100 m cell. Subsequently, we assigned elevation, slope and aspect to forest fragments. Each fragment was assigned its average elevation and slope values. Original aspect data (0 to 360º) were reclassified into four quadrants according to the exposure to cold weather: northern, 316º to 45º; eastern, 46º to 135º; southern, 136º to 225º; and western, 226º to 315º. Then we assigned to each fragment its most frequent aspect, i.e. the mode aspect of the DEM cells within the fragment.

2.2.4. Fragmentation patterns

Landscape level metrics

We used FRAGSTATS (McGarigal et al. 2002) on the raster data to calculate the coverage for all montane forest and for each forest class within the landscape, and the forest class occurrence in terms of percentage of fragments belonging to each class.

Within fragment heterogeneity

We obtained the number and coverage of the different patches included in each fragment, calculating a Simpson's index of within-fragment diversity as $SI = 1/\sum pi2$ (where pi = coverage of the forest class i).

Fragment size, shape and isolation indexes

We used FRAGSTATS to obtain the following characteristics of fragments: fragment size, fragment shape via fractal dimension, and isolation via Euclidean nearest neighbour distance (NND) and proximity index. Fractal dimension (D) characterises the degree of shape complexity of a polygonal fragment, such that the perimeter (P) is related to the area (A) by $P = \surd AD$ (i.e., $\log P = 1/2D \log A$). For simple Euclidean shapes $P = \surd A$ and $D = 1$, whereas for increasingly complex shapes, the perimeter becomes plane-filling and $P = A$ with $D = 2$ (Mladenoff et al. 1993; Pan et al. 2001; McGarigal et al. 2002). Proximity index accounts for the number, the size and proximity of neighbouring fragments within a specific search radius from a focal fragment, higher index values indicating lower isolation (Gustafson & Parker 1992). That is, isolation decreases for fragments surrounded by a higher number of fragments, bigger fragments or/and nearer fragments. Since the choice of a search radius is arbitrary, we firstly checked for differences in the behaviour of the proximity index at different search radii, from $d = 30$ m (the minimum nearest neighbour distance found in the database) to increasing distances in a log scale ($d = 300$, 3000, and 30000 m). We found that proximity values asymptotied at d300 for all forest classes, maintaining the ranking of differences among classes at the higher scales (based on ANOVAR considering the scale of distance as a repeated measure term). Thus, all subsequent analyses involving proximity index were performed at d300. Isolation indexes for each fragment were calculated separately for neighbours of the same class and for neighbours of any class. Additionally, an index of dispersion at the landscape scale was calculated for each forest class as $Rc = 2dc(\lambda/\pi)$, where dc = mean of the same-class NND and λ = density of fragments ($Rc > 1$ indicates patches are regularly distributed, $Rc = 1$ patches are randomly distributed and $Rc < 1$ patches are aggregated; Forman 1995).

2.2.5. Fragmentation and protection status

A fragment was considered under protection when its surface was total or partially included within the territory of an established Protected Area. We derived this information from the GIS database. The regional reserve network included in the studied landscape is currently composed of 4 areas under legal protection: the Regional Reserve and “Man and the Biosphere” Reserve “Reserva Natural Integral de Muniellos”, the Regional Parks and MAB Reserves “Parque Natural de Somiedo” and “Parque Natural de Redes”, and the National Park “Parque Nacional de Picos de Europa” (Anon. 1994). These reserves have been established in the last 20 years, excepting the Picos de Europa National Park, which was established in 1918. Reserves do not exclude traditional land uses such as cattle grazing (excepting in the Muniellos Reserve) but imposse legal restrictions on new land uses such as road construction, mining and timber deforestation.

2.2.6. Statistical analyses

Elevation, slope, fragment size and perimeter were compared among forest classes using ANOVA. We performed ANCOVA with fragment size as a covariable to check for fragment size effects on the differences among classes on heterogeneity. The same procedure was used to compare fractal dimension among forest classes. For that analysis, we included only fragments between 0.56 Ha and 10 Ha, to achieve a range of sizes adequately represented in all forest classes, and to avoid biases resulting from the inclusion of smaller fragments (see also Turner et al. 2001). Aspect and size distributions were compared among forest classes by Chi-square and Median test, respectively. ANOVAR was performed to compare proximity index among forest classes, considering the neighbour type (same-class or any-class neighbours) as repeated measures.

Our analysis of fragmentation in relation to protection level had two steps. First, we checked for the efficiency of the current reserve network to cope with future fragmentation. For that, we compared, between protected and unprotected fragments, fragmentation surrogate variables (fragment size, shape and isolation indexes), and altitude and slope by ANOVA, whereas aspect was compared by Chi-square. Second, we evaluated whether the current reserve network was representing the availability of the different forest classes in the landscape, or conversely, that some forest classes were under-represented relative to others (Gap Analysis; Caicco et al. 1995; Scott et al. 2001). For that, we compared via Chi-square the actual distribution of protected fragments among different forest classes with a theoretical distribution of protected fragments depending on the relative class-availability in the landscape.

Data corresponding to rowan forest were excluded from most analyses, due to the small sample size in relation to remaining forest classes (see Table 1). Type III Sum of Squares was chosen since the design of the database was unbalanced (Shaw & Mitchell-Olds 1993). When necessary, variables were transformed for normality, homocedasticity and linearity, using the arcsine transformation for data expressed as frequencies, and the log-transformation for the remaining ones (Zar 1996). All analyses were performed with JMP statistical package (SAS Institute Inc. 2001).

2.3. RESULTS

2.3.1. Fragmentation patterns

Landscape level metrics

Current forests covered 90336 Ha, accounting for 21.7% of the studied landscape and 23.2% of the potential forest area within this landscape, and occurring in 12228 forest patches that aggregated in 8978 forest fragments. Beech forest was the dominant class, both in terms of number of fragments and coverage in the landscape (Table 1). Oak and birch forests showed intermediate values of these variables, whereas the remaining classes represented together less than 21% of fragments and 9% of total forest area.

Within-fragment heterogeneity

Most of the fragments contained only a single patch type (80-95% of fragments for all forest classes, Table 1) although the maximum number of patches per fragment was as high as 186. The number of patches per fragment and the diversity of patches (Simpson's index) were significantly higher for beech forests than for the remaining classes (Table 1). However, both the number of patches by fragment and the diversity of patches were positively related to fragment size, leading to significant interaction terms in the ANCOVAs considering the forest class as main effect and fragment size as a covariable (number of patches: $F6,8660 = 54.14$, $P<0.0001$; Simpson's index: $F6,8660 = 7.92$, $P<0.0001$).

Topography

Forest classes were distributed differentially in altitude, with pine plantations and ash-maple forests occurring at lowest altitudes on average, oaks, birch and beech at middle altitudes, and holly and rowan above 1100 m a.s.l. ($F6,8914 = 245.20$, $P<0.0001$, one-way ANOVA; Table 1). Aspect differed significantly among forest classes (Chi-square = 992.42, $P<0.0001$, d.f. = 21, Table 1), beech and birch appearing mostly northwards, oaks southwards,

Table 1. Characteristics of forest fragments of different classes related to their occurrence in the landscape and the forested surface, the within-fragment heterogeneity, topography and physiognomy[a].

	Beech	Pyrenean Oak	Sessile Oak	Ash-Maple	Birch	Holly	Rowan	Conifers	All classes
No. of fragments (%)	2417 (26.92)	1442 (16.02)	1593 (17.74)	456 (5.08)	1663 (18.52)	456 (5.08)	56 (0.63)	895 (9.97)	8978
Landscape surface (%)	13.77	1.25	3.69	0.25	1.14	0.20	0.03	1.36	21.73
Forest surface (%)	63.45	5.78	17.02	1.13	5.26	0.94	0.14	6.27	-
Single-patch fragments (%)	83.06	91.18	90.19	91.31	90.64	94.54	80.00	91.55	88.82
No. patches per fragment	1.89±0.14^{a}	1.17±0.03^{b}	1.35±0.07^{b}	1.16±0.04^{b}	1.18±0.02^{b}	1.09±0.03^{b}	1.22±0.06	1.26±0.06^{b}	1.07±0.00
Simpson's Index	1.10±0.01^{a}	1.06±0.01^{b}	1.06±0.01^{b}	1.07±0.01^{ab}	1.06±0.00^{b}	1.04±0.01^{b}	1.13±0.04	1.05±0.01^{b}	968.2±2.5
Altitude (m a.s.l.)	1043.8±4.8^{a}	886.1±3.7^{b}	978.9±5.1^{c}	846.9±6.1^{d}	983.0±7.9^{c}	1129.3±11.2^{e}	1444.2±21.5	799.5±3.6^{f}	654.0±1747.1
Aspect (Mode, %)	N 40.49	S 39.61	S 32.54	E 34.07	N 36.07	W 32.50	N 48.21	E 27.96	-
Slope (%)	20.53±0.19^{a}	18.12±0.20^{b}	21.51±0.19^{c}	17.49±0.41^{be}	14.88±0.23^{d}	16.83±0.40^{e}	19.62±0.89	10.03±0.27^{f}	17.88±0.09
Area (Ha) average	23.72±4.43^{a}	3.63±0.34^{b}	9.65±2.87^{b}	2.25±0.38^{cd}	2.86±0.34^{c}	1.85±0.39^{d}	2.33±0.50	6.33±1.15^{c}	10.06±1.31
Area (Ha) median	1.19^{a}	0.87^{b}	0.87^{b}	0.63^{cd}	0.70^{c}	0.54^{d}	0.89	0.61^{cd}	0.83
Perimeter (km)	3.99±0.55^{a}	1.30±0.07^{b}	2.02±0.29^{b}	0.96±0.08^{cd}	1.03±0.06^{c}	0.79±0.08^{d}	1.01±0.14	1.27±0.12^{cd}	2.06±0.16

[a] Mean (± SE) values followed by different superscript letters are different at $P < 0.05$ after Bonferroni-Dunn test (means) or partial Chi-square (medians). The modal aspect and the percentage of fragments showing this aspect are indicated.

pines and ash-maple eastwards, and holly westwards. Steepness was lowest at pine plantations and highest for sessile oak and beech (F6,8914 = 269.22, P<0.0001; Table 1).

Fragment size (area)

The distribution of fragment size was strongly biased towards small values, with 55.4% of the fragments smaller than 1 Ha. Only 1.4% of fragments were >100 Ha and 0.1% were >1000 Ha. All forest classes showed distributions skewed towards small sizes (Fig. 2), but differed significantly in average fragment size (F6,8915 = 58.81, P<0.0001, one-way ANOVA), perimeter (F6,8915 = 54.71, P<0.0001), and the size distribution (Chi-square = 195.56, P<0.0001, d.f. = 6, Median test). Beech fragments were larger than the other classes, whereas holly and ash-maple forests were, on average, the smallest fragments (Figure 2, Table 1).

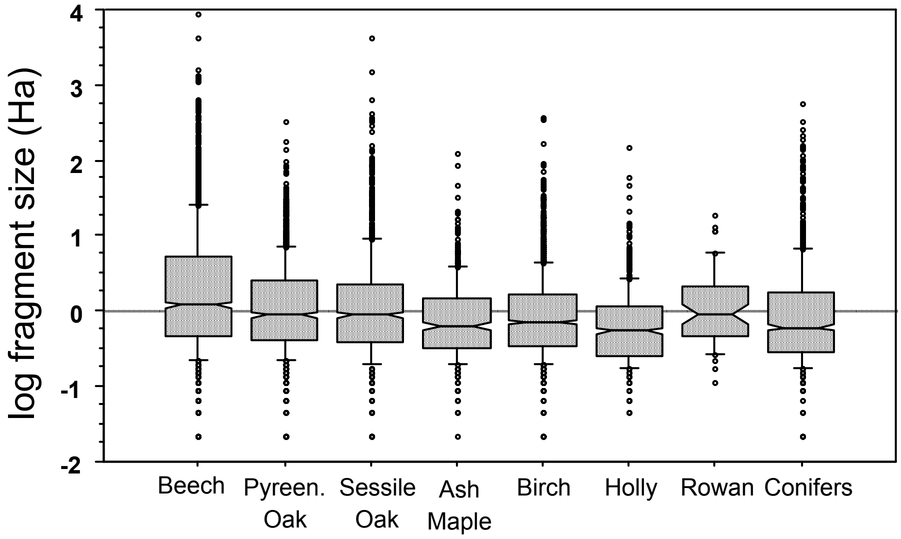

Figure 2. Box plots representing the size distribution of fragments belonging to different forest classes.

Shape (fractal dimension)

Fragment shape differed among forest classes (F6,4753 = 12.42, P<0.0001, ANCOVA), with pine plantations having the lowest average fractal dimension (Fig. 3). Among natural forests, holly and beech were the classes with the most regular shape. Fractal dimension increased proportionally to fragment size for all classes (F1,4753 = 430.90, P<0.0001) while differences in fractal dimension among classes were independent from fragment area (Interaction forest class-area: F6,4753 = 1.36, P = 0.23, Fig. 3).

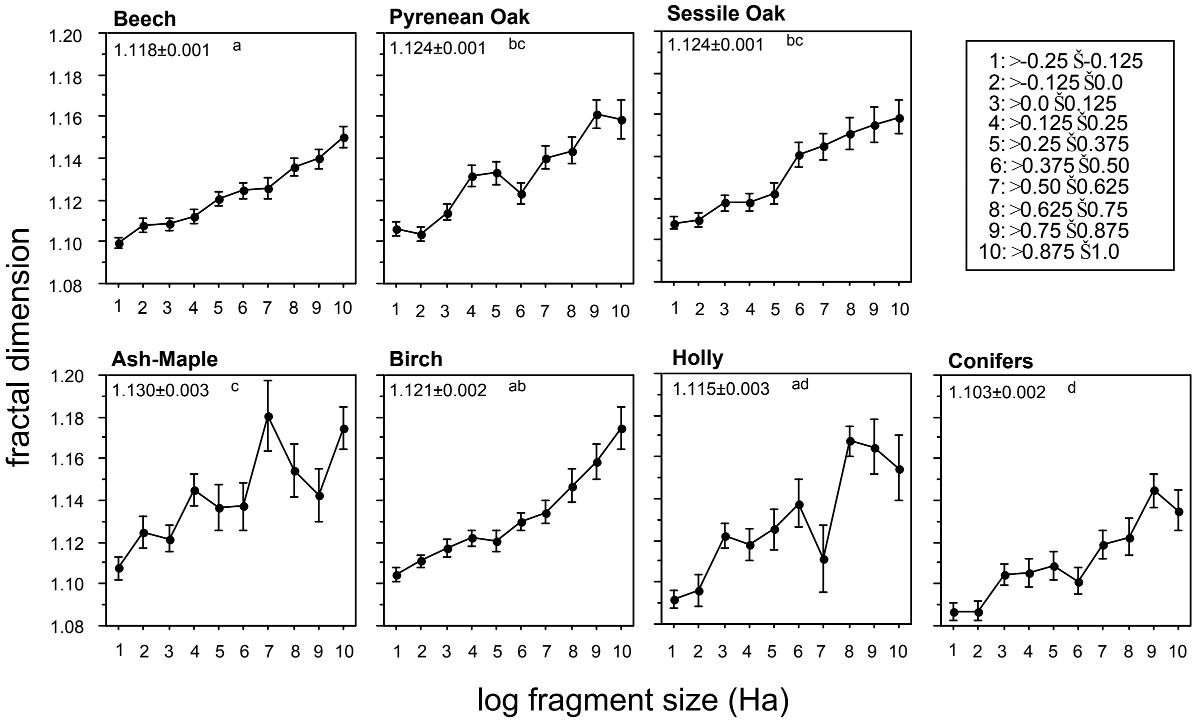

Figure 3. Fractal dimension (mean ± SE) of different forest classes in relation to fragment size (categorized in ten progressive intervals for representation). The mean value (± SE) for all fragments within each forest class is also shown (values followed by different superscript letters are different at P < 0.05 after Bonferroni-Dunn test).

Isolation

Dispersion indexes indicated aggregated distributions for all forest classes (Fig. 4). Birch forest had a comparatively higher Rc value, despite having a density value lower than beech and similar to oaks (Table 1). The dispersion index was minimal for rowan, holly and ash-maple forests, also characterized by larger NND. Averaging all fragments, NND was significantly larger when considered to the same class neighbour (265.01 ± 7.86SE) than to neighbour of any-class (103.52 ± 52SE; t = 45.37, P<0.0001); this difference being consistent for all forest classes (t > 14.0, P<0.0001, for all cases). Proximity index differed among forest classes for both types of neighbour (F6,8915 = 276.22, P<0.0001, ANOVAR, Fig. 5), differences being stronger when considering the same-class neighbours (Interaction forest class-neighbour type P<0.0001). Beech forests were less isolated than the other forests, considering both same-class and any-class neighbours. Ash-maple and holly forest showed the highest isolation, when considering the distance to the same-class fragments (Fig. 5).

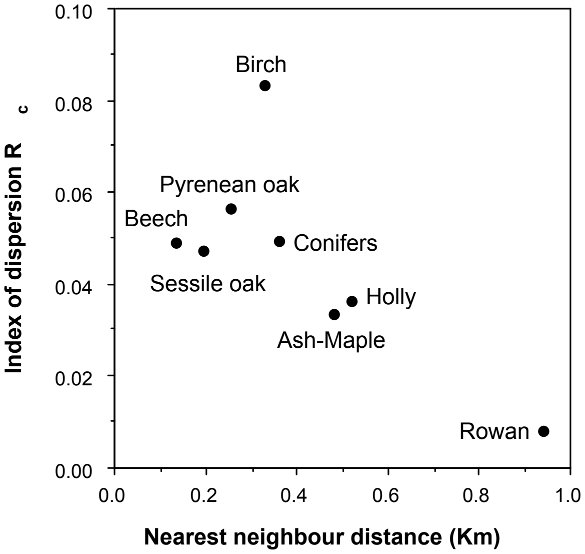

Figure 4. Values of the dispersion index Rc plotted against the average same-class nearest neighbour distance, for different forest types.

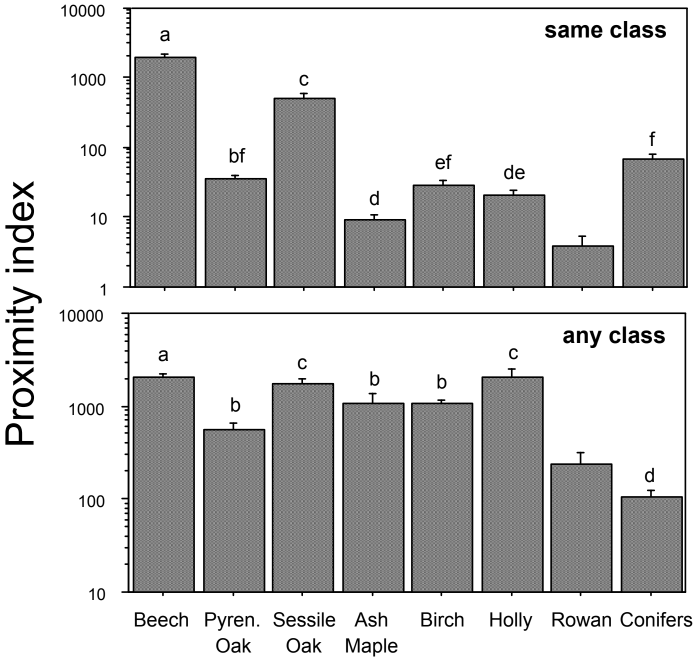

Figure 5. Proximity index (mean + SE) for different forest classes, both considering neighbours of the same class and neighbours of any class.

2.3.2. Fragmentation and protection status

Protected fragments were significantly larger and showed higher values of the proximity indexes than unprotected ones (Table 2). However, fractal dimension and nearest neighbour distances were independent of the protection status of the fragments. Protected fragments were located at higher altitudes and steeper slopes (Table 2). Most protected fragments were oriented northwards, whereas the modal aspect for unprotected fragments was eastwards (Table 2).

Table 2. Fragmentation and topographical variables (mean ± SE) for forest fragments under the coverage o not of a protected reserve of the Asturian Cantabrian range[a].

	Protected	Unprotected	F	P
Fragment area (Ha)	27.41±3.33	6.91±1.42	110.71	<0.0001
Fractal dimesion	1.11±0.00	1.11±0.00	2.27	0.131
NND to same class (m)	264.3±20.1	265.1±8.6	1.45	0.229
NND to any class (m)	88.4±5.5	106.3±2.3	3.12	0.077
Proximity index to same class	1798.4±130.6	444.7±55.7	125.58	<0.0001
Proximity index to any class	2975.8±185.9	1016.5±79.2	127.66	<0.0001
Altitude (m)	1042.2±6.4	954.7±2.7	169.23	<0.0001
Slope (º)	20.39±0.25	17.42±0.10	109.23	<0.0001
Aspect	N (33.58%)	E (27.80%)	χ^2=30.36	<0.0001

[a] F and P values resulting from one-way ANOVAs comparing both types are also shown. The modal aspect (% of fragments) and the results of a Chi-square test comparing the distribution of aspects among fragment types are also indicated.

The percentage of forest area under current protection was 27.6%, which included 18.15% of forest fragments. Protection coverage differed among forest classes, with many natural forest classes, specially holly and birch, showing protection coverage lower than 10% of their total area, but beech and sessile oak having more than 27% of their total area protected (Table 3). These differences also appeared when considering the percentage of fragments under protection. When considering total forest surface under protection, beech and sessile oak forest accounted for ca. 96% of this area, but this percentage was under 2% for the other forest classes. The distribution of protected fragments among forest classes was strongly biased towards beech. Most forest classes showed percentages of occurrence within the pool of protected fragments that differed significantly from their availability in the forested landscape (Tables 1 and 3). Beech fragments are actually over-protected in relation to their availability, whereas oaks, birch and holly were underprotected.

Table 3. Results of the Gap Analysis evaluating the coverage of the different forest classes within the reserve network. The percentages of protected surface and protected fragments respecting to the total area of each forest class, as well as the percentages of surface and fragments respecting to the total protected area in the landscape are indicated[a].

	Within class area		Within protected area		
	% surface protected	% fragments protected	% surface	% fragments	χ^2
Beech	34.25	32.89	78.78	57.65	272.07 ***
Pyrenean Oak	9.83	10.06	2.06	10.51	**18.31** ***
Sessile Oak	27.81	11.36	17.15	13.13	**11.41** ***
Ash-Maple	8.16	19.08	0.34	6.30	1.96 N.S.
Birch	5.53	6.86	1.05	8.27	**64.37** ***
Holly	4.65	8.77	0.16	2.90	**8.63** **
Rowan	9.56	10.71	0.05	0.44	0.61 N.S.
Pine	1.78	1.23	0.40	0.80	**132.91** ***

[a] Chi-square analyses compared, for each class, the proportion of fragments within the protected area with a theoretical distribution of protected fragments following the relative class-availability in the landscape (in bold are shown classes with actual percentages significantly lower than those derived from availability, see also Table 1; N.S.: $P > 0.05$; **: $P < 0.01$; ***: $P < 0.001$).

2.4. DISCUSSION

2.4.1. How fragmented is the Cantabrian forest?

Forests currently cover ca. 23% of the potential forest area in the Cantabrian range. This value of forest occurrence is lower than those described for other temperate (30-50%, Spies et al. 1994; Rebane et al. 1997; Fuller 2001; Pan et al. 2001) and boreal forests (≈50%, Mladenoff et al. 1993; Rebane et al. 1997; Löfman & Kouki 2001) but similar to heavily fragmented forests in agricultural (e. g. Ranta et al. 1998; Carbonell et al. 1998; Santos et al. 2002) or urban landscapes (Iida & Nakashizuka 1995). Other landscape-level fragmentation measures are the size distribution of fragments and the average fragment size (Forman 1995). In our case, fragment size distribution is strongly skewed towards small values, this kind of lognormal distributions indicating high levels of fragmentation (Wilcove et al. 1986). In addition, both the percentage of fragments >1 Ha and the average fragment size are much lower than depicted in other fragmented systems (e.g. Spies et al. 1994; Ranta et al. 1998; Fuller 2001; Pan et al. 2001).

The snapshot of the Cantabrian forest taken by our landscape analysis is the result of a long-term process including natural fragmentation as well as historical deforestation by humans but, in any case, it depicts an habitat situation for forest species characterised by low habitat cover and heavy fragmentation. Even when all forest classes are considered as a single habitat type, forest cover is below the predicted critical threshold for negative effects of fragmentation on biodiversity (Andrén 1994). The effects of low forest coverage could be buffered in some degree by the surrounding matrix, when providing what-suitable habitat for forest species (i.e., when the matrix is composed by second-growth forests, Mönkkönen & Reunamen 1999; Lindermayer & Franklin 2002). This is not the case of the forest fragments considered here, which include both mature and second-growth forest in different stages of development that strongly contrasted structurally with the surrounding pasturelands or heathlands matrix. Thus, additional losses of forest habitat would probably lead to exponential increases in fragments isolation within the agricultural matrix, negatively affecting the persistence of forest species (Andrén 1994; Mönkkönen and Reunamen 1999; Fahrig 2002). This situation could be particularly important for the isolated populations of endangered forest vertebrates still present at the Cantabrian range but highly sensitive to habitat degradation, such as brown bear *Ursus arctos* and capercaillie *Tetrao urogallus* (Naves et al. 2004; Obeso and Bañuelos 2004; see also Rolstad 1991; Kurki et al. 2000).

2.4.2. Differences among forest types

Heterogeneity

Most of the forest fragments in our landscape contain only one forest type, making the comparative analysis among different forest classes possible. This forest landscape is, thus, composed of an ensemble of rather homogeneous forest units standing out from a deforested matrix. However, the internal heterogeneity of fragments is related to the fragment size, with the bigger fragments being more heterogeneous. This is probably due to their higher probability of containing a wider range of habitat conditions related to altitude, soil and topographical characteristics, allowing the establishment and coexistence of different tree species on contiguous patches (Iida & Nakashizuka 1995; Honnay et al. 1999). Thus, the bigger fragments might maintain the structure of once continuous forest, characterised by a mosaic of adjacent forest patches of different composition (Mladenoff et al. 1993; Ripple et al. 1991). On the other hand, this size related effect is the main cause of differences among forest classes on internal heterogeneity: beech forests show a higher internal patchiness mainly because of their comparatively larger area.

Landscape cover and fragment size

Our results show differences among forest classes in terms of landscape cover, size distribution and average fragment size, despite a general trend of lognormal distributions for all classes. Beech forests are the major component of Cantabrian montane landscape in terms of both surface and the number of fragments. In addition, beech fragments are bigger on average than those of the remaining classes. Several historical and proximate causes might explain this dominance. Firstly, beech colonized the Eurosiberian region of the Iberian Peninsula from the early Holocene (7000 years BP) spreading westwards from the Pyrenees, and reaching its current limit at the western part of the Cantabrian range (Huntley and Birks 1983; Peñalba 1994; Muñoz et al. 1997). This species might thus be considered as a climax tree (under the current conditions of Atlantic oceanic climate) replacing early-Holocene species (such as *Quercus petraea* and *Betula alba*) from mid-altitudes after long-term anthropogenic disturbances (Peñalba 1994; Muñoz et al. 1997). Secondly, proximate causes such as higher rates of human-induced disturbance or selective logging for high-quality timber may also account for differences in coverage and average fragment size. This is probably the case for ash, maple and both oaks, species naturally occurring in areas more suitable for agriculture, such as valley bottoms or southern exposures (Spies et al. 1994). Additionally, Pyrenean oak forests have been strongly affected by anthropogenic fires (Luis-Calabuig et al. 2000). The small size of holly and rowan fragments might be mostly related to their character of second-growth forests developed after old-growth tree-line deforestation for high-altitude pastures (Díaz and Fernández 1987; Rebane et al. 1997). Holly woodlands seem to persist long time during succession thanks to herbivore pressure, which allows the presence of these prickly trees but precludes the colonization of more palatable species like beech or birch (Mitchell 1990).

Shape

Shape complexity, measured by fractal dimension, was similar in magnitude to that found in other montane temperate forest affected by human-induced fragmentation (e.g. Fuller 2001; Pan et al. 2001), but showed differences among forest classes. Conifer forests were the most regular in shape, as a result of the man-made structure of plantations located in flattest and lowest areas (average values of slope an altitude are minimal among forest classes). Conversely, ash-maple and oak forests were strongly irregular, probably due to the same reasons explaining their smaller size, the use of valley bottom lands and southwards oriented slopes for agriculture and pastures (Forman 1995). The most important consequence of increased shape irregularity are negative edge effects (Lovejoy et al. 1986; Andrén 1995; Murcia 1995), since, in fragments with larger perimeter/area ratio, edge effects penetrate a larger proportion of the fragment and even big fragments can be entirely physically or biotically modified (Laurance 2000; Davies et al. 2001). On the other hand, lower susceptibility to extinction thresholds are predicted for species living in habitats with lower fractal dimension (Hill & Caswell 1999). Therefore, at similar sizes, stronger negative effects due to shape irregularity might be predicted for ash-maple and oak forests than for the remaining classes in the Cantabrian range.

Shape complexity increased proportional to fragment size for all forest classes (see Krummel et al. 1987; Mladenoff et al. 1993; Pan et al. 2001; for similar patterns in other montane temperate forest). This indicates that different factors may be influencing the shape of small and large patches. For example, small fragments located in low agricultural areas tend to be more regular shaped reflecting their man-made limits (Krummel et al. 1987). In our case, the trend of increasing size and complexity in relation to slope suggests that large patches are usually located on or near hilltops, extending along ridges and generating amoeboid, convoluted or dendritic shapes (see also Forman 1995). In addition, the bigger the fragment, the higher is the probability to enconter with topographical and substrate heterogeneity, altitudinal limits or small-scale disturbances at the borders of the fragment, leading to higher boundary irregularity (Forman 1995; Iida and Nakashizuka 1995). Finally, big fragments probably suffer higher intrusive fragmentation or perforation (sensu Forman

1995) due to the formation of gaps related to fire or human clear-cuts, decreasing the total interior habitat and increasing the boundary length.

Isolation

When considered at the scale of the whole Cantabrian landscape, our fragment distribution may be considered as a fine-grained pattern, since it is mostly composed of numerous small fragments. However, as judged by the low values of the dispersion index, it is better depicted as an array of clusters or local aggregations of small fragments of the same class, with low NND, within a sea of low occupancy and high inter-fragment distances (hierarchical mosaic pattern, sensu Rolstad 1991). The dispersion index varied among forest classes, probably reflecting the requirements and responses of each class in relation to soil, topography, altitude and land use (Forman 1995; Turner et al. 2001). However, under a general trend of increased aggregation proportional to NND (Fig. 4), birch forest showed lower clumping than expected, indicating a less pronounced pattern of hierarchical mosaic than forests like beech and oak, with smaller NND but lower Rc values. These configuration differences may have important biological consequences, in terms of the metapopulation dynamics of organisms living in the respective forest classes. That is, in highly hierarchical patterns, metapopulation dynamics would be probably restricted to within-cluster dynamics, whereas less hierarchical patterns would favour dynamics expanding from local clusters to larger portions of the landscape (Rostald 1991).

Despite a clumped distribution at the landscape level, average nearest neighbour distances in our system indicated greater isolation among fragments than depicted for other fragmented forests (e.g. Löfman & Kouki 2001; average NND ≈ 25 m). Isolation partially encompassed the differences in other fragmentation measures like size or landscape coverage, probably as a result of the covariation in these fragmentation variables (Harris 1984; Andrén 1994; Forman 1995). Thus, biggest forests, such as beech and sessile oak, showed lower isolation than small-sized birch and ash-maple forests. On the other hand, the magnitude of these differences in isolation increased when measured respecting to the fragments of the same class. In fact, for all forest classes, the distance to a fragment of any class was smaller than the distance to a fragment of the same class, indicating that an important fraction of fragments had the nearest neighbour belonging to a different forest class. Habitat structural connectivity might be strongly affected by this fact, since the nearest fragment might not necessarily fit the habitat requirements for forest specialist species (Wiens et al. 1993; Andrén 1994; Tischendorf and Fahrig 2000). Under this perspective, holly and ash-maple forests, heavily affected by within-class isolation, would be less suitable for the maintenance of habitat-specialist species with low dispersal ability than beech and oak forests, but more prone to be inhabited by generalist species, able to move across and survive in a broader gradient of forest habitat types (Kozakiewicz 1995).

2.4.3. Conservation and fragmentation

Our analysis of protection status of fragmented forests shows that the current reserve network in the Asturias region should cope positively with additional fragmentation, since it covers preferentially bigger and less isolated fragments. Additionally, the protection of large fragments could lead to higher levels of biodiversity conservation, due to the positive relationship between fragment size and within-fragment heterogeneity. However, selective protection of largest forests could hinder the conservation of small, but structurally rich forest fragments which have suffered less internal degradation by some management practices as, for example, removal of dead wood and selective logging, as has been shown for other chronically fragmented landscapes (Schwartz 1999; Götmark and Thorell 2003).

The patterns of size-biased protection must be interpreted in relation to the selection of some forest types to the detriment of others within the reserve network. In fact, the relationship between fragmentation surrogates and protection status is probably due to the fact that beech forests, the class with bigger and less isolated fragments, was disproportionately covered by this reserve network. More importantly, this unbalanced protection indicates important gaps in the habitat representativeness. Despite being relatively comprehensive (all the seven natural forest types are protected in some degree), the current reserve network strongly failed on its adequacy for most of habitats, since less than a third of forest classes have protected ≥10% surface. The proportion of "well represented" habitats is even lower than reflected in Gap Analyses from other networks (e.g. Scott et al. 2001). Among natural types, holly forests are the least protected, despite showing high conservation values (besides holly, they contain important populations of yew Taxus baccata, a tree species threatened over its range in Europe, Svenning & Magard 1999; García & Obeso 2003). As previously explained, the maintenance of these second-growth forests seems compatible with moderate land-use like cattle grazing. However, they are not precluded from deforestation by other causes and thus, these under-represented, small habitats should be considered as protection targets for future expansion of the reserve network (see also Reyers et al. 2001; Scott et al. 2001).

The reasons for the current patterns of protection are due to the motivations for establishment of particular reserves. The conservation of mature beech forest as the habitat of threatened species (capercaillie and brown bear) is a major biological motivation (Anon. 1994). In this case, these umbrella (and flagship) species would act as surrogates of biodiversity working efficiently against fragmentation, since they would promote the protection of less fragmented forests (but see Andelman & Fagan 2000). However, the unbalanced protection coverage suggests that reserves have been partially proclaimed in an ad hoc fashion, because they contained areas with high scenic or tourism potential and did not conflict with other forms of land use (Pressey et al. 1993; Reyers et al. 2001; Scott et al. 2001; Götmark & Thorell 2003). The relationship among topographical characteristics of fragments and their protection status support this hypothesis, indicating that reserves have been concentrated in areas of marginal agricultural value (higher altitudes and slopes, and northern exposures; see also Scott et al. 2001). Finally, the uncertain viability of traditional mountain land-use under the current agricultural trends of the European Union, and the consequent search of alternative ways of development such as eco-tourism, are also within the motivations of the current reserve network.

2.4.4. Concluding remarks

This study depicts the current landscape patterns of the montane forest in the Cantabrian range, evidencing severe fragmentation in all forest types and biased representativeness of forest habitats in the protected landscape. Future forest management and reserve network design should take into account these patterns to preclude increasing losses of forest surface and the consequent biodiversity decay. Particularly, the expansion of the reserve network towards new areas in the region should be based in landscape information, not merely in social convenience or opportunity, seeking to protect the less-fragmented forests but also to include those misrepresented forest types with high ecological value.

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CAPÍTULO 3. Cantabrian Capercaillie and deciduous forests: Habitat selection at the forest-stand level

Urogallo cantábrico y bosques caducifolios: Selección de hábitat a nivel de sitios en el interior del bosque

3.1. INTRODUCTION

The Capercaillie (*Tetrao urogallus*), the largest grouse species, is also one of the largest forest birds of Palaearctic, and it is considered an umbrella species and indicator of undamaged ecosystems (Boag & Rolstad 1991; Suter et al. 2002; Pakkala et al. 2003). Although it occupies much of its historical distribution range in Europe, most of their populations are declining since the last decades (Storch 2000). To explain this overall trend, some factors have been proposed to affect concrete populations locally (Klaus & Bergmann 1994; Bevanger 1995; Kurki et al. 1997; Ménoni & Magnani 1998; Moss 2001). In addition, global factors like climate change (Moss et al. 2001) and habitat loss and fragmentation due to human land use (Rolstad & Wegge 1987a, 1989; Rolstad 1991; Klaus & Bergman 1994; Storch 1997; Ménoni et al. 1997) have been also related to the decline.

In such a declining context, populations at the edge of the species' distribution range are subjects of special attention. Peripheral populations are considered more vulnerable to extinction, because they show a lower probability of receiving immigrants from other populations (MacArthur & Wilson 1967) and, as the result of occupying less favourable habitats, present ecological particularities and smaller size and densities (Brown 1984; Brown et al. 1995). On the other hand, the long-term conservation of species depends much on the conservation of peripheral populations (Lesica & Allendorf 1995); genetic divergence, because of isolation, genetic drift and natural selection, is expected to occur in such populations, being also sites of future speciation processes (Lesica & Allendorf 1995).

The Cantabrian Capercaillie subspecies (*Tetrao urogallus cantabricus*) complies with the circumstances formerly mentioned. Inhabiting the Cantabrian Mountains in the northwest Spain (the southwest extreme of the distribution range of the species) it is a relict and the world's most threatened capercaillie population (Storch 2000), with a population size estimated in 500 adults (Obeso & Bañuelos 2003). The subspecies fits the category of endangered according to IUCN criteria (Storch et al. 2006) and, as the result of their long-lasting reproductive isolation, qualifies as an Evolutionarily Significant Unit with a high genetic differentiation compared to the rest of capercaillie populations elsewhere (Rodríguez-Muñoz et al. 2006; Storch et al. 2006).

Capercaillie has been traditionally considered a specialist of coniferous mature forests with moderate canopy cover (Rolstad & Wegge 1987a; Picozzi et al. 1992; Storch 1995a; Bollman et al. 2005). However, this specialization could be relative, and capercaillie might adapt to other habitats on condition that its ecological requirements were satisfied (Rolstad & Wegge 1987b). Bilberry is a key resource, providing Capercaillie with food and shelter during snow-free seasons (Storch 1993; Wegge et al. 2005). In winter, snow cover usually prevents access to ground vegetation, and conifer needles become the main food resource (Gjerde & Wegge 1989). For most populations, Scots pine is positively selected as winter food comparing with other tree species (Gjerde & Wegge 1989), but they actually feed also on fir and spruce. Furthermore, Capercaillie feeds on buds from beech and birch during the spring throughout their distribution range where those species are present (Saniga 1998). Hence, Capercaillie performs as a non-specialist in relation to tree species, differences in the diet among different localities being largely the response to local availability (Saniga 1998, 2004). From this data, the species could be considered ecologically adaptable given an adequate forest structure, an idea that is supported by the mere long-lasting existence of Cantabrian population. Cantabrian forests are almost exclusively deciduous (Chapter II – García et al. 2005; Quevedo et al. 2006a, b), and this radical difference in habitat composition have determined changes in basic ecological adaptations like winter feeding habits (Rodríguez & Obeso 2000). But, in spite of this vegetation differences, Cantabrian forests have constituted a suitable habitat for the species for thousands, basic requirements for the species being fulfilled.

On the other hand, Brown et al. (1995) showed that populations at the edge of the distribution of the species usually occupy poorer habitats than those populations toward the centre of the range. Hence, with these two opposite pictures in mind a question to ask is whether Cantabrian forests could be considered or not an adequate habitat for Capercaillie. Two aspects could be considered as disadvantages of inhabiting this region. First, the absence of conifers might constitute a handicap during winter because, given the less digestibility and the more disaggregated distribution of buds in space, a diet based on buds instead of needles probably increases feeding time and movements, and consequently predation risk (Rodríguez and Obeso 2000). Second, but not less, Cantabrian Capercaillie and its habitat are especially sensible to climatic conditions, a fact that has already been documented to affect viability of Capercaillie in Scotland (Moss et al. 2001). Considered a typical species of boreal forests, Cantabrian population occupies the southwest extreme of the distribution range of the species, a more temperate region in the limit with Mediterranean climate. In a context of global warming, susceptibility of this border region to alterations should not be dismissed. Furthermore, climate is known to change more rapidly with altitude than with latitude, the montane range that constitutes the habitat of Cantabrian Capercaillie becoming a certain scenario for the effects of climate warming. In this sense, a positive significant relation has been found between occupancy and altitude (Quevedo et al. 2006b). The population shrinkage in the last decades then follows the expected direction toward higher elevations, those leks at lower altitudes being progressively abandoned.

In spite of its critical situation, however, knowledge on basic population features of the Cantabrian Capercaillie and ecological relations between the species and their habitat is very scarce, available information about use of habitat being mainly restricted to leks and breeding season (Castroviejo 1975; Martinez 1993; Quevedo et al. 2006b). That way, very little is known about the habitat preferences during other critical moments of the annual cycle, like nesting and chick-rearing season, dispersal of juveniles, or winter season, and whether the birds have or not a seasonal distinctive preference for vegetation characteristics and territories within their annual home range (but see Martinez 1993 and Quevedo et al. 2006b). Although mentioned questions about habitat selection and requirements for Capercaillie at local scale are well documented for other European populations (Gjerde & Wegge 1989; Picozzi et al. 1992; Storch 1993, 1995b; Bollman et al. 2005), distinctive context of the Cantabrian Mountains demands specific work. In that sense, the formerly mentioned study by Quevedo et al. (2006b) is the first published work on habitat selection by the Cantabrian subspecies, though information about use of habitat was still restricted to the lek vicinity.

In this work, we assessed the characteristics of habitat that determine, at the forest stand level, the presence of Capercaillie in the Cantabrian range throughout the year. For that purpose, we examined Capercaillie habitat during two annual cycles, and characterized Capercaillie sites (defined by presence signs) into multi-specific descriptors of vegetation structure, which we subsequently applied to build a forest-stand quality index. With this approach, our main aims were to improve our understanding of the ecological peculiarities of Cantabrian Capercaillie and their habitat, and to develop a procedure that could be used as an instrument for the adequate management of the population.

3.2. METHODS

3.2.1. Study areas

The study areas are located in the Cantabrian Mountains, northwest Spain, a mountain region that runs parallel to the Atlantic coast from east to west (Figure 1), with elevations ranging up to 2648 m and numerous hilltops above 2000 m. Due to their complex geological history and to the proximity to the sea, slope gradient is high (34% in the north and 21% in the south-facing), and the main east-west axis is crisscrossed by many gorges and cliffs. The climate is humid and temperate, influenced by the sea in the north, and with annual variations in snow cover during winter and early spring. Soils are mainly calcareous in the east and central parts, while in the west siliceous beds dominate.

Forests are deciduous, dominated by beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and birch (*Betula alba*), but their composition is not homogeneous throughout the range. Indeed, beech clearly monopolizes over the rest of tree species in the east and central part of the range, while in the west, coinciding with the domain of siliceous soils, sessile oak dominates and birch presence is higher. Brooms (*Cytisus* sp., *Genista* sp.), true heathers (*Erica* sp.), common heather (*Calluna vulgaris*) and bilberry (*Vaccinium myrtillus*) are the main shrub species, all of them occurring in the whole range. However, their relative abundances as well as their location in relation to the forest also differ between mentioned domains. Above 1700 m, climatic conditions prevent forest growth, and shrubs and subalpine vegetation (*Vaccinium myrtillus*, *Juniperus communis*, *Arctostaphylos uva-ursi*) dominates.

Although the grade of management is currently low, Cantabrian forests have a long history of human use and are consequently largely fragmented (Chapter II – García et al. 2005), bearing today a heavy grazing pressure by domestic as well as wild ungulates (Anduix 2001). Forests are mainly mature or semi-natural, second-growth forests being also present where fires or pasture abandonment occur. Thus, the present picture of the landscape consists in forest fragments surrounded by a non-forest matrix of pastures, heath lands and small villages.

In concurrence with forest domain, Cantabrian Capercaillie broadly occupies the range between 800 and 1700 m.a.s.l. As the result of steep orography and forest lost and fragmentation, the population is spatially structured, with local populations interspersed among large gaps of poor habitat. Extremely low bird numbers (Obeso and Bañuelos 2003) together with reported dispersal distances (see Storch and Segelbacher 2000 for a review) suggest that the connectivity between distinct local populations is low (in this sense, Quevedo et al. 2006a suggested that habitat configuration plays an indirect role in the current process of population decline). Occupying in the mid-twenty century the five provinces that conforms the whole range of the Cantabrian Mountains, the metapopulation, from a landscape perspective, has been constrained from the extremes towards the central parts. At present, all occupied leks belong to the provinces of Asturias and Leon, corresponding to the northern and southern slopes, respectively.

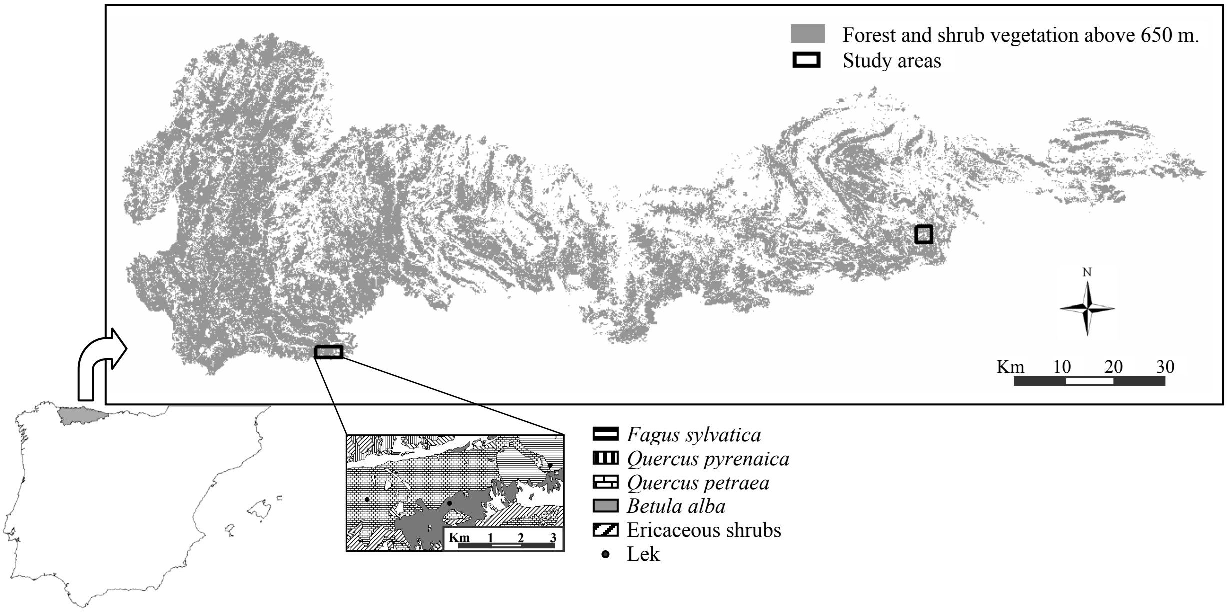


Figure 1. Map of forest and shrub vegetation above 650 m. in Asturias, with location of the two study areas, and detailed vegetation composition of the western study area.

According to a spring survey for lek occupancy performed over the whole northern-exposure by the regional environmental agency (Consejería de Medio Ambiente, Principado de Asturias) between years 2000 and 2001, we selected two separated forested areas of supposed high habitat quality, in terms of occupancy, to conduct this study (Figure 1). These areas were selected trying to cover the two main forest configurations previously described. One was situated in the Degaña District, western part of the range, within the oak-dominant forests on siliceous soils. The other area belongs to the Ponga District, in the eastern part, where beech dominates mostly on calcareous soils. On each zone, we established a study area of 1000 hectares that included some occupied leks, with the purpose of examining an area at least as large as a typical annual home range (which averages five hundred hectares in Central Europe, see Storch 1995a).

3.2.2. Data on habitat use

We carried out the fieldwork every two months during two years, from August 2002 to June 2004. Surveys were conducted basing on UTM cells of 1x1 Km, where we looked for evidence of Capercaillie presence (direct sightings, feathers, droppings, footprints) and measured habitat variables. A survey season then consisted in the inspection of the 10 UTM cells of each study area, signs searching consisting in random itineraries of about three hours within each cell.

Habitat variables were measured in sample plots, which consisted in areas with a radius of 25 metres (two sample plots were located at a distance of at least 50 m to be considered different). When a sign of capercaillie presence was detected, we established a positive sample plot centred in the sign. Besides, as a representation of habitat availability, we randomly located a set of control plots within each cell of the study area, being established every 30 minutes of inspection. In order to analyse habitat selection by Capercaillie, we compared habitat variables between sign-centred (positive) and randomly located (control) plots. Plots were located using GPS and 1:10000 topographical maps.

We recorded, within each sample plot, 31 variables mostly referred to vegetation composition and structure (Table 1). For the species comprising the tree-stratum, we recorded canopy cover, whilst both cover and mean height was recorded for those from the lower strata. Estimation of this understorey and ground cover was not limiting, i.e., the total cover might sum more than 100%. We also recorded abundance of rocks and bare soil (mostly fallen leaves). Measuring of variables was done visually: percentage of cover was estimated to the nearest 5%, and mean height was assigned to the nearest multiple of 10 or 5 centimetres depending on whether shrubs were or not taller than 50 centimetres, respectively.

3.2.3. Data analysis

Data analysis was conducted separately for the two study areas. Firstly, univariate tests were done as a descriptive analysis of capercaillie preference for cover and height of tree and shrub species, using Student t-test to assess differences between positive and control plots. Species appearing in less than 10% of sample plots of any category were not included in analyses because we considered them poorly represented.

In order to go beyond a monospecific vision of habitat selection and explore the multi-specific associations that characterize the habitat used by Capercaillie, we performed Principal Component Analysis (PCA) on data from the positive plots alone. Thus, we could describe Capercaillie habitat as a set of independent habitat structures. Variables used for PCA were those relative to vegetation cover, excluding those relative to height. The exclusion was done in order to avoid the effect of points with 0% cover on height average (when calculating height averages, points with 0% cover would behave like points with a low height value).

To look for actively selected habitat structures, we tested whether or not described habitat structures were used by Capercaillie more often than expected basing on their mere availability. For that, we performed univariate t-test analyses comparing the value of the principal components (PC scores) between positive plots and control plots.

Finally, we used PCs (i.e., habitat structures) as new explanatory variables to build a habitat suitability index. We formulated a set of predictive models, which consisted in multiple logistic regressions (GLM, binomial distribution, logit link function) that contrasted positive versus control plots and resulted in probabilistic predictions of Capercaillie presence. For model development, we used half of sample plots of both categories, keeping the rest for model validation. Akaike Information Criterion (Akaike 1973) was used to select the best logistic model for each study area.

In order to assess model accuracy, we transformed back probabilistic outputs into presence-absence data (Guisan and Zimmermann 2000). This was made by truncating probabilities at a cut-off value that best performed in maximizing both Cohen's kappa coefficient (Cohen 1960) and overall percentage of correct classification.

3.3. RESULTS

3.3.1. *Descriptive analysis*

We found 196 positive sites, 145 corresponding to Degaña and 51 to Ponga. Additionally, 284 control plots were established in Degaña and 214 in Ponga. Positive sites corresponded mostly to droppings (174 sites, 88%), followed by sightings (32 sites), feathers (25 sites), snow tracks (11 sites), and roosting sites (7 sites); obviously, different types of capercaillie signs could appear in the same positive plot.

Results of the univariate analysis are shown in Table 1. Five of the seven canopy species were poorly represented in Ponga District, only beech and holly appearing with a frequency large enough to perform the analysis. Both variables showed significant differences between positive plots and control plots, although in the case of holly the significance was only marginal. Canopy cover of beech was larger in those plots with presence signs, while holly cover performed the opposite. Total canopy cover showed no differences in relation to Capercaillie presence. In reference to understorey and ground vegetation, Capercaillie seemed to prefer sites without beech regeneration. If beech or holly regeneration occurred, taller sizes were avoided, as they were also taller ferns. On the contrary, birds preferred taller heathers, bilberry and common heather, cover of this last shrub being also positively selected (Table1).

In the case of Degaña District, two canopy species, pine and maple, did not appear within the study area. From the rest, three canopy variables showed differences between positive and control plots. They were total canopy cover, birch cover and rowan cover, all showing a higher value in Capercaillie occupied plots than in absence plots. As it happened in Ponga, Capercaillie preferred taller heathers. In this area, abundance of *Vaccinium* and meadows was significantly higher in sites with Capercaillie (Table1).

Table 1. Vegetation variables in relation to Capercaillie presence in Ponga and Degaña districts. Values shown are untransformed variable means (± standard deviation). Statistical differences based on t-test were assessed after variables transforming.

Variable	Description	Ponga			Degaña		
		Capercaillie	Control		Capercaillie	Control	
CANOPY	% canopy cover in the sample plot	52.78±16.32	48.33±23.04		69.14±9.92	60.21±24.57	***
FAGUS	% canopy of beech (*Fagus sylvatica*)	45.92±16.07	33.33±24.73	**	10.10±21.80	9.48±15.84	
ILEX	% canopy of holly (*Ilex aquifolium*)	4.10±5.12	7.55±11.84	#	2.10±5.04	2.07±6.12	
QUERCUS	% canopy of oak (*Quercus petraea*)	0.00	0.69±3.74	--	18.16±23.61	20.19±26.31	
BETULA	% canopy of birch (*Betula alba*)	1.49±4.66	1.67±9.88	--	29.32±19.09	21.54±21.02	**
SORBUS	% canopy of rowan (*Sorbus aucuparia*)	0.59±1.91	0.10±0.70	--	9.41±9.33	5.78±7.99	***
ACER	% canopy of maple (*Acer pseudoplatanus*)	0.00	0.00	--	0.18±1.00	0.03±0.33	--
PINUS	% canopy of pine (*Pinus sylvestris*)	0.39±2.20	3.43±11.73	--	0.00	0.00	--
%FAGUS	% understorey beech	2.65±5.03	5.59±9.63	#	0.55±3.54	0.69±4.95	--
hFAGUS	Mean height (cm) of understorey beech	24.01±49.56	55.47±68.44	**	3.52±22.10	1.79±12.62	--
%ILEX	% understorey holly	1.96±3.62	3.33±4.20		0.31±2.58	1.10±5.09	--
hILEX	Mean height (cm) of understorey holly	20.10±40.72	46.57±65.69	*	3.93±24.22	8.97±41.28	--
%QUERCUS	% understorey oak	0.00	0.00	--	0.10±0.93	1.62±6.06	--
hQUERCUS	Mean height (cm) of understorey oak	0.00	0.00	--	1.38±11.94	9.83±36.36	--
%BETULA	% understorey birch	0.00	0.00	--	0.10±0.93	0.66±3.74	--
hBETULA	Mean height (cm) of understorey birch	0.00	0.00	--	1.38±11.94	4.14±23.11	--
%CYTISUS	% cover of brooms (*Cytisus* sp., *Genista* sp.)	8.82±11.43	8.63±13.86		0.72±3.77	3.83±10.17	--
hCYTISUS	Mean height (cm) of brooms	117.2±121.2	127.7±127.6		8.48±36.79	40.35±81.99	--
%ERICA	% cover of heathers (*Erica* sp.)	12.35±18.30	6.61±16.31		23.66±15.60	24.21±19.74	
hERICA	Mean height (cm) of heathers	51.96±53.74	30.39±50.79	*	91.51±45.63	80.33±50.44	*
%ULEX	% cover of gorse (*Ulex sp.*)	0.19±0.98	2.55±11.15	--	0.00	0.00	--
hULEX	Mean height (cm) of gorse	2.54±14.54	6.96±22.87	--	0.00	0.00	--
%FERN	% cover of ferns	10.92±16.49	14.90±20.26		9.93±16.91	12.10±19.94	
hFERN	Mean height (cm) of ferns	24.41±33.83	44.31±50.94	*	19.09±25.60	23.00±31.34	
%CALLUNA	% cover common heather (*Calluna vulgaris*)	6.57±13.21	2.06±6.65	*	0.00	4.04±12.81	--
hCALLUNA	Mean height (cm) of common heather	6.57±11.55	2.16±7.09	*	0.00	4.09±12.12	--
%VAC	% cover of bilberry (*Vaccinium myrtillus*)	19.55±18.78	13.43±23.74		28.45±17.03	23.81±16.95	*
hVAC	Mean height (cm) of bilberry	15.52±10.45	8.90±12.24	**	29.44±9.75	28.03±13.23	
%MEADOW	% cover of meadows	21.53±22.12	14.80±20.54		27.59±20.77	20.17±19.60	**
%SOIL	% cover of bare soil (mostly leaves)	3.47±6.56	1.96±4.70		6.10±10.37	7.72±13.12	
%ROCK	% cover of rocks	12.45±19.19	12.94±18.82		6.17±13.77	6.97±17.78	

#P < 0.06, *P < 0.05, **P < 0.01, ***P < 0.001.

-- Not tested, variables insufficiently represented.

3.3.2. Multi-specific associations

We used vegetation cover of the species present at least in 25% of positive plots in each locality to perform independent PCA for Ponga and Degaña (Table 2, see Table 1 for representativeness of variables), retaining for subsequent analysis those PCs with higher eigenvalues. We considered these resulting PCs as supra-specific descriptive variables of habitat structure.

Table 2. Eigenvalues and eigenvectors' coordinates of principal components (PCs) for Ponga and Degaña. Statistical differences of PCs related to Capercaillie presence-absence based on t-test are shown (#P < 0.10, *P < 0.05, **P < 0.01). Scores of the variables with relatively high weights in each PC are shown in bold.

	Ponga					Degaña				
	PON1	PON2	PON3	PON4	PON5	DEG1	DEG2	DEG3	DEG4	DEG5
	*		*			**			#	
Eigenvalue	2.44	1.95	1.57	1.39	1.24	2.72	1.96	1.26	0.95	0.90
Percent	20.30	16.23	13.09	11.59	10.35	27.19	19.60	12.64	9.51	8.99
FAGUS	-0.194	-0.096	**-0.642**	0.088	0.240	**-0.363**	**0.402**	0.016	0.096	**0.360**
ILEX	-0.283	-0.149	0.294	**0.501**	-0.283					
QUERCUS						**-0.344**	**-0.463**	-0.098	-0.204	**-0.356**
BETULA						**0.488**	0.109	-0.054	0.122	0.119
SORBUS						**0.461**	0.108	0.024	-0.080	0.171
%FAGUS	**-0.389**	0.132	0.046	**-0.361**	0.182					
%ILEX	**-0.453**	-0.071	0.315	0.108	-0.025					
%CYTISUS	0.039	**-0.367**	0.137	-0.337	-0.341					
%ERICA	**0.407**	-0.022	0.042	0.132	**0.513**	**0.359**	-0.214	0.316	0.043	0.181
%FERN	-0.006	**-0.383**	-0.229	**-0.430**	-0.271	-0.092	0.137	**-0.753**	0.257	0.188
%CALLUNA	0.248	-0.216	**0.499**	-0.210	0.304					
%VAC	-0.085	**-0.543**	-0.232	0.149	0.111	0.132	**-0.522**	-0.191	-0.224	0.217
%MEADOW	**0.330**	0.243	-0.153	0.268	**-0.452**	0.150	**0.436**	0.054	-0.111	**-0.669**
%ROCK	-0.015	**0.472**	-0.038	**-0.380**	-0.147	-0.122	-0.221	0.309	**0.840**	-0.098
%SOIL	**-0.426**	0.202	-0.005	0.011	0.213	**-0.327**	0.155	**0.430**	-0.302	**0.358**

Scores in the principal components that showed significant differences between capercaillie sites and random sites are marked in green (positively related to capercaillie presence) and red (negatively related).

In Ponga, the five retained PCs (PON1 … PON5) accounted for 72% of data variation from the 102 positive plots. Looking at weightings (Table 2), high PON1 scores reflected sites with abundance of heathers and meadows, and low covering of beech and holly regeneration and bare soils (fallen leaves). High PON2 reflected rocky places and absence of brooms, ferns and bilberry. High PON3 scores indicated high cover of common heather and low beech canopy. PON4 showed holly abundance in the positive axis and abundance of ferns, beech regeneration and rocky soils in the negative axis. High PON5 scores reflected abundance of heathers and low presence of meadow. Figure 2A shows weightings of cover variables in PON1 and PON3 scores. These two principal components showed significant differences when related to Capercaillie presence-absence (Table 2).

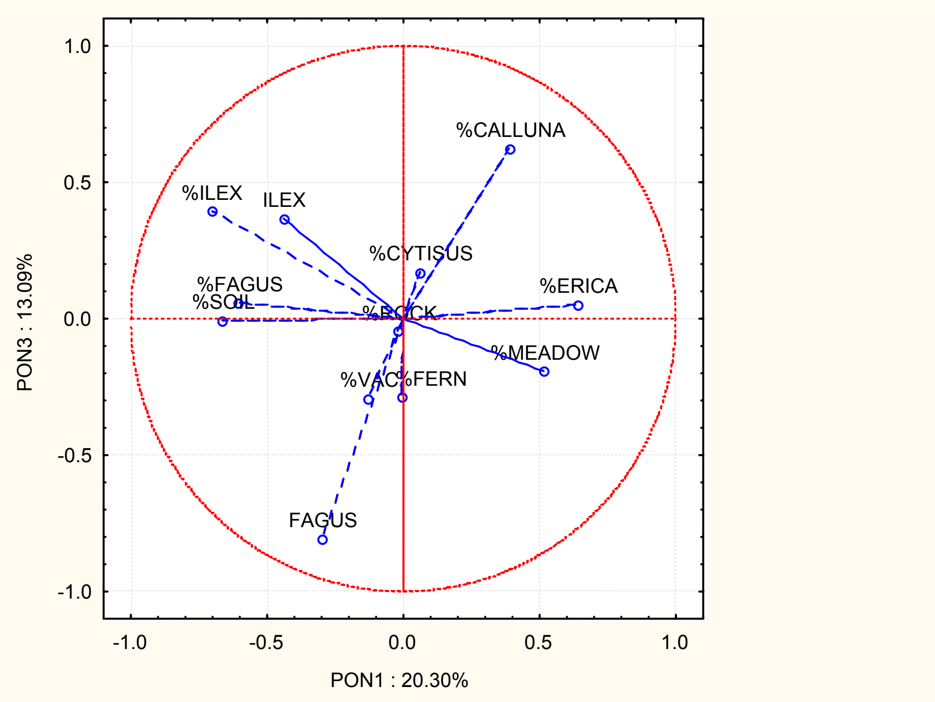
Five PCs (DEG1 … DEG5) were also retained for Degaña, accounting for 78% of data variation from 290 Capercaillie sites. High DEG1 scores indicated abundance of birch, rowan and understorey heather, and low presence of beech and oak. High DEG2 scores reflected abundance of beech and meadow and absence of oak with understorey bilberry. High DEG3 scores indicated abundance of bare soils against abundance of ferns, DEG4 abundance of rocks, and DEG5 high beech canopy without ground vegetation opposite to oak canopy with meadow (Table 2). When compared between positive and random plots, two PCs showed significant (DEG1) and marginally significant (DEG4) differences (Table 2). Weightings of cover variables in such PC scores are shown in Figure 2B.

3.3.3. Habitat suitability model

The five retained PCs in the role of descriptors of habitat structure were used as new explanatory variables in multiple logistic regressions. For each area, we formulated a set of potential models consisting in different combinations of their five PCs. No variables had to be rejected from any model because of correlation between them, as PCA ensured independence of variables.

Figure 2. Relative weights of cover variables in the PCs that showed statistically significant differences in Capercaillie presence-absence at A) Ponga and B) Degaña.

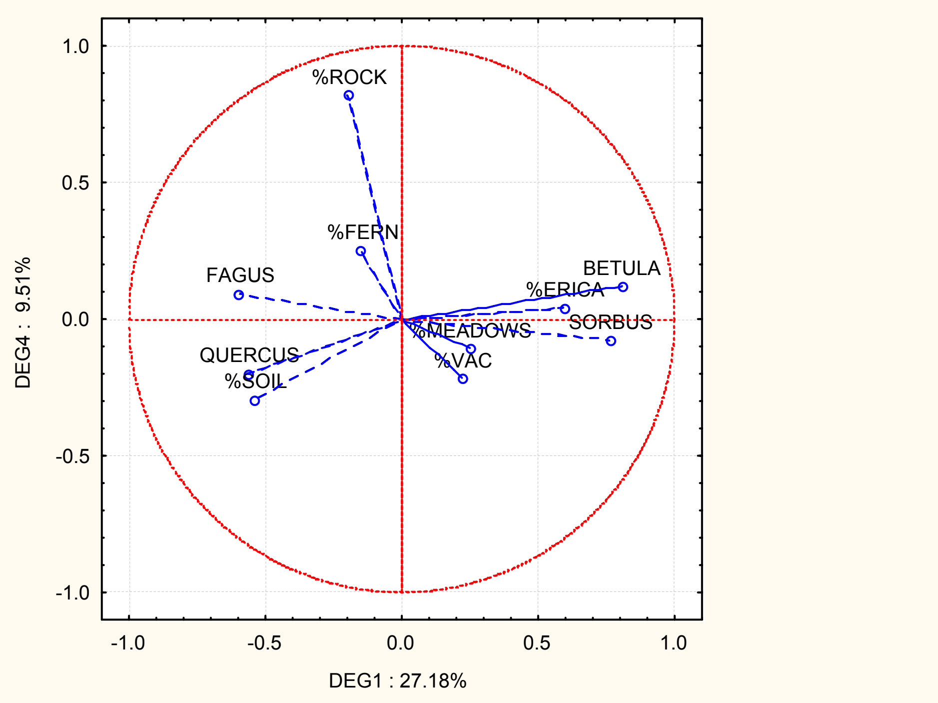
A)



PON1 groups sites with abundance of heathers and meadows at positive loadings, in opposition to abundance of beech and holly regeneration and bare soils at negative loadings.

PON3 reflects abundance of common heather against high beech canopy in the opposite axis.

B)



DEG1 groups sites of birch and rowan as predominant tree species with understorey heather at positive loadings, in opposition to sites with abundance of beech and oak at negative loadings.

DEG4 accounts for abundance of rocky soils at positive loadings.

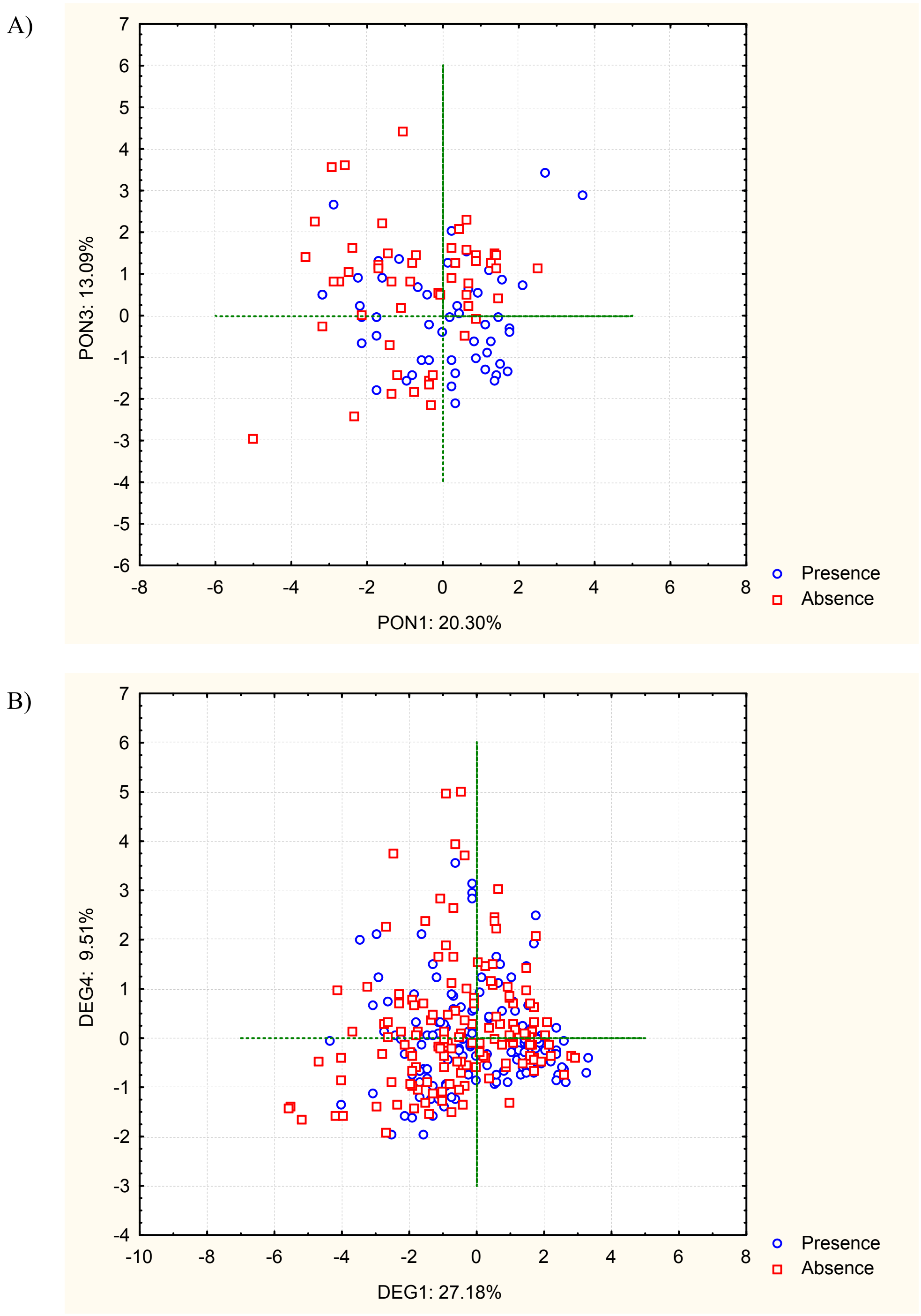
For both areas, model with the lowest Akaike (AIC) value retained only two PCs, whose scores are plotted in Figure 3. Best model for Ponga (Table 3) combined PON1 (+, positive parameter estimate) and PON3 (-, negative parameter estimate). Therefore, a look into Figure 2A showed that Capercaillie preferred a) sites with abundance of heather (*Erica* sp.) and meadow instead of low ground cover and beech and holly regeneration, together with b) sites with beech canopy but no common heather (*Calluna vulgaris*). The cut-off threshold for presence-absence discrimination was 0.43 with a Cohen's kappa coefficient = 0.35. The model correctly classified 78% of positive plots as occupied, and overall correct prognoses was 62% of the sample plots (Table 3).

The two variables included in the best model for Degaña were also those PCs previously mentioned in the univariate tests, DEG1 showing positive and DEG4 negative parameter estimates (Table 3). Thus, Capercaillie in Degaña preferred a) sites with abundance of birch and rowan rather than beech or oak in the upper stratum, and abundance of heather (*Erica* sp.) instead of scarce ground cover, and also b) sites without rocky soils (Figure 2B). Cut-off level was 0.44 with a value of Cohen's kappa coefficient = 0.30. Model correctly classified 57% of sample sites, and positively identified 83% of Capercaillie sites (Table 3).

Table 3. Parameter estimates and model accuracy of the best models for Ponga and Degaña.

	Model parameters					Model information						
	Variable	Estimate	Std. Error	Wald Stat.	P	Deviance	AIC	Cohen's kappa	Cut-off	Sensitivity	Specificity	Correct prognoses
Ponga						11.84	135.56	0.35	0.43	0.784	0.451	0.618
	Intercept	0.2303	0.2197	1.10	0.294				0.5	0.647	0.569	0.608
	PON1	0.3205	0.1348	5.65	0.017							
	PON3	-0.3695	0.1560	5.61	0.017							
Degaña						11.05	396.98	0.30	0.44	0.828	0.317	0.572
	Intercept	0.0755	0.1217	0.38	0.535				0.5	0.586	0.552	0.569
	DEG1	0.1995	0.0708	7.94	0.005							
	DEG4	-0.2053	0.1095	3.52	0.061							

Figure 3. Scores of the positive (blue circles) and control (red squares) plots for the two PCs that showed statistically significant differences in Capercaillie presence-absence at A) Ponga and B) Degaña.



3.4. DISCUSSION

In this work, we assess the characteristics of vegetation that determine, at a microhabitat level within home range, the occurrence of capercaillie in the Cantabrian range throughout the year. Our results show that vegetation variables measured are adequate to correctly characterize capercaillie used sites at the forest stand level differentiating them from available habitat. These results add new insights into the study of the ecological particularities of Cantabrian Capercaillie, improving the global picture of habitat use and selection that other recent works have drawn for either a higher (landscape) or a lower (lek vicinity) scale (Quevedo et al. 2006a and b, respectively).

This work represents the first study dealing with habitat selection by Cantabrian Capercaillie at the spatial and temporal scales of the total home range and the entire year, respectively. In contrast to the unique previous published work (Quevedo et al. 2006b), which was focused in the lek vicinity, our two study areas comprised some display grounds as well as 900-1000 hectares surrounding them, where we conducted random field surveys every two months during two annual cycles. The size of those areas was in accordance with large annual home ranges in Central Europe (Storch 1995a). Besides, the more detailed field data at different canopy levels and the employ of an approach based on principal components analysis allowed us to finely describe vegetation composition and structure of the habitat and find independent structures that determine capercaillie presence at the forest stand level. Furthermore, our data will allow us to conduct subsequent analysis for describing in more detail the seasonal pattern of habitat selection. Both actual and subsequent results should be taken in mind for the adequate conservation of the population in its distinctive habitat.

3.4.1. Habitat selection

Habitat selection can be conceptualized as a hierarchical spatial process, being primarily based, at the scale under study, on intentional search for resources, mainly food and shelter, by individuals (Hildén 1965; Rolstad et al. 2000). According to that, we assumed habitat selection by individuals taking place at a scale higher than that determined by mere abundance of plant species individually. Instead, we supposed the close environment of individuals being selected at the level of overall forest composition and structure, as a global picture of food and shelter availability. Consequently, when examining forest structure from vegetation cover variables in order to determine habitat preference, spurious correlation between abundances of different plant species could lead us to wrong interpretations. The employ of an approach based on principal components analysis (Picozzi et al. 1992; Moss et al. 2001) allowed us to describe forest structure as a combination of meaningful independent variables that we related to resource availability.

An example of the aforementioned “contradictory interpretation” is the case of common heather (*Calluna vulgaris*) in Ponga. In the univariate analysis, its abundance was positively related to Capercaillie presence (Table 1). Nevertheless, when analysing in combination with the rest of vegetation variables (Table 2) the result changed. The preference for *Calluna* seemed to be mediated by other species, resulting in preferred sites when appearing together with predominant heathers (*Erica* sp.) and meadows (see principal component PON1 in Table 2). On the contrary, principal component PON3 showed that the birds avoided sites where *Calluna* was the unique dominant shrub. Another example is the preference for heather (*Erica* sp.) in Degaña. Looking at the univariate analysis (Table 1), abundance of heather was very similar in positive and control plots. However, the first principal component (DEG1, see Table 2) showed that abundance of heather was an attribute of preferred sites.

According to our study, Cantabrian Capercaillie shows differences in habitat selection at local scale in comparison to other capercaillie populations (Gjerde and Wegge 1989; Picozzi et al. 1992; Storch 1993; Saniga 2003; Bollman et al. 2005). Though probably influenced at some extent by the different variables and methods employed in the different studies, we consider these results an evidence for further investigations on the ecological particularities of Cantabrian subspecies.

In general terms, Cantabrian Capercaillie showed preference for sites with relative abundance of shrubs dominated by heather (*Erica* sp.), a result that we supposed related to the role of this plant as shelter, but also as food resource for the birds. Indeed, consumption of heather as winter food is already documented for Cantabrian Capercaillie (Rodriguez and Obeso 2000).

In Ponga, preferred sites were mainly those with *Erica* appearing in concert with meadows abundance and tree regeneration absence (principal component PON1). The PON1 score reflects a trade-off between intense tree regeneration, with almost no shrub cover, and consolidated heather lands (*Erica* sp.) with presence of herbaceous species. Preference for heather lands could be interpreted in terms of higher food availability. In Degaña, the DEG1 score reflects a dichotomy between sites with very low shrub cover under beech-oak as canopy dominant species, and heather (*Erica* sp.) abundance under birch-rowan canopy cover. Preference for *Erica* under birch and rowan was interpreted in terms of both higher food availability and better protection. The second meaningful principal component, DEG4, reflects abundance of rocky soils, whose avoidance could be caused by their low productivity.

3.4.2. Conservation and management

The persistence of the Cantabrian Capercaillie depends, to a great extent, on the preservation of their habitat. Our results show that, at the scale under study, capercaillie habitat is selected at the level of multi-specific plant associations.

Regional conservation plans for the subspecies, however, seem to be focused almost exclusively on dominant trees and bilberry cover. It is clear the importance of mature forest with moderate canopy cover and the subsequent bilberry abundance in the ecology of capercaillie. Nevertheless, our results appoint also to other plant formations, mainly ericaceous shrubs (*Erica* sp.) and mountain meadows, as essential elements of the habitat. Moreover, in the western part of the range the presence of some non-dominant tree species, such as birch and rowan, is positively related to capercaillie presence, probably due to their spatial association with ericaceous shrubs. Conservation policies and management should not obviate the importance of maintaining such a complex mosaic of microhabitats for the fulfilment of capercaillie requirements. A badly understood habitat improvement, actually exemplified in supported birch and rowan removal (e.g. Leitariegos, own observations in 2006) as well as under-canopy clearings for theoretically favouring bilberry growth in currently occupied forests with considerable bird numbers, could lead to an excessive structural simplification of the habitat, resulting in unexpected negative effects on the population instead of the intended benefits.

In spite of that, conservation management should focus primarily on enhancing effective protection of the best remaining inhabited forests and their vicinity, as already appointed by Quevedo et al. (2006b). Protection of good areas should be interpreted basically in terms of both avoiding human traumatic activity (as opening of new tracks across the forest or aforementioned canopy and under-canopy clearings) and preventing overgrazing by domestic ungulates. Firstly, the species is proved to be highly susceptible to human disturbance; again, even the desired benefits of a well intentioned human activity could be surpassed by the disturbances caused by the activity itself to the birds of an already good area. Secondly, high herbivory levels on *Vaccinium* cause a decrease in fruit production in the following years (Tolvanen et al. 1993), and this could have a detrimental effect on the quality and availability of bilberry for capercaillie (Fernández-Calvo and Obeso 2004). Restricting the access of domestic ungulates, not only to currently occupied good areas but also to areas actually managed for improvement, would have a better effect for favouring bilberry growth (Klaus and Bergmann 1994; Côté et al. 2004) than the aforementioned under-canopy clearings (whose efficacy is not proved), and would make human disturbances unnecessary as well. Common sense tells us that when two possibilities for the same purpose exist, it is always better to test firstly the conservative solution, that is, the one in which fewer factors operate. Removing both human activities and overgrazing by domestic ungulates from the equation should be the first management measures to test if the purpose is the effective conservation of the population.

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CAPÍTULO 4. Spatial habitat models for endangered Cantabrian Capercaillie: A bidimensional approach

Modelos espaciales de hábitat para el urogallo cantábrico: Una aproximación bidimensional

4.1. INTRODUCTION

Conservation of endangered species in human modified landscapes is a leading topic in conservation biology. Due to the continuous growing of human impact, declining of the species comes to be faster and many of them are brought near extinction even before we attain to know their population status. In this situation, conservation research gets involved in the need of developing new frameworks and tools for improving our understanding of the relationship between environmental factors and habitat requirements of the species, and how they respond to the changes in their habitat.

Particularly important in this topic is to understand habitat selection, since it determines the spatial structure of populations (Morris 1987) and consequently population viability. For many species, however, there is a lack of knowledge relative to habitat requirements, and obtain this information may require considerable monitoring effort (Revilla et al. 2000) as well as time. This is especially problematic in high endangered as well as relict species or populations, where we are challenged to provide urgent management criteria with not enough knowledge of their ecology.

The Cantabrian Capercaillie (*Tetrao urogallus cantabricus*) is a clear example of the situation above mentioned. The Cantabrian Mountains, in the NW of Spain, present a long history of human use and, as a consequence, the forests the capercaillie inhabits are largely fragmented (Obeso and García 1990; Chapter II – García et al. 2005). Cantabrian subspecies shows marked differences in comparison to the rest of the European populations, living also in the edge of the distribution range of the species and being a relict population, as the nearest ones are those in the Pyrenees, 300 kilometres away. Although the Capercaillie is supposed to be a conifer specialist (Picozzi et al. 1992; Storch 1995), this is not the case in the Cantabrian Mountains, where the bird inhabits almost exclusively deciduous forest fragments composed mainly by beech (*Fagus sylvatica*) and oak (*Quercus petraea*) highly interspersed with ericaceous shrubs (Castroviejo 1975; Chapter II – García et al. 2005). Therefore, other factors like ground vegetation and subsequently feeding habits also differ from the populations in North and Central Europe (Rodriguez and Obeso 2000). The Cantabrian Capercaillie was considered endangered in the Red Data Book in 1979, going since then through a pronounced decline estimated in more than 50% of the birds and 42% in lek occupancy (Storch 2000). In spite of this situation, only very recently have basic ecological questions begun to be answered. In this sense, a habitat model restricted to the province of Asturias (Quevedo et al. 2006) showed that large-scale habitat suitability for Cantabrian Capercaillie is very low, and that habitat configuration plays a role in the current process of population decline at a scale that goes beyond the average size of forest fragment in the range (see Chapter II – García et al. 2005 for details about configuration of forest fragments).

Habitat modelling has become an important field in conservation biology as it helps to resolve the questions previously mentioned. Predictive distribution models based on species-landscape associations are useful tools for compensating lacks of knowledge on population ecology, and have been used in that way (Boyce 1999). Models using logistic regression have increased particularly and have been used for several species (Donazar et al. 1993; Mladenoff et al. 1999; Schadt et al. 2002; Naves et al. 2003), being particularly useful to investigate conservation problems of species with large habitat requirements and high sensitivity to habitat alterations (Carroll et al. 2001). They work in situations where no more than presence-absence data are known and they don't show the restrictions of other methods about normality distribution of errors. The method basically consists in contrasting used versus unused habitat units with a set of potentially explanatory variables, in order to determine habitat suitability by predicting the probability of occupancy (Manly et al. 1993; Tabachnick and Fidell 1996); the regression function can then be extrapolated and mapped over the entire area of interest.

We should take in mind population ecology that lies behind presence-absence data. In order to make correct inferences, habitat quality should be explicitly linked to demographic features (Thomas and Kunin 1999). In that way, it would be more realistic to construct two sets of models, one for survival and one for reproduction, instead of one-dimensional model.

However, the objection to this approach lies on the rare availability of information about demographic features. What we here propose is to generate two independent sets of models with the same and only available dependent variable presence/absence variables (Naves et al. 2003). The basis of this framework is to relate each landscape variable to one of the key demographic features survival and reproduction, generating two independent sets of explanatory variables. The critical assumption is that human related variables, in terms of disturbance and pressure on the habitat, are the main causes of mortality, while on the other hand variables related with food availability determine reproduction. Abundance of food is a prime factor determining habitat selection (Wiens 1989a), and therefore conditioning home range size (Storch 1995) and reproductive and breeding success (Selås 2000). On the opposite, human induced mortality is considered the main cause of death for long-lived species with large spatial requirements and low densities (Woodroffe and Ginsberg 1998), particularly in highly humanized and fragmented landscapes. Zones perceived by the individuals as good habitats in terms of abundance of resources but with a high risk of mortality are reported in the literature as ecological traps (Dwernychuk and Boag 1972; Gates and Gysel 1978; Schlaepfer et al. 2002). These deceptive sources act functionally as attractive sinks (Delibes et al. 2001a, b), and are usually associated with human activities (Schlaepfer et al. 2002).

By applying our framework, we try to contribute with new approaches to improve our understanding of the capercaillie-landscape relationship and overcome the urgent need for knowledge on demographic parameters that Quevedo et al. (2006) demanded in their model.

In that sense, our spatial models will help us to get knowledge on Cantabrian Capercaillie source-sink dynamics, identifying areas of high conservation value and otherwise areas to be managed for their improvement. Finally, we will apply the obtained models to test the relative influence of a high mortality rate and a low reproduction rate on the extinction dynamic of the population.

4.2. METHODS

4.2.1. Study area

The area of study was included in the Cantabrian Mountains, northwest Spain (Figure 1). The mountains run parallel to the Atlantic coast from east to west, with elevations ranging up to 2648 m and numerous hilltops above 2000 m. Due to the proximity of sea in the north, average elevation is lower and slope gradient higher than in the south-facing slopes (700 m and 34%, and 1300 m and 21%, respectively). Soils are mainly calcareous in the east, while in the west some siliceous beds also appear. Forests are deciduous, dominated by European beech (*Fagus sylvatica*) and sessile oak (*Quercus petraea*). Above 1700 m climatic conditions prevent forest growth, and shrubs and subalpine vegetation (*Vaccinium myrtillus*, *Juniperus communis*, *Arctostaphylos uva-ursi*) dominates. Once mostly covered by deciduous forest, the Cantabrian range has a long history of human use and deforestation. Today, Cantabrian forests are largely fragmented (Chapter II – García et al. 2005) and bear a heavy grazing pressure by domestic as well as wild ungulates, being cattle grazing the main economic activity.

Basing on published data on dispersal distance (Wegge et al. 1981; Storch & Segelbacher 2000; Sachot 2002; Moss et al. 2006), we chose a potential area of 12 kilometres around the historic distribution of capercaillie leks, resulting in a study area of 8092 km^2 that comprised almost the totality of the range above 650 m.

4.2.2. Spatial scales and capercaillie data

The units for our analysis were raster cells derived from a grid comprising the whole Cantabrian range. We chose a spatial resolution of 0.25 km^2 in order to capture landscape information in a scale finer than the birds' home ranges, which varies from 0.5 to 12 km^2 according to local conditions (Storch 1995).

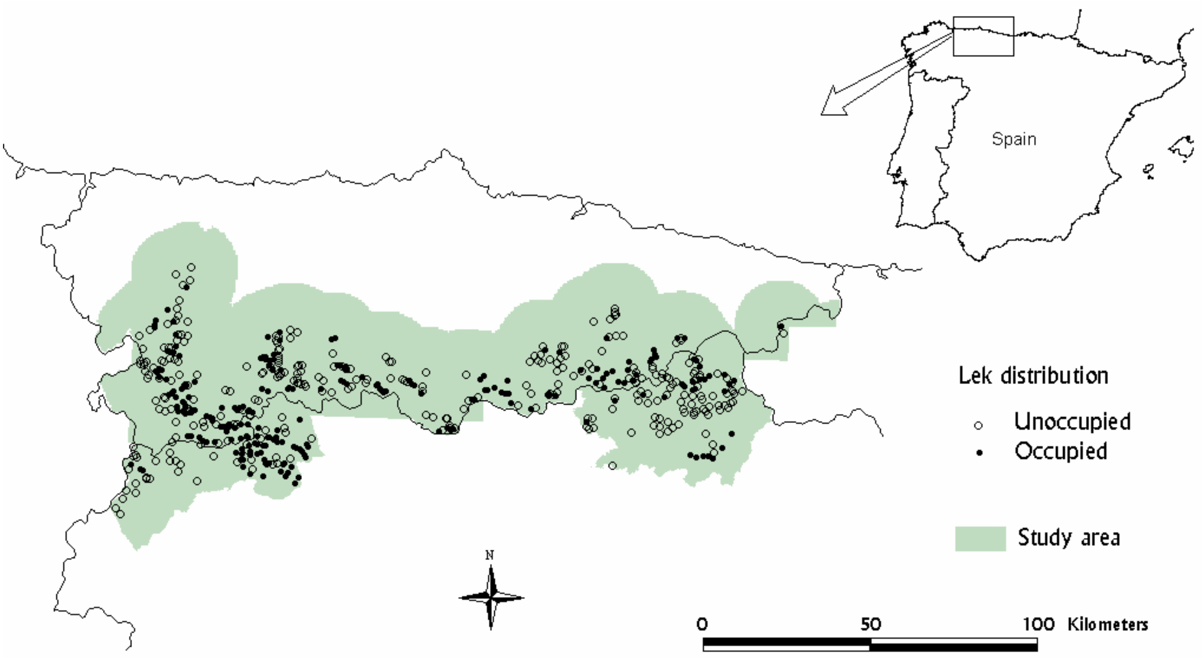


Figure 1. Study area representing potential habitat for Cantabrian Capercaillie. Occupied leks are shown as filled circles, and empty circles are extinct ones. Regional limits are represented with black lines.

However, it is known that there is no single correct spatial scale at which to describe species-habitat relationships (Wiens 1989b); birds might perceive the landscape at different scales, and the effects of human presence on birds might also be greater at a coarser scale. In that sense, it has been appointed that habitat models, particularly large-scale ones, should be conducted with multi-scale approaches (Graf et al 2005). According to that, we also generated, from the original explanatory variables, scale-dependent variables to test the landscape-species relation over areas larger than the arbitrarily chosen spatial grain, in order to capture the real scale at which that interaction takes place.

We considered as positive or presence cells those cells containing or intersecting with leks, whether they are occupied or not. The study area then consisted on 538 presence cells in a total of 32541 cells. Lek location was proportioned by the regional environmental agencies (Principado de Asturias, Castilla-Leon), mostly corresponding to traditionally known lek territories occupied in the 70´s. Since then, various censuses have been performed to collect information about lek occupancy, which was assumed when any kind of signs of presence (direct sightings, droppings, footprints) was detected.

4.2.3. Landscape variables

Election of the variables was done in order to allow subsequent modelling steps. In that way, variables not a priori showing ecological relevance were avoided, trying not to choose many potentially explanatory predictors that may complicate model interpretability and inference (Burnham and Anderson 1998). Nine landscape variables were selected and summarized in the sampling units after being processed with a geographic information system (ArcView GIS 3.1, ESRI Inc. 1998). They were mostly derived from digital thematic cartographies, provided by the regional agencies (Principado de Asturias, Castilla-Leon), which are composed of Arc-Info vectorial layers with a resolution of 25 m based on the Spanish National Topographic Map 1:25,000. Besides, two variables were derived from the national municipality databases (CERCA, Instituto Nacional de Estadística). Because of the coarser spatial resolution of this latter source of data (at least one order of magnitude larger than the spatial grain of our grid), we made use of it only when no other way to process a chosen predictor was possible.

<u>Natural variables</u>

Four variables were compiled for the reproduction models attending to their relation to shelter and food availability. Three of them (*For*, *Shrb* and *Edge*) were vegetation variables obtained by processing the digital thematic cartographies (Principado de Asturias, Castilla-Leon). Forest cover (*For*) and shrub cover (*Shrb*) represent respectively the proportion of the cell covered by forest and shrub vegetation, which act both as shelter and food sources. The length of edge between shrub and forest patches within the cell (*Edge*) is a measure of the density of ecotones; we used this variable as an indirect estimate of bilberry (*Vaccinium myrtillus*), as no other source of data about bilberry presence was available. Finally, the number of equivalent large stock units in the cell (*UG*) was supposed to take effect on bilberry availability, due to the high cattle pressure the Cantabrian Mountains actually bear; this variable was derived from the national municipality databases (CERCA, Instituto Nacional de Estadística).

Human variables

We chose five potential predictors describing human presence and access to birds. We supposed these variables to be related to both direct and indirect disturbances and mortality. Variables related with direct human pressure were number of villages (*Vill*) and population (*Popul*). In relation with indirect pressure or human access to birds, we compiled road density (*Road*) and topographical features slope (*Slop*) and elevation (*Elev*). Human variables were derived from several sources. The municipality databases (CERCA, Instituto Nacional de Estadística) provided human population, while number of villages and road density were derived from the digital thematic cartographies (Principado de Asturias, Castilla-Leon). We also generated a Digital Elevation Model so that mean elevation and slope of the cells could be derived.

Scale-dependent variables

Although spatial resolution was chosen trying to fit capercaillie home range, cell size is anyway arbitrary. In order to take into account the species' perception of their habitat we generated, from the five local scale variables obtained from the fine-grained digital thematic cartographies, new variables at larger scales. We used a moving window algorithm (Wiegand et al 1999; Schadt et al 2002; Naves et al 2003; Wiegand and Moloney 2004) to describe connectivity or diffusion of a given variable at different growing scales, assigning to each cell the average value of the surrounding cells. At a scale R, diffusion was measured with a circular window of radius R, while to calculate connectivity we employed a ring-shaped moving window. Diffusion was employed with human variables villages, population and road density, and connectivity was applied to vegetation variables forest and shrub. We enlarged scales from focal cell to radius-10 (i.e. up to 5 kilometres), obtaining 50 supplementary variables.

4.2.4. Analysis and Model building

We used univariate analysis with our landscape predictors (Table 1), using t-test to describe differences between presence and absence cells. We retained for each set of scale-dependent variables (e.g. *Vill*, *VillE1* … *VillE10*) the scale at which the variable showed the most explanatory significance (e.g. *VillE3*). Then, a Spearman correlation matrix was calculated with all the variables retained in order to avoid multicollinearity between the variables entering each model. Spatial autocorrelation in the dependent variable was assessed to avoid pseudo-replication and model overfitting (Lennon 1999).

The models were formulated previously to their analysis. This a priori formulation of models was made to avoid “data dredging” (Burnham and Anderson 1998) and consequently overfitting of models. In addition, this procedure may be a prerequisite for model inference (Burnham and Anderson 1998), which is the ultimate purpose of modelling when the aim is the management of an endangered population. We formulated a total of 33 models divided in two blocks, 24 corresponding to reproduction and 9 to survival (Table 2). As forest and shrub cover showed a high significance when radius equalled 2 km, adjusting to the reported capercaillie home range (Storch 1995), we worked on different hypothesis about the scale (grid cell or home range) at which those vegetation variables could be more important for capercaillie, including them at both local and radius-4 scale in separate reproduction models.

Multiple logistic regression was then applied to the formulated models. For model development, we used 269 randomly chosen leks (i.e. half of presence cells), keeping the rest for model validation. Both development and validation were accomplished by contrasting presence cells versus the same number of absence cells randomly distributed over the study area.

Multiple logistic regression is a form of GLM (Generalized Linear Model) with a binomial error distribution and a logit link function. It is formulated as follows:

$P = e^{\mathrm{logit}\,(P)} / 1 + e^{\mathrm{logit}\,(P)}$

being P the probability of obtaining a positive response in a cell. Logit (P) is a traditional multiple regression:

$\mathrm{logit}\,(P) = \alpha_{0\,+}\,\alpha_1\,x_1 + \alpha_2\,x_2 + ... + \alpha_n\,x_n$

with α_0 the intercept, x_i the predictors entering the model and α_i the coefficients assigned to the predictors during the regression procedure.

Logistic models were evaluated using Akaike Information Criterion (AIC) and a second order transformation of it, AIC_c (Table 2). AIC (Akaike 1973) is an objective model selection criterion for the selection of the best approximating model for data and inference (Burnham and Anderson 1998), which is based on simplicity and parsimony. By choosing from each of the two blocks the model with the lowest AIC (which in all cases had also the lowest AIC_c), one survival model and one reproduction model were selected for posterior inferences. We tested for uncertainty in model selection by calculating Akaike weights for all the models basing on the lowest AIC value in each block (Burnham and Anderson 1998).

Given a model, we selected a cut-off value that best discriminated between used and unused habitat. That was made by plotting probability outputs versus sensitivity (correctly classified bird presence), specificity (correctly classified absences) and global correct prognoses. Besides, as a measure of model accuracy independent of the cut-off value, we represented a Receiver Operating Characteristic curve (Guisan and Zimmermann 2000; Pearce and Ferrier 2000) plotting sensitivity against false positive proportion of predicted presences (i.e. 1 – specificity). The area under the curve (AUC) is the proportion of correct discrimination between two presence and absence cells randomly chosen, that is, model assigning a higher probability value to the presence cell (Pearce and Ferrier 2000).

Validation of the models was done with data not used during model development. With the discrimination value previously selected, proportion of correct classification of observations and non-observations was calculated over 269 leks and 269 random points.

For model application and map building, logistic functions were calculated in all cells of the study area using the logit link function previously described, the value obtained for each cell being assumed as its habitat quality. According to our two-dimensional framework, we obtained, for each cell, two indexes of habitat quality. The combination of both survival and reproduction indexes (*P-Surviv* and *P-Reprod*, respectively) allowed us to classify the habitat into five categories (Figure 3): Matrix (avoided habitat, very low survival and reproduction), sink (low survival and reproduction), attractive sink (high reproduction but low survival), refuge (high survival but low reproduction), and source (high survival and reproduction) habitats.

Finally, we applied our framework to explain the extinction dynamic of the population. The suitability indexes of the two selected logistic models (*P-Surviv* and *P-Reprod*) were used as new predictive variables to test the relative influence of either a high mortality rate or a low reproduction rate on population current status. In order to take into account the spatial autocorrelation in the dependent variable, we generated at growing scales a set of variables describing the number of occupied cells in the vicinity of each occupied cell (*OcupE1* ... *OcupE10*); with this, we tried to detect the scale at which a hypothetic aggregation of occupancies occurred. This measure could be considered an estimate of demographic spatial stochasticity, whose great relevancy on the extinction process of such a very small metapopulation might conceal the effect of habitat variables. We then formulated a set of logistic models (Table 4) with cell occupancy as dependent variable and different combinations of *P-Surviv*, *P-Reprod* and demographic stochasticity as predictors.

Table 1. Definition and contrast of the means (± standard deviation) of the landscape variables measured in 538 absence cells and 538 leks (presence cells). Statistical differences based on *t*-test are indicated by asterisks (* indicates significant differences at $P < 0.05$ and ** differences at $P < 0.01$).

Variable	Description [units]	Leks	Absence cells	
For	Forest proportion inside the cell [proportion]	0.664 ± 0.263	0.229 ± 0.291	**
ForE4	Forest proportion inside a ring of 1 cell width and radius 4 around the cell [proportion]	0.361 ± 0.162	0.236 ± 0.167	**
Shrb	Shrub proportion inside the cell [proportion]	0.211 ± 0.231	0.263 ± 0.300	*
ShrbE4	Shrub proportion inside a ring of 1 cell width and radius 4 around the cell [proportion]	0.325 ± 0.181	0.288 ± 0.197	*
Edge	Density of ecotones between forest and shrubs [m / Ha]	52.5 ± 37.2	35.8 ± 37.8	**
UG	Stocking rate [Livestock units / Ha]	0.130 ± 0.079	0.161 ± 0.111	**
Popul	Human population [inhabitants / Ha]	0.177 ± 0.174	0.219 ± 0.402	
VillE3	Number of villages inside a circle of radius 3 around the cell [Nº villages / Ha]	0.0004 ± 0.0007	0.0020 ±0.0029	**
Road	Road density [m / ha]	8.19 ± 20.08	15.95 ± 24.95	**
Elev	Mean elevation of the cell [m.a.s.l.]	1326.8 ± 201.3	1052.5 ± 467.9	**
Slop	Mean slope of the cell [%]	39.89 ± 23.35	35.32 ± 20.22	*

4.3. RESULTS

4.3.1. Univariate and Correlation Analysis

After exploring correlation between each variable at a particular scale and the same variable at the rest of scales, we selected eleven variables for model building. Number of villages at cell scale was substituted for villages at radius-3 scale (*VillE3*), that is, number of villages in the surrounding 1.5 kilometres. Both forest and shrub cover at scale 4 (*ForE4*, *ShrbE4*) didn't show a strong correlation with the original vegetation variables, so that they were added to the pool without rejecting local scale variables (*For*, *Shrb*).

All these eleven variables showed significant differences between presence and absence cells (Table 1) exception made of *Popul*. Forest cover proportion was as expected higher in presence than in absence cells at both local and radius-4 scales. It is important to note that radius-4 scale adjusts to the reported home range for capercaillie (Storch 1995), being also in relative accordance with the results of other multi-scale studies on capercaillie habitat (Miettinen et al. 2005; Quevedo et al 2006).

So as expected, positive cells had larger density of ecotones (*Edge*) and less stocking units (*UG*) than negative ones. Shrub cover showed a different behaviour depending on the scale. It was negatively related to bird presence at local scale, but the relation turned into positive at radius-4 scale. Human variables behaved also as expected. Number of villages, human population and road density were larger in negative cells, while mean elevation and slope were higher in positive cells. No variable had to be rejected from any model, as no pair of variables in the same a priori formulated model showed a Spearman correlation coefficient $r > 0.7$.

Table 2. Logistic predictive models for capercaillie presence formulated a priori, and selection evaluators. Δi = AIC – minAIC.

Model		Deviance	AIC	AICc	Δi	Weights
Reproduction models						
	Home range and local scales					
1	*For ForE4 Shrb ShrbE4 Edge UG*	0.4205	446.176	446.448	3.451	0.088
2	*For ForE4 Shrb ShrbE4 Edge*	0.4202	444.373	444.584	1.648	0.217
3	*For ForE4 Shrb ShrbE4 UG*	0.4200	444.562	444.773	1.837	0.198
4	*For ForE4 Edge UG*	0.3815	471.261	471.419	28.536	0.000
5	*For ForE4 Shrb ShrbE4 Edge*	0.3804	470.117	470.23	27.392	0.000
6	*For ForE4 Shrb ShrbE4 UG*	0.381	469.427	469.54	26.702	0.000
7	*For ForE4 Shrb ShrbE4*	0.4199	442.725	442.883	0	0.495
8	*For ForE4*	0.380	468.236	468.311	25.511	0.000
	Local scale					
9	*For Shrb Edge UG*	0.3996	457.823	457.981	15.098	0.000
10	*For Shrb Edge*	0.394	459.945	460.058	17.22	0.000
11	*For Shrb UG*	0.399	455.904	456.017	13.179	0.001
12	*For Edge UG*	0.370	477.738	477.851	35.013	0.000
13	*For Edge*	0.3618	482.044	482.119	39.319	0.000
14	*For UG*	0.370	475.803	475.878	33.078	0.000
15	*For Shrb*	0.394	457.954	458.029	15.229	0.000
16	*For*	0.3618	480.044	480.089	37.319	0.000
	Home range scale					
17	*ForE4 ShrbE4 Edge UG*	0.229	584.879	585.037	142.154	0.000
18	*ForE4 ShrbE4 Edge*	0.226	585.777	585.89	143.052	0.000
19	*ForE4 ShrbE4 UG*	0.227	584.23	584.343	141.505	0.000
20	*ForE4 Edge UG*	0.200	604.42	604.533	161.695	0.000
21	*ForE4 Edge*	0.194	606.865	606.94	164.14	0.000
22	*ForE4 UG*	0.1968	605.116	605.191	162.391	0.000
23	*ForE4 ShrbE4*	0.223	585.353	585.428	142.628	0.000
24	*ForE4*	0.190	607.98	608.025	165.255	0.000
Survival models						
25	*Popul VillE3 Road Elev Slop*	0.319	519.718	519.929	0	0.688
26	*Popul*	0.039	720.887	720.932	201.169	0.000
27	*Popul Road*	0.097	679.756	679.831	160.038	0.000
28	*VillE3*	0.228	579.805	579.85	60.087	0.000
29	*VillE3 Road*	0.241	571.804	571.879	52.086	0.000
30	*VillE3 Elev Slop*	0.312	521.296	521.409	1.578	0.312
31	*Road Elev Slop*	0.289	538.069	538.182	18.351	0.000
32	*Elev Slop*	0.286	538.235	538.31	18.517	0.000
33	*Road*	0.061	704.009	704.054	184.291	0.000

4.3.2. Reproduction models

Model with the lowest AIC value contained the four vegetation variables *For*, *ForE4* (forest connectivity at a radius of 4 cells), *Shrb* and *ShrbE4* (Table 2). The second and third best models included those same variables and *Edge* and *UG*, respectively. A closer look to the weights of reproduction models supported the hypothesis of vegetation cover being decisively important at both local and home range scales, as the sum of weights for that hypothesis accounted for more than 99.8% confidence in selecting the best model (Table 2). The simplest model was therefore selected (it was also the first in the AIC ranking) for further applications. We selected 0.5 as cut-off value as it fell between the value for least error and the value for optimum prognoses (Table 3, Figure 2(A.1)). Sensitivity of the model with that discrimination value was 0.84 and specificity equalled 0.78 (Table 3). AUC, that is, discrimination power, was 0.87 (Figure 2(A.2)).

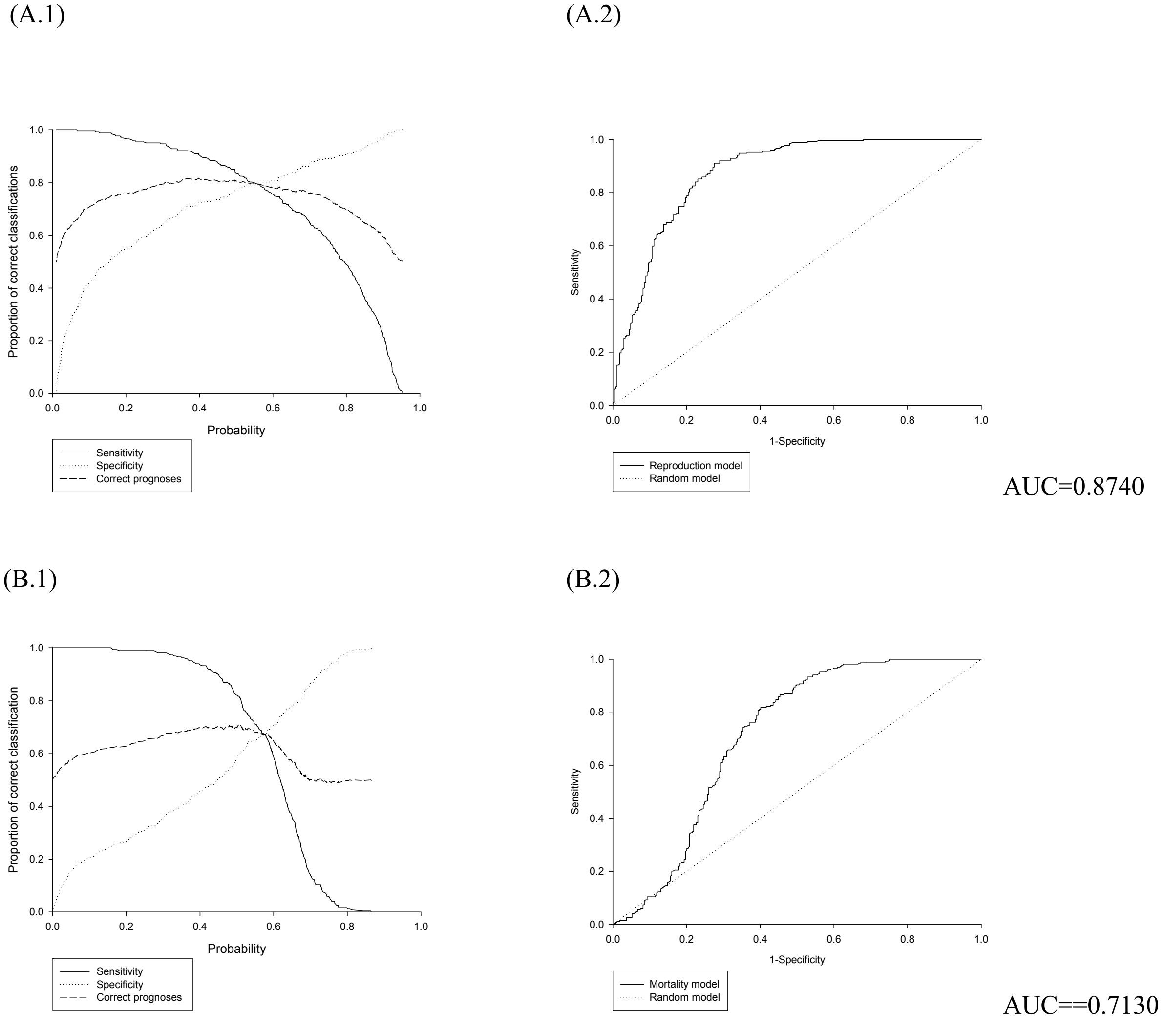
Model validation, with 0.5 as cut-off value, showed high classification accuracy very similar to the obtained with the training data set. Model correctly classified 79.7% of the cells, sensitivity equalling 0.79 and specificity 0.80. A map describing the selected habitat suitability model for reproduction is shown in Figure 3A.

Table 3. Results of the logistic regressions for the best reproduction and survival models. Numbers in brackets are referred to Table 2.

		Model parameters						**Model information**							
	Model	Parameter	Estimate	Std Error	Chi-Sq	P	Std Estimate	Deviance	AIC	AICc	Weight	Cut-off	Sensitivity	Specificity	Correct prognoses
Reproduction	Best AIC (7)							0,37871	473,375	473,533	0,495428	0,5	0,836431	0,776952	0,806691
		Intercept	-4,6053	0,5361	73,7904	<.0001						0,55643 Least error	0,795539	0,795539	0,795539
		For	5,8867	0,5882	100,1494	<.0001	1,1436					0,39737 Optimum	0,910781	0,724907	0,817844
		ForE4	1,6218	0,9162	3,1333	0,0767	0,1570								
		Shrb	2,5412	0,6116	17,2644	<.0001	0,3769								
		ShrbE4	2,2880	0,7923	8,3398	0.0039	0,2394								
	+ Edge (2)							0,37912	475,065	475,276	0,217331	0,5	0,840149	0,765799	0,802974
		Intercept	-4,6744	0,5543	71,1135	<.0001						0,56399 Least error	0,795539	0,795539	0,795539
		For	5,8634	0,5916	98,2127	<.0001	1,1391					0,357140 Optimum	0,921933	0,710037	0,815985
		ForE4	1,5792	0,9175	2,9622	0,0852	0,1529								
		Shrb	2,5862	0,6225	17,2617	<.0001	0,3836								
		ShrbE4	2,2370	0,7993	7,8322	0.0051	0,2341								
		Edge	0,00175	0,00315	0,3077	0.5791	0,0370								
	+ UG (3)							0,37872	475,367	475,578	0,197734	0,5	0,836431	0,773234	0,804832
		Intercept	-4,6300	0,6078	58,0313	<.0001						0,55522 Least error	0,795539	0,795539	0,795539
		For	5,8906	0,5901	99,6598	<.0001	1,1444					0,429978 Optimum	0,907063	0,724907	0,815985
		ForE4	1,6416	0,9447	3,0195	0.0823	0,1589								
		Shrb	2,5478	0,6163	17,0875	<.0001	0,3779								
		ShrbE4	2,2838	0,7938	8,2774	0,0040	0,2390								
		UG	-0,1153	1,3340	0,0075	0,9311	0,00621								
Survival	Best AIC (30)							0,16215	632,889	633,002	0,844814	0,5	0,821561	0,579926	0,700743
		Intercept	-1,6900	0,5731	8,6969	0,0032						0,5756 Least error	0,672862	0,672862	0,672862
		VillE3	-513,2	107,6	22,7487	<,0001	-0,6285					0,50518 Optimum	0,817844	0,598513	0,708178
		ELEV	0,00131	0,000359	13,2135	0,0003	0,2774								
		SLOP	0,0140	0,00477	8,6328	0,0003	0,1695								
	+ Pobl + Road (25)							0, 16295	636,297	636,508	0,153717	0,5	0,825279	0,587361	0,706320
		Intercept	-1,6887	0,5978	7,9791	0,0047						0,56743 Least error	0,665428	0,665428	0,665428
		Popul	0,2547	0,3630	0,4923	0,4829	0,0435					0,49833 Optimum	0,832714	0,587361	0,710037
		VillE3	-518,3	108,8	22,7114	<,0001	-0,6348								
		Road	-0,00161	0,00461	0,1212	0,7277	-0,0203								
		ELEV	0,00130	0,000366	12,5825	0,0004	0,2758								
		SLOP	0,0135	0,00484	7,8330	0,0051	0,1638								

Figure 2. (A) Best reproduction model. A.1) Sensitivity, specificity and total proportion of correct classifications as a function of probability for selecting an adequate cut-off value. A.2) ROC (Receiver Operator Characteristic) curve for the best reproduction model (solid line) and for a random model. Quality in discriminating presence from absence cells (0.87) is given by the area under the curve (AUC).

(B) Best mortality model. B.1) Proportion of correct classification of the best mortality model plotted against P. B.2) ROC plot for the same best survival model. As an overall fit of the model, AUC equalled 0.713.



AUC=0.8740

AUC==0.7130

4.3.3. Survival models

Best survival model included three variables: *VillE3* (number of villages in a radius of 3 cells)*, Elev* and *Slop* (see Table 2 and 3 for details). AIC weight of the model was 0.84 showing not high selection uncertainty. Together with the second best model they accounted for 99% in selection confidence, being the second best model the global model (that is, the one including all the five survival variables). We chose also in this case 0.5 as cut-off value for discrimination (Figure 2(B.1)), sensitivity being 0.82, specificity 0.58 and global correct prognoses then 0.70 (Table 3). Discrimination power (AUC) was 0.72 (Figure 2(B.2)).

Predictive accuracy of the model for validation data was even higher than for the training data. Correct prognoses equalled 0.77, with sensitivity 0.87 and specificity 0.67. Figure 3B shows a map describing the selected habitat suitability model for survival.

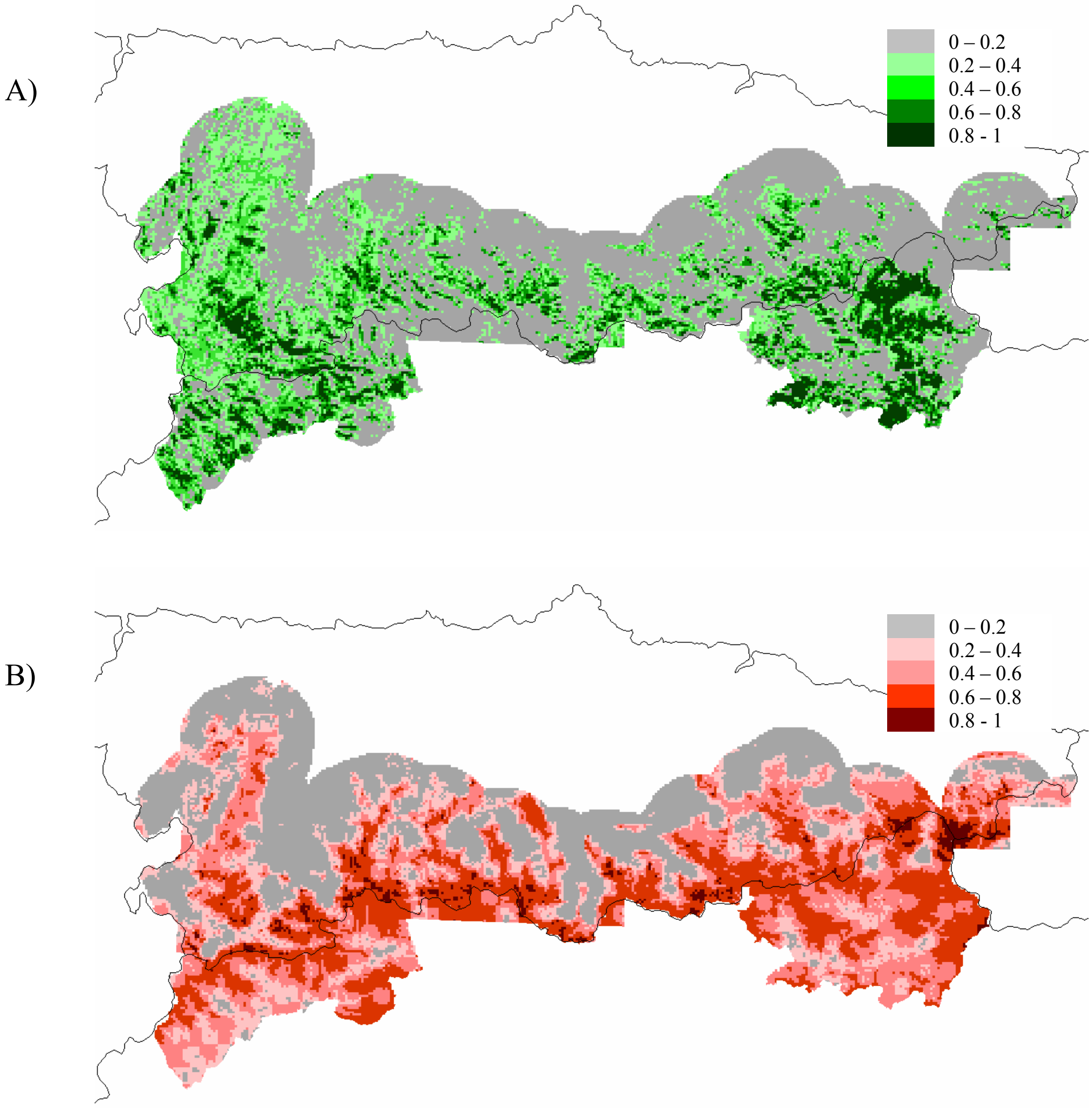


Figure 3. Habitat quality maps for A) reproduction and B) survival. Higher values imply higher habitat suitability.

4.3.4. Habitat map

According to our two-dimensional framework, we divided the study area into five habitat types: Matrix, sink, attractive sink, refuge, and source habitats. For defining avoided habitat a threshold value $P = 0.21$ was chosen, so that less than 5% of the presence cells fell inside matrix. To delimit source habitat we selected a discrimination value $P = 0.65$ (Figure 4).

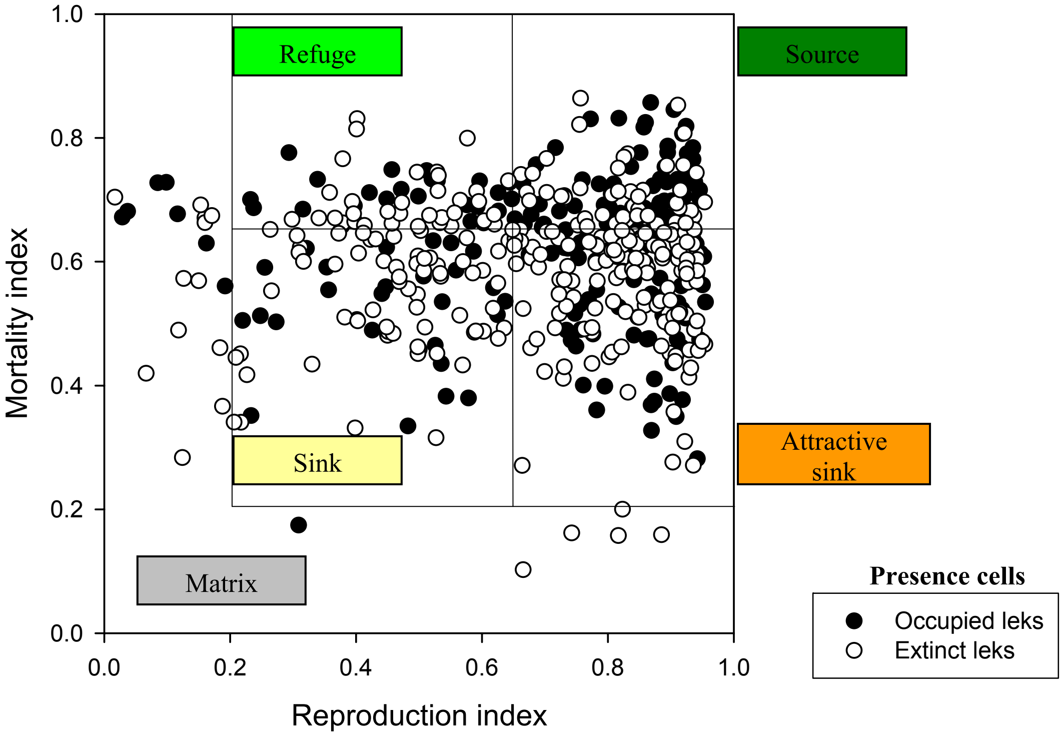


Figure 4. Bidimensional classification of all the leks in accordance to the quality (probability) index of the human and natural models (y-axis and x-axis respectively). Occupied and extinct leks are discriminated to assess the spatial structure of extinction probability among the different habitat types defined. Thresholds are 0.21 for matrix and 0.65 for source habitat.

The map representing the study area categorized into these five habitat types is shown in Figure 5. Availability of good habitats for capercaillie was poor and they were strongly patched, source habitat representing only 2.47% (200 km^2) of the study area and being located mainly in the north-facing slopes. Seven main zones accounted for 71.3% of this source habitat (Muniellos 24.5 km^2, Fuentes del Narcea 15.2 km^2, Degaña 20 km^2, Genestoso 26.7 km^2, Aller 20 km^2, Caso-Ponga 14.7 km^2, Casasuertes 21.5 km^2). Spatial conformation of these areas was complex, source habitat being interspersed mainly with areas of refuge, but also with attractive sink areas. Matrix occupied 59.1% of the potential habitat (4779 km^2). Sink areas accounts for 20.4% of the study area, while 12.2% corresponded to attractive sink and 5.6% to refuge areas.

4.3.5. Spatial allocation of extinction

We assessed the spatial distribution of extinctions according to the five defined habitat types. For that, we explored the actually status of lek occupancy in relation to that in the 80's. Of the 538 leks used for logistic modelling, 302 become extinct before last census (which took place in 2000). In addition, 9 leks were not visited in that census and were so excluded from de analysis. In summary, there were 302 extinct cells of a total number of 529 cells.

Matrix (0.70) and sink (0.69) showed the highest likelihood of extinction, and they were followed by attractive sink (0.61) and refuge habitat (0.60), although differences were not significant among these four groups. Only source habitat differed significantly from all the rest, its probability of extinction being 0.39.

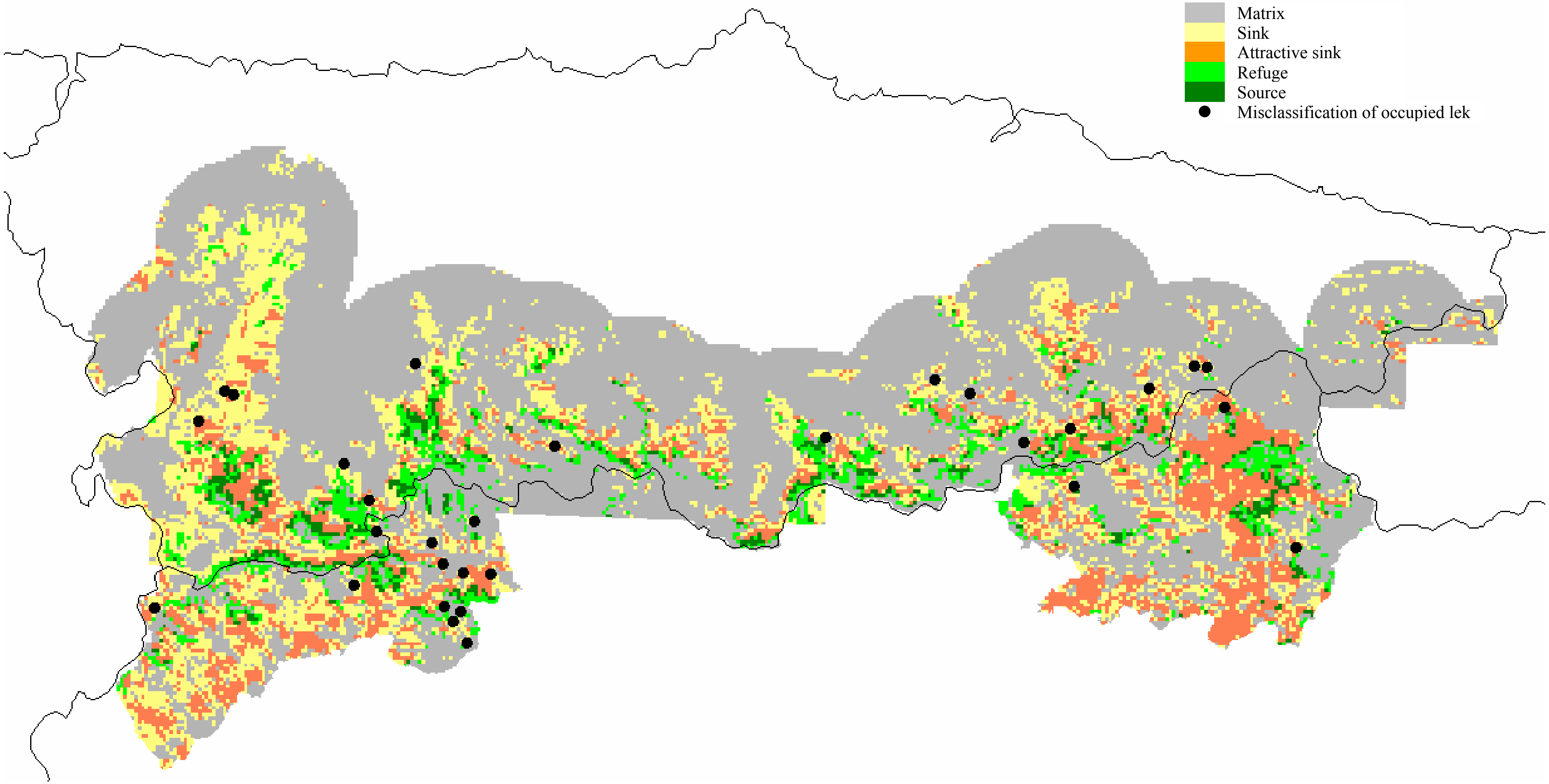


Figure 5. Habitat quality map, categorized into matrix (*P-Reprod* < 0.21 or *P-Surviv* < 0.21), sink (*P-Reprod* < 0.65 and *P-Surviv* < 0.65), attractive sink (*P-Reprod* > 0.65 and *P-Surviv* < 0.65), refuge (*P-Reprod* < 0.65 and *P-Surviv* > 0.65) and source (both > 0.65). Black circles represent actually occupied leks not classified as located in source habitats.

4.3.6. Extinction model

The spatial aggregation of occupancy was significant in a vicinity of 5 cells surrounding a given occupied cell, so we selected *OcupE5* as estimate of spatial demographic stochasticity. Best extinction model following AIC included the variables *OcupE5* and *P-Surviv* (Table 4). The addition of *P-Reprod* (second best model) did not add significant meaning, so the former model was selected due to its higher simplicity (Burnham and Anderson 1998). Extinction was therefore explained basically from survival model, though *OcupE5* revealed as the factor with the highest significance (Table 5). At a cut-off value of 0.6, selected model correctly classified 69% of the leks into occupied and unoccupied classes. Sensitivity equalled 0.66 and specificity 0.71 (Table 5). ROC plot indicated a discrimination power (AUC) of 73%.

Table 4. A priori proposed extinction models, and information estimators for model selection.

	Extinction models	Deviance	AIC	AICc	Δi	Weights
1	*P-Reprod P-Surviv OcupE5*	0.1165	646.482	646.596	0.006	0.419
2	*P-Reprod OcupE5*	0.1091	649.751	649.826	3.275	0.082
3	*P-Surviv OcupE5*	0.1138	646.474	646.551	0	0.420
4	*OcupE5*	0.1056	649.829	649.874	3.353	0.079

Table 5. Best extinction models. Numbers in brackets are referred to Table 4.

	Model parameters						**Model information**								
Model	Parameter	Estimate	Std Error	Chi-Sq	P	Std Estimate	Deviance	AIC	AICc	Weight	Cut-off		Sensitivity	Specificity	Correct prognoses
Best (3)							0.1138	646.47	646.55	0.420	0.6		0.6589	0.7137	0.6863
	Intercept	2.3439	0.5346	19.2240	<.0001						0.5895	Least error	0.6788	0.6784	0.6786
	OcupE5	-0.3496	0.0461	57.4041	<.0001	-0.4580					0.6144	Optimum	0.6490	0.7665	0.7078
	P_Surviv	-1.9416	0.8546	10.2823	0.0231	-0.1264									
Second (1)							0.1165	646.48	646.60	0.419	0.6		0.6623	0.7269	0.6946
	Intercept	2.7632	0.6183	19.9710	<.0001						0.5843	Least error	0.6954	0.6960	0.6957
	P_Reprod	-0.6213	0.4430	1.9671	0.1608	-0.0763					0.63786	Optimum	0.6126	0.8062	0.7094
	P_Surviv	-1.9338	0.8576	5.0844	0.0241	-0.1259									
	OcupE5	-0.3414	0.0464	54.0736	<.0001	-0.4474									

4.4. DISCUSSION

In this work we provide a functional characterization of Cantabrian Capercaillie habitat based in the incorporation of demographic features into a bidimensional habitat model. This approach also allows us to assess the spatial structure of the extinction process of the population, and to differentially evaluate the role of demographic aspects on that process.

4.4.1. Current population status

Availability of good habitat is a main problem for capercaillie in the Cantabrian range according to our model, a result in agreement with the first work published on Cantabrian Capercaillie habitat suitability (Quevedo et al. 2006). Representation of habitat obtained from our model shows that Cantabrian Capercaillie inhabits a complex patchwork of high but mostly low quality areas, a usual condition in many peripheral populations of endangered species (Channell and Lomolino 2000). Source habitat represents only 2.5% of potential habitat, and that situation does not look much better considering that refuge habitat reaches only 5.6%. Birds appear to be confined to small unconnected good areas surrounded by a larger proportion of sink and matrix habitat, these two habitat types with the lowest quality accounting for 80% of the potential habitat. Besides, good areas not occupied seem to be very few and also small to allow persistence of birds after a supposed colonization.

If model assumptions are correct, our results also appoint to some meaningful questions about the causes and the status of the extinction process the population is undergoing. In that sense, the extinction model appoint to a high mortality risk as the main factor determining lek occupancy, rejecting the effect of a hypothetic poor reproductive condition. Besides, the comparative high significance of *OcupE5* in the model also suggest that population numbers might be close to reach (if not yet) a lower threshold value for demographic stochasticity to become the governing factor in the current process of population decline, a circumstance that is present in other endangered capercaillie populations as well (Sachot et al. 2006).

4.4.2. Model benefits and shortcomings

Habitat modelling is a necessary first stage in conservation planning. It allows us to detect unoccupied suitable areas to be promoted, zones located between actually isolated occupied areas to be also promoted and managed as ecological corridors, and areas in which humans and species under study are particularly in conflict.

Though landscape-scale habitat models have been already developed for some other capercaillie habitats in Europe (Storch 1997; Sachot 2002; Suchant et al. 2003; Graf et al. 2005), it is nevertheless important to note that application of habitat models outside the area for which they were developed should be undertaken with caution, as the relationship of species occurrence to predictor variables can differ in both direction and strength (Graf et al. 2006). In that sense, the marked differences between Cantabrian and the rest of capercaillie habitats as well as the critical status of the population call for distinctive studies in that region.

Efficacy (precision) and applicability (generality) of models to conservation depends considerably on two aspects, the data employed to develop them and the distinctive conditions of the areas where model is going to be applied. Regarding the last point, we used pooled data from all available sub-regions for model calibration in order to increase predictive power (see Graf et al. 2006) over the whole Cantabrian range. Respecting the availability of the data, is not unusual a lack of them for many endangered populations in spite of the urgency of their management. Cantabrian Capercaillie is a clear example of such a challenging situation, an urgent need for demographic data being already demanded (Quevedo et al. 2006). In such a situation, the lack of ecological knowledge could be balanced by the use of methodological approaches that efficiently take into account the relationships between landscape features and distribution and dynamics of the populations. We here developed a bidimensional framework based on the construction of independent logistic models for the different demographic features. With this, we tried to make the best of available data, making a functional characterization of capercaillie habitat which incorporates refuge and attractive sink habitats to the classic source-sink theory (Delibes et al. 2001 a, b).

Probably the main shortcoming of this model is about the assumptions in relation to the bidimensional framework about independent natural and human related variables. This situation is more likely to take place in small and fragmented populations, and accepted to occur in the case of large carnivores (Naves et al. 2003). In our model, variables were selected basing on their simplicity and easy interpretability to facilitate that dissociation. Of course interrelationships also occur, but we assume their role to be of less significance. We suppose vegetation variables are related mainly to reproductive success in terms of food availability; being the capercaillie strictly linked to forest, we assume that a lost in forest cover implies a lost in resources availability more than a predation risk associated with fragmentation. On the other hand, human related variables, like number of villages and road density, of course might affect food availability by removing forest habitats when they are built, but we assume their role is of larger significance in terms of mortality by increasing access to birds. We found that reproduction models performed better than survival models in reproducing the distribution of historical capercaillie territories, while on the other side survival models performed better in reproducing the observed pattern of local extinctions. This supports our aforementioned assumptions that variables related with food availability determine reproductive success, and human related variables are the main causes of mortality, being also in accordance with previous works which showed that currently occupied leks support less human disturbances (Suárez-Seoane & García-Roves 2004; Quevedo et al 2006).

Another weakness of our model could be the different temporal origins of the dependent variable and the measured factors potentially influencing it. Capercaillie data are based on historic distribution of leks, while predictive variables come mostly from cartography generated in last years. This could lead to a conflict if variables controlling demographic dynamics had varied in the last decades. Nevertheless, that is not the case in our model. Forest cover has remained almost unchanged since the mid-twenty century, or even has grown slightly. Contrary to Central and North Europe forests where other Capercaillie population inhabits, Cantabrian montane forests are not managed for timber exploitation. However, cattle grazing still remain as the main economic activity. Moreover, apart of these historic considerations, the results of the model confirm that factors determining extinction dynamics are related to human variables, mainly to number of villages, and that vegetation variables are of little effect. Forest cover is the main factor influencing lek distribution, but not lek occupancy, as both occupied and unoccupied leks are located in forest habitat. These differences also support our main idea of analyzing human and natural variables separately.

4.4.3. Future conservation and management

Some authors have argued that the long-term persistence of species depends much on the maintenance of genetically distinct populations. This genetic divergence, as a result of isolation and natural selection, is expected to occur in peripheral populations (Lesica and Allendorf 1995), which are in addition subjects for new speciation events. Cantabrian Capercaillie, being considered a subspecies (del Hoyo et al. 1994), fulfils and goes beyond all these considerations for its conservation to be judged highly valued. The deciduous forests the subspecies inhabit and the complete isolation from the rest of the capercaillie populations are both factors accounting for genetic divergence (in terms of divergent natural selection and reduced gene flow, respectively), making its conservation become the conservation of the evolutionary process itself (Lesica and Allendorf 1995).

Occupied areas and source habitat and their vicinity should be the main subject of conservation efforts. Particularly, four of the seven main good areas constitute a macro-area of the highest conservation value in the western part of the range, comprising almost half of the total source habitat in the Cantabrian Mountains. These areas are Muniellos, Fuentes del Narcea, Degaña and Genestoso. Conservation management should focus primarily on enhancing effective protection of this large zone if the goal is the creation of a connected high quality area big enough for maintaining a viable population. In addition, non-occupied zones in the periphery of occupied ones should also be protected and its natural habitat improved. Protection of good areas should be interpreted basically in terms of limiting human traumatic activities and infrastructures; in this sense, we should take in mind that the disturbances caused by the human labours of a badly understood improvement of already occupied habitat may be greater than the intended benefit, especially when species are proved to be sensitive to human activities.

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CAPÍTULO 5. Assessing the importance of dispersal in the recent decline of the Cantabrian Capercaillie using Pattern-oriented modelling

Determinación de la importancia de la dispersión en el declive reciente del urogallo cantábrico mediante modelado orientado por patrones

5.1. INTRODUCTION

Habitat selection during dispersal is a key process in population ecology. Individuals' perception of habitat heterogeneity and subsequent contrasting use of space during dispersal are main factors affecting spatial structure (Morris 1987) and dynamics (Pulliam and Danielson 1991; Thomas 2000) of populations. This becomes particularly important in the case of metapopulations inhabiting heterogeneous landscapes, since individual dispersal movement leads to the connection or isolation of habitat subunits of different suitability and subsequently to local colonization or extinction (Levins 1970). Considering individual behaviour as the key for understanding the dispersal process, we need to understand how the spatial structure of the landscape and individual behaviour interact (Revilla et al. 2004). Quantifying landscape structure has become a leading topic in ecology and conservation, being considered to affect population dynamics in many ways (Dunning et al. 1992; Fahrig and Merriam 1994). When individual behaviour provides a functional link between spatial structure and population dynamics, the spatial structure of the landscape must be explicitly considered (Wiegand et al. 1999).

Spatially explicit population models (SEPMs) were developed to cope with the complex relations among individual behaviour, landscape structure, and population dynamics and provide a useful and powerful tool to test the effect of landscape spatial structure on population dynamics (Pulliam et al. 1992; Dunning et al. 1995; Wiegand et al. 1999, 2004). These models consider the species-habitat relationship explicitly by applying a population model on an underlying landscape map. This landscape map usually represents habitat quality, and it derives from a geographic information system (GIS). The other basic component is the population model, which simulates demographic features of the species. One meaningful aim of this type of models is linking individual and population scales. Individual-based SEPMs include rules of individual behaviour in response to the species' habitat perception. With the development of these models, individual habitat selection and dispersal connects to population dynamics in an explicit way (Pulliam and Dunning 1995; Wiegand et al. 1999).

Traditional approaches based on the theory of island biogeography assumed a homogeneous and unsuitable matrix, where metapopulation structure and dispersal can be explained by simple factors like distance between suitable habitat patches or buffer measures (Hanski 1994; Wiegand et al. 1999). However, recent field and modelling studies have shown that variation in matrix quality affects (meta)population dynamics (e.g., Vandermeer and Carvajal 2001; Revilla et al. 2004; Wiegand et al. 2005). Thus, when studying metapopulation key features such as dispersal, matrix heterogeneity must be considered explicitly, as it is the scenario where individual behaviour occurs during dispersal (Ricketts 2001). Individual-based SEPMs can easily include simple rules of individual behaviour in response to spatial variation in matrix quality to establish a link between matrix structure and metapopulation dynamics (Revilla et al. 2004).

However, a major criticism on the use of SEPMs is parameter uncertainty due to the intrinsic difficulty of obtaining information about the behaviour of individuals as well as from the lack of validation of the models (Wiegand et al. 2004a). Errors in demographic and dispersal parameters can propagate into larger errors in model predictions (Wennergren et al. 1995; Wiegand et al. 2003, 2004) and it has been argued that one will hardly access enough field data for populations of conservation concern to estimate demographic and dispersal parameters with sufficient exactitude to prevent error propagation (Ruckelshaus et al. 1999). Only recently, pattern-oriented modelling has been proposed as an answer to the uncertainty problems (Grimm et al. 2005; Wiegand et al. 2003, 2004). Although our knowledge of individual behaviour during dispersal in a heterogeneous matrix is still poor (Storch 2000; Rickets 2001), the pattern-oriented approach can resolve this problem by accessing additional sources of data for an indirectly estimation of model parameters or selecting an appropriate process structure. This additional data stem from a higher organizational level than the individual level, e.g., observed population trends. Population-level data such as time-series (Wiegand et al. 1998, 2004) or presence-absence data in spatially structured populations (Hanski 1994) is a rich source of data that might reflect underlying ecological processes. By comparing systematically the observed population data with the model output obtained for different model versions and different model parameterizations we could detect implausible model structures and parameterizations. The observed population-level data thus act as a filter to discriminate between probable and improbable model variants and parameterizations, and so diminishing both sources of uncertainty (Wiegand et al. 2003; Grimm et al. 2005).

In this article, we develop an individual-based spatially explicit dispersal model for Cantabrian Capercaillie (*Tetrao urogallus cantabricus*), a subspecies at the edge of the distribution range (Storch 2000). The subspecies was considered as endangered in the IUCN "Red Data Book" in 1979 and in the "Libro Rojo de las Aves de España" (Obeso 2004), but knowledge on basic population dynamics processes is still scarce. Only recently ecological questions like habitat use and selection by the Cantabrian Capercaillie (Quevedo et al. 2006a) and habitat suitability at large scale (Quevedo et al. 2006b) begin to be answered. Because of its secretive behaviour and low population number, little is known about the behavioural rules governing dispersal in the fragmented Cantabrian landscape and about the role dispersal plays in the dynamic of the Capercaillie metapopulation. However, data are available on long-term population trends stemming from 1982 to 2000 presence-absence censuses in 444 displaying sites covering the entire known range of the metapopulation. We will follow the approach of indirect pattern-oriented modelling outlined above to infer individual level dispersal behaviour from population level data. The specific aims of this study are:

1) To develop a dispersal model that could be included in a spatially explicit population model. Explicit consideration of the space will be based on underlying GIS-derived habitat quality maps. We will use observed data from population trends to reduce the uncertainty of parameter estimation and model structure. This will enable us to identify a dispersal behaviour that performs consistently with our data.

2) To improve our understanding of the role the dispersal process plays in the dynamic of the metapopulation, an essential prerequisite for the conservation of the most endangered capercaillie population (Storch 2000; Obeso and Bañuelos 2003).

5.2. METHODS

5.2.1. The study area and the metapopulation

The study area is located in the Cantabrian Mountains, northwest Spain, a mountain region that runs parallel to the Atlantic coast from east to west (Figure 1). Due to the proximity to the sea, average elevation is lower and slope gradient higher in the north than in the south-facing slopes (700 m and 34%, and 1300 m and 21%, respectively), with elevations ranging up to 2648 m and numerous hilltops above 2000 m. Soils are mainly calcareous in the east, while in the west some siliceous beds also appear. Forests are deciduous, dominated by European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and birch (*Betula alba*). Above 1700 m, climatic conditions prevent forest growth, and shrubs and subalpine vegetation (*Vaccinium myrtillus*, *Juniperus communis*, *Arctostaphylos uva-ursi*) dominates. As the result of a long history of human use, Cantabrian forests are largely fragmented (see Chapter II – García et al. 2005), bearing also a heavy grazing pressure by domestic as well as wild ungulates (Anduix 2001; Obeso and Bañuelos 2003).

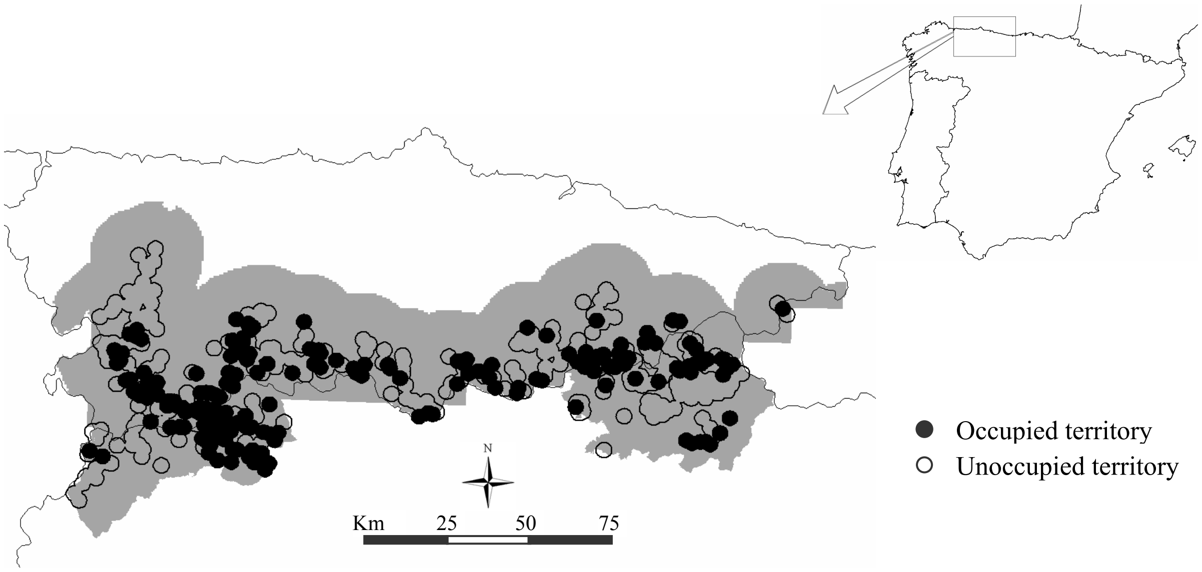


Figure 1. Study area representing potential habitat for Cantabrian Capercaillie. Occupied territories of 2Km radius are shown as filled circles, and empty circles are extinct territories. Regional limits are represented with thin black lines.

The Cantabrian Capercaillie lives at the edge of the distribution range of the species and is a relict population; the nearest ones are those in the Pyrenees, 300 kilometres away. The population was considered endangered in the "Red Data Book" in 1979 and in the "Libro Rojo de las Aves de España" (2004), going since then through a pronounced decline in number of birds and lek occupancy (Storch 2000; Obeso and Bañuelos 2003) that leaves an estimated adult population of 500 birds (Obeso and Bañuelos 2003). Because located at the edge of the species distribution, the Cantabrian subspecies shows marked habitat differences in comparison to the rest of the European Capercaillie populations and inhabits almost exclusively deciduous forest composed mainly by beech, oak and birch highly interspersed with ericaceous shrubs (Chapter II – García et al. 2005, Quevedo et al. 2006a, b).

5.2.2. Model strategy

Our working hypothesis was that the dispersal behaviour of individual birds varied in response to habitat heterogeneity. Our model therefore explicitly considered species-habitat relationships. We represented the landscape of the Cantabrian Mountains by two habitat maps describing natural habitat quality and human habitat quality (see section "*The habitat model*" and Chapter IV), which we supposed to influence mortality and dispersal movement.

The structural uncertainty related with the behavioural rules of capercaillie dispersal was relatively high. To nevertheless advance in our understanding of capercaillie dispersal of the Cantabrian population we hypothesized four simple and biologically plausible individual-based dispersal models. We used inverse pattern-oriented modelling, based on the data on the observed long-term population trends and theoretical expectations on "optimal" dispersal models, to evaluate the ability of the four models to reproduce the patterns of the observed data and our expectations. Failure of a dispersal model to reproduce essential aspects of the observed data was taken as evidence against the model. These patterns, described in more detail in section "*Patterns and criteria used to evaluate model performances*", emerged from the internal model performance due to the interaction among landscape structure and individual behaviour. As the observed patterns of population dynamics were the result of that interaction, our assumption was that parameter calibration could be achieved by selecting model parameterizations yielding predictions that were consistent with the population level data. We simulated each of the four models repeatedly for 625 different parameterizations, and we systematically compared model outputs to observed population pattern. Model outputs used to evaluate model performance were simulated data on mortality, habitat use, dispersal distances, and the simulated connectivity between territories.

5.2.3. Population-level data

We used data on presence-absence collected at 444 displaying areas from two consecutive spring visits to the leks performed over the whole area of study. The regional environmental agencies provided us with the location and occupancy of displaying areas. These areas correspond to traditionally known leks occupied at least until the 70's of the twentieth century. The first official survey for lek occupancy was performed in 1982 over most of the Cantabrian range, and a second one was carried out in 2000-2001. Lek occupancy was assumed when any kind of signs of presence (direct sightings, feathers, droppings, footprints) were detected. Every lek domain (displaying area and surrounding forest usually up to 1Km^2) was examined carefully to assess occupancy (details of the performance of the surveys can be provided by the regional environmental agencies – Consejería de Medio Ambiente del Principado de Asturias and Consejería de Medio Ambiente de Castilla-León).

5.2.4. The habitat model

The underlying habitat model was developed from the known location of the aforementioned 444 leks, which are distributed overall the Cantabrian Mountains. Basing on published data of average dispersal distance (Koivisto 1963; Wegge et al. 1981; Storch 1993;

Beshkarev et al. 1995; Moss et al. 2006; see Storch and Segelbacher 2000 and Sachot 2002 for a review), we chose a potential area of 12 kilometres around the historic distribution of capercaillie leks. This resulted in a study area of 8092 km^2 that comprised almost the totality of the elevation range above 650 m. The units for our analysis were raster cells derived from a grid comprising the whole Cantabrian range. The grain of the model was 0.25 Km2 (i.e., square cells of 500 x 500 meters) in order to capture landscape information in a scale finer than the birds' home range, which varies from 0.5 to 12 km^2 (Storch 1995).

We categorized landscape variables into natural and human variables. Under the assumption that variables related with food availability determine reproduction, while human related variables are the main causes of mortality, independent models were constructed for reproduction (natural quality) and mortality (human quality). Proportion of forest was the most important factor in the natural model, following by proportion of tall shrubs and forest fragmentation in a radius of 2 Km. In the mortality model, number of villages in an area of 1.5 Km around the cell was the most relevant variable.

Habitat models consisted in multiple logistic regressions, a form of Generalized Linear Model with a binomial error distribution and a logit link function. Logistic function informs on the probability of occupancy of habitat units, which is assumed as their habitat quality. Therefore, these models can be graphically represented as habitat quality maps. Best models were selected using Akaike Information Criterion for simplicity and parsimony (Akaike 1973; Burnham and Anderson 1998). For model development, we used half of available data, keeping the rest for model validation. The resulting best models describing the natural and human habitat quality indexes Q_N and Q_H, respectively, are shown in figure 3 of Chapter IV (see Chapter IV for further information).

5.2.5. Dispersal model

Capercaillie reproduction is based on displaying at leks. Males are site tenacious displaying on the same lek every spring, while females can visit several leks within their home range before copulating. In our model, the spatial social structure is based on the distribution of individuals in territories, which were defined, according to reported home range size (Storch 1995), as the circular neighbourhood area of 2 Km radius surrounding a given lek. Individual habitat selection takes place on the natural habitat quality map, dispersal behaviour being affected only by the natural habitat quality index Q_N. On the other hand, dispersal mortality is determined by both natural and human indexes Q_N and Q_H (Figure 2).

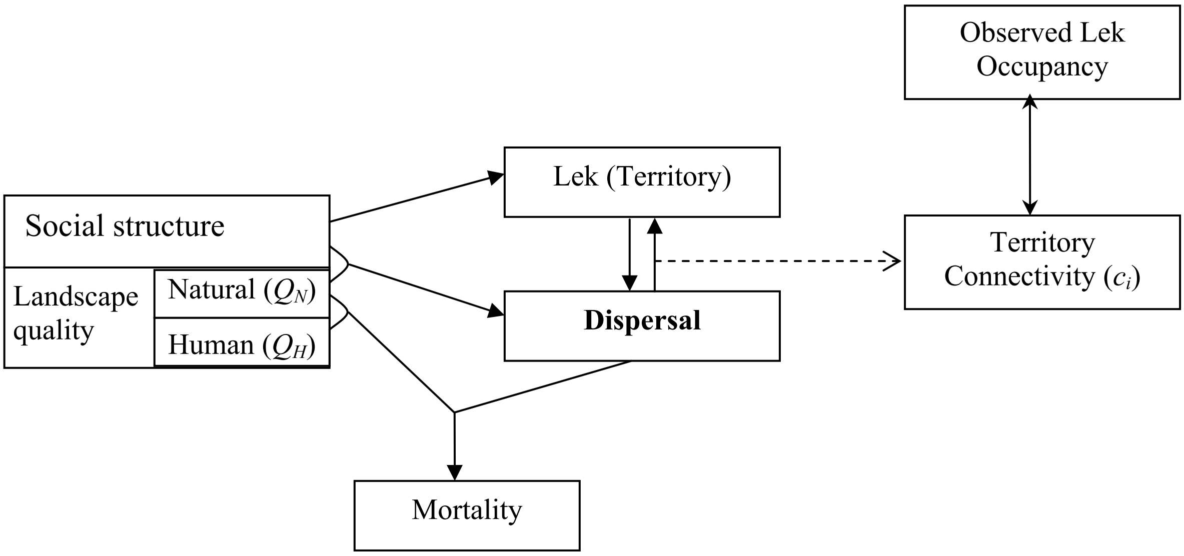


Figure2. Scheme of model processes and relations. Individual behaviour during dispersal between territories is influenced by the social structure and the landscape quality, which also determines mortality. Connectivity of territories is the main model output; a given parameterization is considered plausible when the obtained connectivity pattern is consistent with the observed pattern of lek occupancy.

Steps moved per day. —After independence at the end of summer, young birds disperse in autumn from their natal area until they reach a territory (Moss 1985; Moss et al. 2006). For simulating dispersal movement from an individual perspective, we divided the dispersal season into a fixed maximum number of days (*MaxDays*). Every day each bird performed a certain number of steps that was determined stochastically, separately for each dispersing bird, from a Poisson probability function:

$$P(N) = \frac{e^{-\lambda} \cdot \lambda^{N}}{N!}$$

being N the number of cells for that day, and λ the mean value of the Poisson distribution. According to the little available data on dispersal distance, which approximately averages 1 and 5 Km for males and females, respectively (see Storch and Segelbacher 2000 for a review), we previously tested different parameters for males (λ_m) and females (λ_f) and selected those that best fitted the desired dispersal distance. The selected mean values for the number of daily dispersal steps were $\lambda_{\mathrm{m}}=1$ for males and $\lambda_{\mathrm{f}}=3$ for females, which resulted in simulated mean dispersal distances of approximately 1 and 4 Km, respectively.

Wandering behaviour. — Results reported from some studies with radio-marked dispersers and empirical observations of very diverse species describes the behaviour of subadults that often wander prolonged periods over large areas of suitable habitat before they settle (e.g., radio-marked Spotted Owl in Forsman et al. 1984; empirical observation of Brown Bear in Wiegand et al. 2004b). According to those observations, we introduced a parameter *Wander* in order to reproduce mentioned behaviour. At the beginning of the dispersal season, juveniles are not allowed to settle until their wandering period comprising *Wander* days is finished.

Dispersal mortality. —We assumed that birds that moved larger distances and visited areas of lower habitat quality should have a higher risk of mortality (Hannon & Martin 2006). In our model, survival of dispersing birds was stochastically determined on a daily basis depending on the distance covered (parameter *mmov* - mortality associated with movement) and on the quality of the visited cells (parameter *mhab* – mortality associated with habitat). The daily movement mortality rate was zero for no-movement and linearly increasing with the number of daily dispersal steps, the slope if this relation being was the parameter *mmov*. The daily habitat mortality was determined in a similar way based on the habitat quality (computed as the average of the natural and human quality) of the cells visited that day. Here, the mortality rate is interpolated linearly between zero and a maximal (*mhab*), which corresponds to maximal and minimal habitat quality recorded in the entire map, respectively.

Stopping rule —Dispersal stops if juvenile birds encounter a territory or if they die. We adjusted the parameter *MaxDays* describing the length of the dispersal season in a way that almost all juveniles will complete the quest in absence of mortality. In the rare case that dispersal was not successful at the end of the dispersal season the unsuccessful disperser dies.

We tested four different types of dispersal movement:

1) Random movement

Dispersing juvenile moved randomly to one of their eight neighbouring cells or stayed at their present location, regardless of the underlying habitat quality. During one day, this random selection was repeated as many times as steps were drawn from the Poisson function.

2) Weighted random movement

As in the previous movement model, juveniles moved randomly to one of their neighbouring cells. However, in this case the probability to select a neighbouring cell was directly proportional to the natural habitat quality of that cell.

3) Threshold movement

As in the previous model, movement behaviour depends on natural habitat quality. Birds move to one of their neighbouring cells as many times as steps are drawn from the Poisson function for that day. However, in this model we distinguished between dispersal behaviour in dispersal habitat, matrix, and dispersal barriers. Dispersal habitat was defined as cells with a natural habitat quality Q_N higher than a threshold parameter *dQN*. Matrix was defined as cells with a value of natural habitat quality Q_N between *dQN* and a second threshold parameter *dSTOP*. Cells with a value of Q_N lower than *dSTOP* are considered as dispersal barriers that cannot be selected.

If a dispersing juvenile was located in a cell of dispersal habitat, it moved randomly to one of the nine neighbouring cells, regardless on its type (this movement is a type of "fine search" within spatially aggregated good habitats) However, if the bird has moved to a matrix cell, a relatively directional movement is assumed until the bird re-enters dispersal habitat (this rule reflects a behaviour attempting to leave poor and dangerous habitat as quick as possible). If the movement outside dispersal habitat leads to a barrier, refection occurs and the bird turns back.

To model this behaviour, space around a cell was divided into eight possible directions, corresponding to the movements to the eight neighbouring cells. Following the hands of a clock, direction values vary from 1 if the bird moves to northeast to 8 if it moves to north. Then, when a bird abandons dispersal habitat to matrix with a given direction, it selects randomly among the previous direction plus or minus one for all movements inside matrix yielding a directed movement. Finally, reflection when the bird moves to a barrier is done by adding four (i.e., the direction corresponding to turning back) to the previous direction.

4) Straight movement

This type of movement is qualitatively different from the first three dispersal movement models. Here the bird did not move in small steps cell by cell, but the entire daily distance was moved at once in a straight line. The cells surrounding the bird up to the maximal distance defined by the Poisson function were divided into 8 sectors corresponding to the directions south, south-east, east, north-east, etc., and every day dispersers selected a random sector out of these eighth sectors. Next, the Poisson function is used to randomly determine the daily distance to be moved. Birds will move the given distance through the selected sector if there is dispersal habitat (i.e., cells with $Q_N > dQN$) available at the selected distance. If the birds cannot find dispersal habitat at the given distance, a new distance is drawn from the Poisson distribution until dispersal habitat is found in sector. In the very rare case that there is not dispersal habitat at all inside the sector selected (note that the sector area comprises almost 20 Km^2), birds are forced to turn back to the initial cell and we count for this day a default distance of 2 cells for calculation of dispersal mortality.

5.2.6. Model parameterization

Some parameters (Table 1) were determined previously to the bulk model simulations in order to simplify the model analysis. The length of the dispersal season (*MaxDays*=60 days) and the habitat quality threshold for a cell to be considered a dispersal barrier (*dSTOP*=0.03) were selected, respectively, to be large enough and small enough to maintain individual behaviour temporally and spatially unrestricted (almost all juveniles should reach a territory in absence of mortality). The mean number of female and male steps per day ($\lambda_f = 3$ and $\lambda_m = 1$), were determined so that simulated dispersal distance fitted the published data on dispersal distance (see Storch and Segelbacher 2000, and Sachot 2002 for a review of available data).

As our knowledge of individual behaviour and mortality was poor, we varied four parameters over a broad range of values. We varied maximum daily mortality rates (both movement mortality -*mmov*- and habitat mortality -*mhab*) between 0 and 0.08. That way, we considered both the extreme possibilities that mortality during dispersal was insignificant or critical (note that mortality is applied every day). The threshold of natural habitat quality dividing matrix and dispersal habitat (*dQN*) was varied between 0.20 and 0.40, so that dispersal habitat comprised also poor and suitable habitat in the extreme case of *dQN* =0.20 and mostly good habitat in the other extreme with *dQN* =0.40. For the days of wandering

(*Wander*, the period when dispersers move but do not settle), we adopted a wide range from 0 to 20 days.

Table 1. Variables and parameters of the model, and their range of variation. Five parameters have a previously fixed value. Ranges of variation for the parameters whose values vary between simulations are shown in bold.

		Symbol	Range
(A)	Variables		
	Natural habitat quality index	Q_N	0 - 1
	Human habitat quality index	Q_H	0 - 1
(B)	Spatial parameters		
	Maximum number of days for dispersal	*MaxDays*	60
	Territory-Home range radius (cells)	*R*	4
	Mean number of female dispersal steps per day	λ_f	3
	Mean number of male dispersal steps per day	λ_m	1
	Days of wandering behaviour	*Wander*	**0 - 20**
	Threshold of Q_N for dispersal habitat	d_{QN}	**0.20 - 0.40**
	Threshold of Q_N for barrier	d_{STOP}	0.03
	Daily per step movement mortality	*mmov*	**0 - 0.0057**
	Maximum daily habitat mortality	*mhab*	**0 - 0.08**

5.2.7. Bulk simulations and model output

We performed bulk simulations for 2,500 model parameterizations obtained by variation of five factors. One of these factors was the model structure itself, (i.e., one of the four dispersal movement models), and the other four factors were the dispersal parameters *mmov*, *mhab*, *dQN*, and *Wander*. For each dispersal movement model, we generated 625 model parameterisations through independent variations of the four dispersal parameters, with uniform distributions between the minimum and the maximum values adopted.

For a given model parameterization, a model simulation consisted in simulating for each territory *i* the dispersal of 1000 juvenile birds. Based on these simulations we calculated for the juveniles released in territory *i* the mean quality of the habitat used during dispersal (*MeanQuality*), the proportion of dispersers dying (*MeanMortality*), the mean dispersal distance (*MeanDistance*, Euclidean distance between natal site and new home range), and the proportion P_{ij} of disperser reaching territory *j*.

5.2.8. Patterns and criteria used to evaluate model performances

Connectivity of a given territory *i* was calculated as

$$c_i = \sum_{j \neq i} P_{ij}$$

where P_{ij} is the sum of the proportions of dispersers starting from any territory $j \neq i$ and arriving at territory *i*. Thus, smaller values of the connectivity c_i indicate that few dispersers from other territories may reach territory *i*, whereas larger values of c_i indicate that territory *i* is well connected to all other territories

Pattern 1, Overall occupancy.— Gross accordance between model predictions for territory connectivity and the population-level data was assessed by comparing the simulated connectivity for all territories with the observed occupancy pattern of the leks they contain. To this end, we assumed that a lower connectivity would imply a higher risk of lek extinction, and consequently we expect that the observed unoccupied leks should be those in territories with a lower connectivity. In order to evaluate this relation we calculated for each parameterisation an ANOVA test relating the territory connectivity c_i to observed population pattern (occupied vs. unoccupied leks).

Pattern 2, regional occupancy trends.— Pattern 1 evaluated the gross relation between occupancy and connectivity simultaneously over the entire study area. However, we suspected that the occupancy data might contain additional information on more subtle regional population trends. To be able to access this information we categorized the study area into five sub-regions, as the result of a latitudinal and longitudinal division of the Cantabrian range (Figure 1). On one hand, we treated separately north and south facing slopes. On the other hand, we divided the range from east to west into three areas that are usually considered almost unconnected. This way, we evaluated the occupancy-connectivity relation with separate ANOVA test for each sub-region, obtaining five sub-patterns (giving that the south facing slopes in the central area are completely deforested and not inhabited by capercaillie).

Pattern 3, temporal occupancy trends.— The occupancy data contained also information on the temporal population trends. To be able to access this information we classified the leks into three categories depending on the moment they went extinct (if so), based on the information from the successive surveys. We defined old-extinct leks (class1) as those already unoccupied before the 1982-census, while recent-extinct ones (class2) were those occupied in 1982 but unoccupied in the 2000-census, and currently occupied leks were defined as class3. To evaluate a model parameterization with respect to its ability to distinguish among these three classes we performed ANOVA tests comparing territory connectivity among all pairs of classes, thus obtaining 3 sub-patterns. The underlying assumption of our evaluation was that a given territory around a lek that went extinct first should have the lowest connectivity.

Patterns 4, 5, and 6, ecological plausibility of dispersal movement model.— For selecting the ecologically most plausible dispersal movement model we introduced three additional conditions based on published data on capercaillie dispersal distance (see Storch and Segelbacher 2000, and Sachot 2002 for a review) and general expectations for an evolutionary optimal dispersal. We demanded that the best dispersal movement model should, besides fulfilling previously mentioned patterns, minimize dispersal mortality (pattern 4) and maximize the average habitat quality of the cells used during dispersal (pattern 5). We also checked whether or not the predicted dispersal distances were consistent with the ranges reported from the literature (pattern 6).

Evaluation of the different dispersal movement models.— We evaluated the different dispersal movement models basing on their ability to fulfil patterns 1, 2, 3 (occupancy patterns), and by checking the three patterns 4, 5, and 6 of minimizing mortality, maximizing the habitat quality of the area moved through, and producing plausible dispersal distances.

Parameter adjustment.— To select parameterizations that produce dispersal movement in accordance with our data we tested for simultaneous fulfilment of the occupancy patterns 1, 2, and 3. The parameterizations fulfilling simultaneously patterns 1, 2, and 3 represent the remaining process and parameter uncertainty after model calibration with the occupancy data and are used for deriving model predictions. However, we cannot use patterns 4, 5 and 6 for parameter adjustment since we do not simulate the entire metapopulation dynamics but release 1000 birds to disperse from every territory.

Identifying critical areas for conservation.— We calculated for each territory the average connectivity and the standard error, based on the accepted model parameterizations. The predicted connectivity values were used to identify critical areas for conservation. To this end, we classified the territories into four classes of excellent, good, poor, and low connectivity.

Evaluating the role of landscape pattern in connectivity.— Territory connectivity may be influenced by two factors, the spatial layout of neighbouring territories and by habitat structure. To find out to which extend the landscape pattern canalizes dispersal we contrasted the predicted connectivity values (i.e., average connectivity based on the accepted model parameterizations) to the predictions of the metapopulation connectivity that assumes a random walk:

$$c_i = \sum_{j \neq i} \exp(-\alpha d_{ij})$$

where d_{ij} is the distance between leks in the centre of territories i and j, and α is a constant related to the dispersal ability of the species. If landscape structure would be unimportant for dispersal, simulated connectivity should be in good accordance with metapopulation connectivity. To find the best value of α we calculate the Spearman rank correlation between the simulated connectivity values and the metapopulation connectivity for several values of α.

5.3. RESULTS

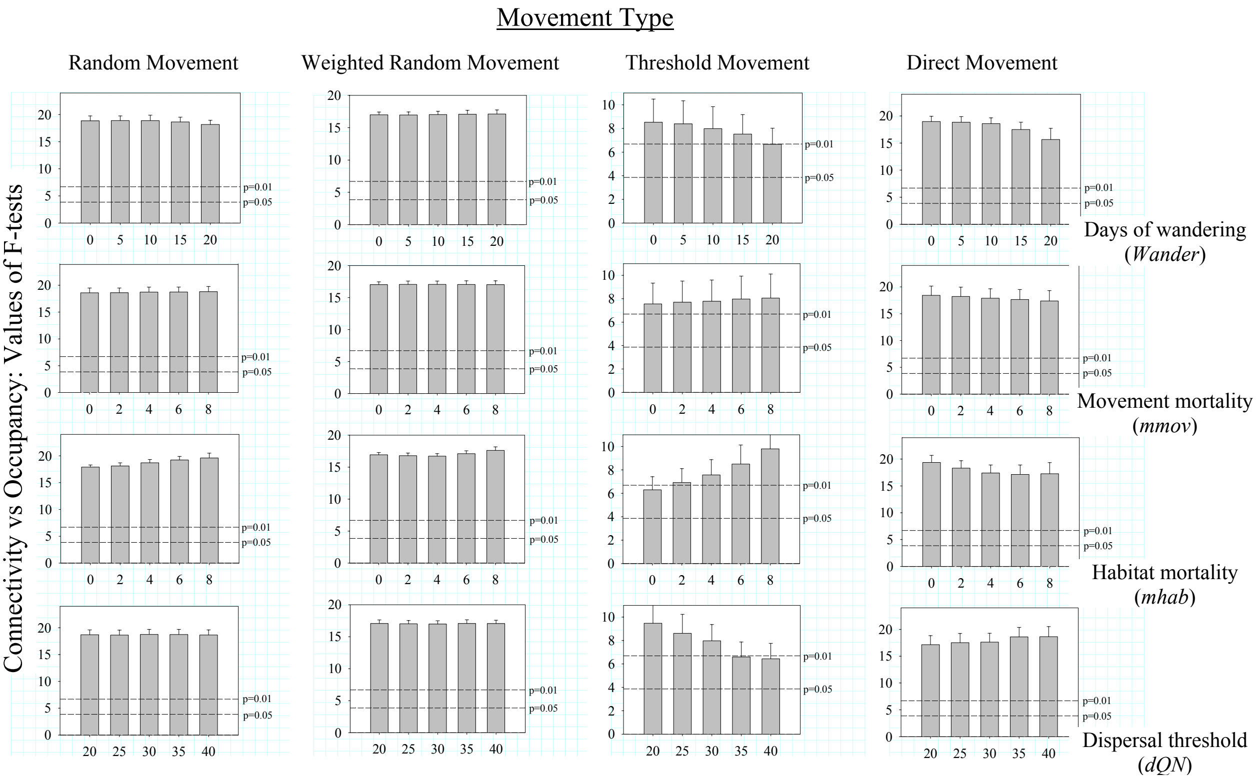
5.3.1. Selection of movement type (Structural uncertainty)

The four proposed dispersal movement models performed well in reproducing the expected gross relation between observed lek occupancy and simulated territory connectivity (pattern 1). Regardless of the type of dispersal behaviour, every model parameterization produced connectivity values which were significantly larger for territories with an occupied lek than for territories with an unoccupied one (Figure 3.A), with a statistically level of $p<0.05$. On the one hand, this result shows that the observed gross occupancy pattern alone is not able to distinguish among the four alternative dispersal movement models. On the other hand, the overall consistency and robustness of the results for the four dispersal movement models indicates that the observed occupancy pattern, and thus capercaillie population dynamics, is presumably strongly affected by a decreasing success in the dispersal processes.

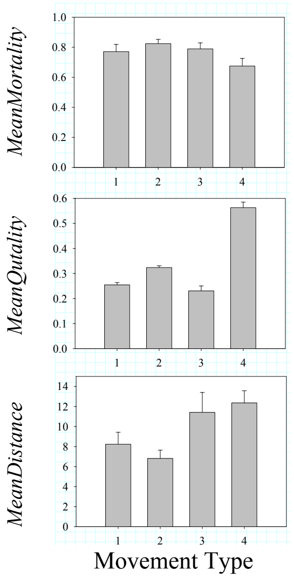
When contrasting the dispersal movement models with our additional conditions (i.e., patterns 4, 5, and 6), however, a clear ranking appeared. The best dispersal movement model in terms of ecological plausibility was the "straight movement" model. Mean mortality predicted with this model (pattern 4) was significantly lower than for the competing models (Figure 3.B), while mean quality of the habitat used during dispersal (pattern 5) was significantly higher (Figure 3.B).

The differences in predicted mortality were statistically significant among all four types. After "straight movement", the model with the lowest mortality was "random movement", followed by "threshold movement" and finally "weighted random movement". Predicted mean habitat quality showed also statistically significant differences among all types. In this case, the second best model was "weighted random movement", followed by "random movement" and finally "threshold movement".

Figure 3.A. F-Values of ANOVA tests comparing predicted connectivity of territories containing observed occupied leks versus predicted connectivity of territories with observed unoccupied leks. Each chart represents the performance of the parameter (row) and dispersal behaviour (column) in reproducing the expected positive relation between observed lek occupancy and simulated territory connectivity. Thresholds of test significance (p=0.05 and p=0.01) are shown in all charts. Regardless of the type of dispersal behaviour, every model parameterization produced connectivity values which were significantly larger for territories with occupied leks.



3.B. Comparison of mean values of model predictions among the different movement types (1: Random movement; 2: Weighted random movement, 3: Threshold movement; 4: Direct movement). Following our assumptions and expectations, the best model should minimize mortality and maximize quality of the used habitat. In that sense, Direct Movement (Type 4) is the most plausible dispersal behaviour.



Predicted dispersal distance ranged from 6 to 11 Km, with “weighted random movement” and “straight movement” showing the lowest and highest dispersal distances, respectively. Though relatively high, we considered these results plausible for all dispersal movement types (Moss et al. 2006; see Storch and Segelbacher 2000, and Sachot 2002 for a review of available data on dispersal distance), taking in mind that we were not properly simulating the entire population cycle but only a single process. Therefore, this condition was not used for model selection.

5.3.2. Model adjustment (Parameter uncertainty)

Pattern 1.— To define accordance between model predictions and the observed population pattern we used the p-values of the statistical tests at which the relation between connectivity and occupancy was significant. Significance was tested for successively decreasing p-values (0.1, 0.05 and 0.01), assuming a better accordance with the observed pattern for those parameterizations that predicted a significantly higher connectivity for territories containing occupied leks at lower p-values.

As seen before, all parameterizations were in accordance with the gross presence-absence pattern (i.e., pattern 1) at a statistically level of p=0.05 for all dispersal movement types. We found that this remained true even for the lowest p-value tested (i.e., p=0.01). However, when testing for more detailed spatial and temporal patterns extracted from the occupancy data, the filter became much more restrictive.

Pattern 2.— For two of the five main zones, there was no significant relation at all (neither positive nor negative) between the simulated connectivity and the observed occupancy for any model parameterization. Interestingly, these zones were those showing a meaningful lower habitat quality in the mortality habitat model (see “*The spatial scale and the habitat model*” and Chapter IV). This suggests that in these areas occupancy may be more strongly influenced by mortality than by inter-territory connectivity. Therefore, we used only the simulated data from the three remaining zones for testing plausibility of individual model parameterizations. At the p=0.05 level, 36 model parameterizations (5.8%) of the staring movement model predicted a territory connectivity that was in accordance with the spatial pattern of lek occupancy, simultaneously in the three main areas considered. Between these three areas, the three alternative models failed always in reproducing the pattern in the main area situated northeast, fulfilling only the sub-patterns for the two main areas in the west (both north and south facing slopes).

Pattern 3.— We did not detect significant differences in connectivity values when comparing occupancy class1 (old-extinct leks) to occupancy class2 (recent-extinct) or class3 (occupied leks). This indicated that dispersal was not a key process in determining older lek extinctions (here perhaps local hunting pressure was much more important than connectivity). Consequently, we used only the differences in simulated connectivity values between territories containing recent-extinct leks and occupied ones for testing the accordance with the observed temporal pattern of lek occupancy. At the p=0.05 level, 353 model parameterizations (56%) satisfied pattern 3 that assumed a lower connectivity for territories with recently extinct leks compared with those with actually occupied leks. In this case, the three alternative models performed in very different ways. The “random movement” and “weighted random movement” models performed very well in satisfying the pattern, with 99% model parameterizations predicting a lower connectivity for territories containing recently extinct leks. On the contrary, only 13% parameterizations from the “threshold movement” model reproduced the temporal pattern of lek occupancy.

Overall, we identified 28 model parameterizations (4.5%), all of them stemming from the “straight movement” model, which reproduced at the p = 0.05 level both the temporal and the spatial patterns of lek occupancy.

5.3.3. Impact of parameters on model predictions

We performed multiple linear regressions relating the four parameters as independent variables to the model predictions as dependent variables (Table 2). This is not a true sensitivity analysis because we only used the restricted set of parameterizations that were in accordance with the population-level data. However, we investigate how the uncertainty in our model predictions, remaining after model calibration, was influenced by the different parameters. This analysis provides us evidence on the priority of data to be acquired for reducing uncertainty and improving model plausibility. We also performed principal component analysis to test for multicollinearity between dependent variables, which did not occur.

The parameter with a stronger impact on model predictions was *mhab*, which informs on the maximum per day mortality due to the habitat quality of the cells the bird uses each day. The impact of this parameter on predicted mortality was stronger than that of *mmov*, which informs on the maximum per day mortality due to the distance covered each day. Mean dispersal distance was impacted mainly by *mhab, mmov* and *Wander* (days at the beginning of dispersal period when birds move but cannot settle), while the biggest impact on mean habitat quality came from *dQN*, parameter defining threshold of suitable habitat.

Table 2. Obtained mean value of predictions (model outputs) based on the 28 model parameterizations whose obtained pattern of territory connectivity was in accordance with observed lek occupancy at all steps. The table also shows the relative weights of parameters in predictions based on multiple linear regressions relating the four parameters as independent variables to the model predictions as dependent variables.

			Impact of Parameters			
Predictions	Units	Mean±SD	*Wander*	*mmov*	*mhab*	d_{QN}
MeanMortality	Rate	0.72±0.01	11.8	32.7	42.6	-4.6
MeanQuality	Rate	0.57±0.02	2.1	12.6	19.7	306.9
MeanDistance	Km	10.78±0.39	40.6	-49.3	-49.5	22.0

5.3.4. Identifying critical areas for conservation

We calculated the mean territory connectivity values and the standard error that resulted from the 28 accepted parameterizations. Connectivity for territories varied between 0.016 and 0.62, and the standard error, averaging 0.06, was surprisingly small (Figure 4). Only for smaller connectivity values (< 0.2), it exceeded sometimes values of 0.1. This is an important result, which showed that the predictions for the 28 accepted parameterizations were consistent and that the population level data were indeed able to prevent error propagation.

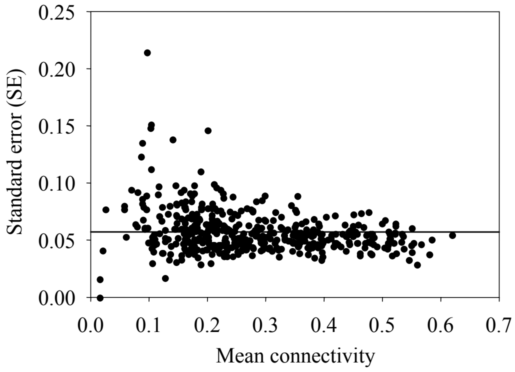


Figure 4. Mean connectivity, calculated from the 28 accepted parameterizations, and the corresponding standard error (=SD/mean) for all 444 territories.

Next, we divided the territories into four connectivity classes comprising excellent, good, poor, and low connectivity (Figure 5). We found very clear spatial patterning of the four classes. As expected, territories with poor and low connectivity were located at the periphery of the distribution or in between the eastern and western sub-population. Territories with excellent connectivity formed basically six clusters, four of them located in the western sub-population and two in the eastern sub-population. This result is in good accordance with that obtained from our previously developed bi-dimensional habitat model (Chapter IV), which showed very similar areas as source habitat and appointed to them as the main subject of conservation efforts and effective protection.

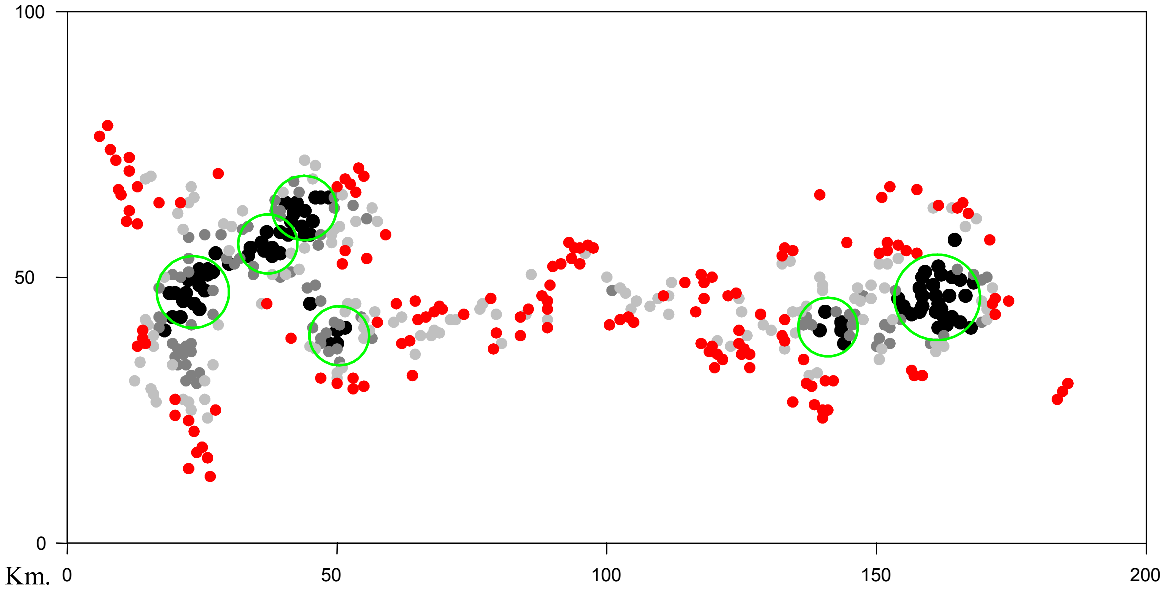


Figure 5. Map showing the mean connectivity of capercaillie territories that resulted from the 28 accepted parameterizations. Black circles: connectivity > 0.4, dark grey: connectivity >0.3, light grey: connectivity > 0.2, and red circles: connectivity < 0.2. The green circles indicate areas of potentially high connectivity values characterized by clusters of highly connected territories.

5.3.5. Evaluating the role of landscape pattern in connectivity

We compared the mean connectivity predicted by our model to theoretical connectivity predicted by the metapopulation connectivity, which assumes basically diffusion movement and no habitat structure. Correlation analysis showed that the best accordance resulted for parameter $\alpha = 0.11$ of the metapopulation connectivity (Figure 6A). At inter-territory distances $d_{ij} > 25$ cells the term $\exp(-\alpha d_{ij}) < 0.1$, thus notable contributions to connectivity stem only from leks nearer than 12.5 km. Though information is very scarce on juvenile dispersal distances (Storch 2000), our result is in good accordance with the few available data reported in the literature, with averages ranging between 2.7 Km in Sweden (Wegge et al. 1981) and 12.8 Km in Finland (Koivisto 1963), or median values of 11 Km in Scotland (Moss et al. 2006). However, the maximum was quite flat only with values $\alpha < 0.03$ showing substantially lower correlations. Comparison of simulated connectivity and metapopulation connectivity with $\alpha = 0.11$ showed that there are substantial variation in simulated connectivity for the same values of metapopulation connectivity (e.g., the grey box around a value of 12 in Figure 6B). Thus, although territory connectivity showed a clear signal of distance dependence as depicted by the metapopulation connectivity, there were substantial individual variations caused by the interaction of local habitat structure and dispersal behaviour.

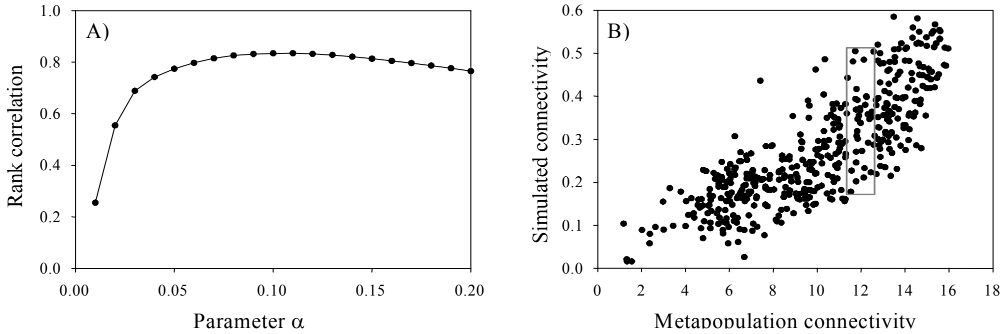


Figure 6.A) Rank correlation between mean connectivity values that resulted from the 28 accepted parameterizations and the metapopulation connectivity $c_i = \sum_{j \neq i} \exp(-\alpha d_{ij})$ for different parameters α. The d_{ij} is the distance between focal territories i and j, measured in units of 500m among their centres.

6.B) Relation between simulated connectivity and metapopulation connectivity for $\alpha = 0.11$, the value with the highest correlation. At distance $d > 25$ the term $\exp(-\alpha d_{ij}) < 0.1$, thus notable contributions to connectivity stem only from territories nearer than 12.5 km. The grey box illustrates how individual behaviour causes substantial variation in simulated connectivity for a given value of metapopulation connectivity.

5.4. DISCUSSION

5.4.1. Metapopulation status

One important conclusion of our work is that dispersal is playing a key role in the current dynamic of the Cantabrian metapopulation. Our results suggest that the observed lek extinction pattern, with a decrease in lek occupancy down to 42.6% over the last 30 years (Obeso and Bañuelos 2003), can be explained largely by the spatial structure of territories' effective isolation. We estimated effective isolation by simulating the probability of dispersing birds of settling in a given territory (where the same number of birds dispersed from every territory).

Dispersal is key factor in recent population dynamics.— We tested a wide range of plausible dispersal movement behaviour, including a random walk, directed random walk, habitat based random walk, and straight movement and found for all dispersal movement behaviours and parameterizations consistently that connectivity values were significantly larger in currently occupied territories than in non occupied ones. The underlying assumption was that local lek extinctions would take place preferably in territories with a higher effective isolation. This robust result indicates that dispersal success is a key factor in determining the dynamics and trends of the endangered Cantabrian metapopulation.

Metapopulation decline and extinction debt.— Recent theoretical metapopulation studies suggest that metapopulations may show considerable time-lags in response to landscape changes (Nagelkerke et al. 2002; Ovaskainen and Hanski 2002), especially if the landscape after the change is close to the extinction threshold. This could be the case of the Cantabrian Capercaillie. After a long-lasting and regular hunting pressure on displaying males, only in the last two or three decades the metapopulation was perceived as endangered and hunting became illegal in the 70s. However, bird numbers and lek occupancy decreased since then in a continuous way.

We suggest that the ongoing decrease in the metapopulation size might have its roots in the habitat change and the strong human pressure before hunting became illegal. Because of a long lag in its response to these perturbations, the population numbers may have remained relatively high for some time, but eventually collapsed after the transient time passed. After the collapse, landscape fragmentation and low bird numbers may interact resulting in intensification in the population decline mediated by density dependent phenomena such as the Allee effect (Stephens and Sutherland 1999). In this situation dispersal might become the key process in the dynamic of the metapopulation, determining which territories become firstly extinct. This hypothesis is supported by our finding that the observed population level pattern of lek occupancy was significantly related to the (dispersal-estimated) connectivity of their territories. Additional evidence comes from our analysis of the observed time pattern of extinction, which suggested that the importance of dispersal on population persistence has increased only recently. We found no differences in connectivity between territories containing leks classified into class1 (old-extinction) and the rest classes (recent-extinction and occupied leks), showing that dispersal success was not related with local extinctions until the last decades. However, under the more recent low bird numbers, dispersal success became a limiting factor and more isolated territories showed a higher probability of extinction. Indeed, we found that class2-leks (recent-extinction) are in territories that showed significantly lower connectivity values than those containing class3-leks (occupied leks).

Source-sink dynamics.— The absence of a relationship between simulated connectivity and observed occupancy within two of the five main zones could be explained with the information provided by the underlying habitat model. These zones showed a very low habitat quality in the mortality habitat model. In accordance with our bi-dimensional habitat model, they were classified as attractive sinks, which are defined as areas of high natural habitat quality but low survival habitat quality (Delibes et al. 2001). In our model, attractive sinks are perceived by the birds as areas of good habitat because they settle in areas of high natural resources, but they perform actually like sinks because of a non-perceived high human-induced mortality, leading into maladaptive habitat selection. Therefore, in these areas occupancy may be strongly influenced by mortality itself rather than by dispersal success. In summary, local extinctions in these areas may not depend primarily on inter-territory connectivity but on source-sink dynamics.

5.4.2. Parameters, Predictions, and Dispersal movement

It is important to note that our model does not simulate the dynamic of the entire population, but only the dispersal process. Instead of simulating the complete annual cycle, each model simulation consisted in forcing a thousand birds to disperse successively from each territory. According to that, model predictions such as mean quality of used habitat, mean mortality and mean dispersal distance were not used for model adjustment, as they cannot be considered as actual population features that a valid model parameterization should fulfil. However, they provided additional arguments for selecting the most plausible model structure.

Selection of ecologically plausible dispersal movement model.— Even if the parameters of the different dispersal movement model were largely unknown, we could safely demand that the ecologically most plausible dispersal model should robustly minimize mortality during dispersal over a wide range of parameters. Hence, we compared model predictions among the different behaviours, treating movement type as a four-levels parameter that resulted in different rates of mortality (Figure 3.B). We found that the "straight movement" model showed the lowest dispersal mortality. The behaviour in this model was characterized by a one-day move in a straight line between separated areas of relatively good natural quality. Although one might argue that this behaviour should be universal for birds, this assumption is not trivial in the case of Capercaillie, which is a very big and heavy species whose behaviour is in many respects more similar to mammals than to other bird species. Indeed, capercaillie “lives” on the ground. Additional evidence came from the result that this dispersal movement behaviour also produced consistently the highest habitat quality at the movement track.

However, the strongest evidence for selection of the “straight movement” dispersal model behaviour stemmed from the comparison of the detailed temporal and spatial lek occupancy data with simulated connectivity. None of the other three alternative models was able to reproduce all patterns simultaneously as occurred for 5% of the parameterizations of the “straight movement” model. A closer look at the patterns where the other three models dropped out showed that they were not able to reproduce regional occupancy trends (pattern 2). Those three models fulfilled at most only two of the five sub-patterns tested. The only two regions where they reproduced the expected pattern were those in the west range (both in the north and south slopes), which correspond to the best-conserved areas.

Besides, the “random movement” and “weighted random movement” models showed an undesired behaviour. Both models, but specially the “weighted random movement” model, showed a very weak relation, if any, between parameterizations and pattern fulfilling, reproducing or not all the sub-patterns regardless of the values of the parameters.

Our analyses voted consistently for the “straight movement” dispersal model. This evidence will allow us to include it in subsequent analysis into the complete spatially explicit population model for simulation the entire capercaillie population dynamics. Since our analyses did not allow us to determine a single optimal model parameterization, we need to run the population model with all 28 parameterizations, which represent the remaining uncertainty after model selection and parameterization.

5.4.3. Gains of inverse pattern-oriented modelling

Our study population, the Cantabrian Capercaillie, is a typical case for an endangered species where the knowledge about key processes and parameters of population dynamics are scarce but the immediate risk of extinction high. In such situation we cannot wait until detailed field studies may eventually allow us to determine the unknown population dynamics' parameters and processes precisely enough before investigating key factors responsible for the population decline (Wiegand et al. 2003). Inverse pattern-oriented modelling offers a feasible way to nevertheless access valuable information hidden in observed population patterns on the individual dispersal movement behaviour and allowed us to substantially advance our understanding of the factors driving the population decline. A string argument in favour of our approach is the low variation in the predicted territory connectivity values among the accepted model parameterizations. In contrast, model predictions showed a standard error one order of magnitude larger when all tested parameterizations were analyzed (averaging 0.4). This demonstrates that the population level data indeed contained strong information that was able to constrain the model predictions to a viable level.

Compared with our understanding previously to our modelling exercise we gained substantial understanding. First, we were able to distinguish clearly among different candidate models of dispersal movement. Second, we found robust evidence that the dispersal process was a key process in the recent population decline. This was not clear a priory, for example, a decline in local habitat quality might also produce the observed population decline. Indeed, for two of the five sub-regions studied we found no relationship between lek occupancy and territory connectivity. A detailed habitat model indicated that these areas were attractive sinks having high, non-perceived, human-caused mortality that probably dominated over connectivity. This result again provided a piece of the puzzle completing our understanding of the demographic conditions of the Cantabrian Capercaillie.

An important ingredient of our approach was extraction of several patterns from our population level data, i.e., the occupancy pattern at different sub-regions (pattern 2) or the temporal patterns of occupancy (pattern 3). It was relatively simple to reproduce one feature of a system, e.g., the overall gross occupancy pattern (pattern 1); however, we showed that the more detailed information provided by the patterns 2 and 3 constrained the valid parameterizations considerably. As outlined by Wiegand et al. (2003), a critical assessment of the ‘‘quality’’ of the patterns, i.e., the magnitude of error connected with data collection, is required when formulating the criteria for pattern fulfilment. If the pattern has larger associated errors the criterion needs to be conservatively wide to not be affected by the errors, but may nevertheless serve for excluding extremely improbable model behaviour. Indeed, several of such weak patterns taken together may be very effective (e.g., Wiegand et al. 2004a). Clearly, taking a purported pattern with possible observer bias and misinformed interpretation too seriously (i.e., using too restricted criteria for their fulfilment) may bias the model results. However, when adequate criteria for deciding when the simulated patterns matches the observed one are selected the indirect and simultaneous model selection and parameter adjustment prevents error propagation, as may happen in conventional models based on point-estimates of parameter values. The degree to which the initial uncertainty is reduced depends on the amount of information that is carried by the observed patterns, and on how well the model describes the most important processes and the major constraints that generate the observed patterns (Wiegand et al. 2003).

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CAPÍTULO 6. A spatially-explicit and individual-based population model for Cantabrian Capercaillie

Un modelo de población espacialmente explícito basado en el individuo para el urogallo cantábrico

6.1. INTRODUCTION

The capercaillie (*Tetrao urogallus*) is the greatest forest bird of the Palearctic, with a widespread distribution ranging from eastern Siberia to south-western Europe. It is the largest species among the family of grouses, and it is considered an umbrella species and indicator of undamaged ecosystems (Boag and Rolstad 1991; Suter et al. 2002; Pakkala et al. 2003). Though occupying much of its historical distribution range in Europe, most of capercaillie populations are declining since the last decades, with a decrease of both area of distribution and number of birds (Storch 2000). This decline is especially severe in Central and South-western Europe, where populations are small and highly fragmented mostly because of the patched distribution of the forests and the habitat loss (Rolstad and Wegge 1987, 1989; Rolstad 1991; Klaus 1991, 1994; Klaus and Bergman 1994; Storch 1997).

The Cantabrian Capercaillie (*T. urogallus cantabricus*), one of the 12 capercaillie subspecies (Potapov and Flint 1989; del Hoyo et al. 1994), lives at the south-western edge of the distribution of the species, occupying an area of approximately 2000 square kilometres in the Cantabrian Mountains, northwest Spain (Quevedo et al. 2006a, b; Storch et al. 2006). It constitutes a relict population and, as the result of a long-lasting reproductive isolation, presents a high genetic differentiation compared to the rest of capercaillie populations elsewhere, hence qualifying as an Evolutionarily Significant Unit (Rodríguez-Muñoz et al. 2006; Storch et al. 2006). After a high and long-lasting hunting pressure on displaying males, about three decades ago the metapopulation began to be perceived as declining, and finally hunting became illegal in the late 70’s. Cantabrian Capercaillie was firstly considered as endangered in the IUCN “Red Data Book” in 1979, going since then through a pronounced decline estimated in more than 50% of the birds and 42% of lek occupancy (Storch 2000). The subspecies actually adapts to the "threatened" category according to the IUCN criteria (Storch et al. 2006), mainly because of the severe fragmentation of the forests and the high direct and indirect human pressure. As the result of those factors and the steep orography, the population is spatially structured, with local populations interspersed among large gaps of poor habitat. The metapopulation, from a landscape perspective, has been constrained from the east and west extremes towards the central parts. Occupying in the mid-twenty century the whole Cantabrian range, all remaining occupied territories belong to the provinces of Asturias and Leon, corresponding to the northern and southern slopes, respectively. With a population size estimated in 500 adults in year 2000 (Obeso & Bañuelos 2003), it is the world most endangered capercaillie population (Storch 2000).

However, little is known about the population dynamics of *T. urogallus cantabricus* (but see Castroviejo 1975, Martinez 1993, and Quevedo et al. 2006b). By contrast to the rest of capercaillie populations that occur in coniferous forests, Cantabrian Capercaillie inhabits pure deciduous forests, and this singularity affects basic ecological adaptations (Rodríguez and Obeso 2000), also advising against the extrapolation of the ecological studies from other areas. Hence, conservation of Cantabrian Capercaillie manifests itself as a complex mission that demands us to urgently find a response to some basic questions, like habitat requirements at different scales, and demographic features and processes playing a key role in the dynamics of the population.

Spatially explicit population models (SEPMs) constitute a useful approach that can overcome to a large extent the lack of ecological information about the spatial and temporal dynamics of the populations. This approach considers the species-habitat relationships explicitly, providing a powerful tool to test the effect of demographic features and landscape spatial structure on population dynamics (Pulliam et al. 1992; Dunning et al. 1995; Wiegand et al. 1999, 2004). It usually consists in the application of a population model, which simulates demographic features of the species, on an underlying GIS-derived landscape map usually representing habitat quality. Additionally, individual-based SEPMs provides the link between individual and population scales, connecting individual habitat selection to population dynamics in an explicit way (Pulliam and Dunning 1995; Wiegand et al. 1999).

In this chapter, we develop an individual-based spatially explicit model that reproduces the behaviour of the whole metapopulation by simulating, during successive annual cycles, the behaviour of the individuals in relation to the rest of individuals and their habitat. Basing on observed data from long-term population trends and following the approach of indirect pattern-oriented modelling, the model recreates the decline of the population in the last decades and discriminates between plausible and implausible model parameterizations. Taking into account that no information on this matter is available for Cantabrian Capercaillie, our aim is to identify the key demographic features and processes driving the recent decline of the population.

6.2. METHODS

6.2.1. Study area and capercaillie data

The Cantabrian Mountains represent the south-western boundary of the Atlantic biogeographical region (Polunin and Walters 1985; Chapter II - García et al. 2005). These mountains run parallel to the north Atlantic coast of Spain (Figure 1), with elevations ranging up to 2648 m and numerous hilltops above 2000 m. Due to their complex geological history and the proximity to the sea, slope gradient is high (34% in the north and 21% in the south-facing slopes), and the main east-west axis is crisscrossed by many gorges and cliffs. The climate in the range is humid and temperate, influenced by the ocean. However, geographic orientation causes differences between northern and southern slopes, with a high rainfall on the north-facing slopes and a rain shadow on the southern slopes (annual rainfall averages 900–1,900 mm and 400–700 mm, respectively). Soils are mainly calcareous in the east and central parts, while in the west siliceous beds dominate. Forests are deciduous, dominated by European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and birch (*Betula alba*); beech clearly monopolizes over the rest of tree species in the east and central part of the range, while in the west, coinciding with the domain of siliceous soils, sessile oak dominates and birch presence is higher. Above 1700 m, climatic conditions prevent forest growth, and shrubs and subalpine vegetation (*Vaccinium myrtillus*, *Juniperus communis*, *Arctostaphylos uva-ursi*) dominates. The present picture of the Cantabrian Mountains consists in a largely fragmented landscape (see Chapter II – García et al. 2005), with forest fragments surrounded by a non-forest matrix of pastures, heath lands and small villages.

Our capercaillie data consisted in information about presence-absence of the species at 444 leks distributed over most of the Cantabrian range. These population-level data came from two temporally separated surveys of the displaying areas, performed by the regional environmental agencies. They provided us with the location and occupancy of those areas, which correspond to historically known leks occupied at least until the early 70's. The first official survey for lek occupancy was performed in 1982, and the second one was carried out in 2000-2001. Every displaying site and surrounding forest up to 1Km^2 was examined carefully to assess occupancy (details of the performance of the surveys can be provided by the regional environmental agencies – Consejería de Medio Ambiente del Principado de Asturias and Consejería de Medio Ambiente de Castilla-León), which was assumed when any kind of signs of capercaillie presence (direct sightings, feathers, droppings, footprints) were detected. In order to encompass the potential distribution area of capercaillie in the Cantabrian Mountains, the study area was established as the montane range above an altitude of 650 m that was within a distance of 12 Km from the centre of any known capercaillie lek (i.e., the study area of the underlying GIS-derived landscape map – see section "*Habitat model and spatial scale*" and Chapter IV). These conditions were based on the altitudinal distribution of Cantabrian forests (see Chapter II – García et al. 2005) and the average dispersal distances of capercaillie (Wegge et al. 1981; Storch and Segelbacher 2000; Sachot 2002; Moss et al. 2006), respectively.

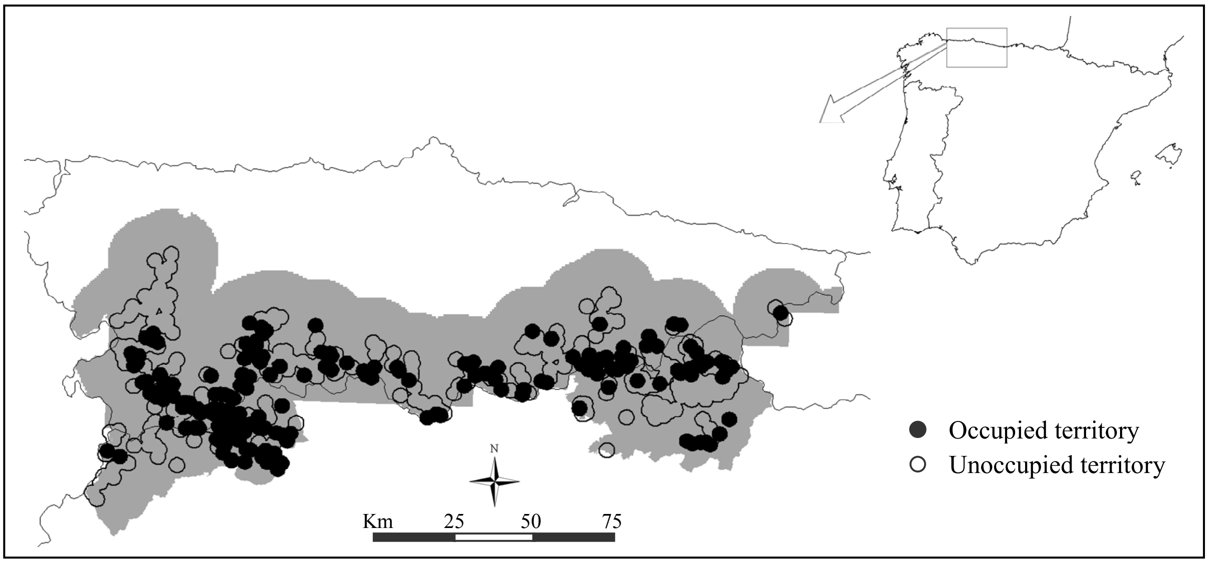

Figure 1. Study area representing potential habitat for Cantabrian Capercaillie. Occupied territories of 2Km radius are shown as filled circles, and empty circles are extinct territories. Regional limits are represented with thin black lines.

6.2.2. Model strategy

Our model explicitly considered species-habitat relationships, as our working hypothesis was that habitat heterogeneity affected the behaviour of individuals. We represented the landscape of the Cantabrian Mountains by two habitat maps describing natural habitat quality and human habitat quality (see section "*Habitat model and spatial scale*" and Chapter IV), which we supposed to influence mortality and behaviour during the successive phases of the annual cycle.

To deal with parameter and structural uncertainty we used inverse pattern-oriented modelling, based on the data on the observed long-term population trends. These observed patterns, described in more detail in section "*Population patterns and Model adjustment*", emerged from the internal model performance due to the interaction among landscape structure and individual behaviour. As the observed patterns of population dynamics were the result of that interaction, our assumption was that parameter calibration could be achieved by selecting model parameterizations (i.e. sets of model parameters) yielding predictions that were consistent with the population level data.

Though beginning in 1957, the model tried to reproduce the population tendency between 1982 and 2000, for which we have spatially detailed information about lek occupancy in those years. Through independent variations of the 17 model parameters we obtained 10,000 different parameterizations, whose outputs were systematically compared to observed population pattern. Failure of a parameterization to reproduce essential aspects of the observed data and our expectations was taken as evidence against that parameterization. The obtained parameterizations served us to assess the extinction risk of the population.

6.2.3. Habitat model and spatial scale

The underlying habitat model was developed from the known location of 444 leks distributed over almost the whole Cantabrian Mountains (exception made of the areas located at both extremes of the east-west axis of the distribution range, which could not be included due to the absence of geographical data). The resolution of the model was 0.25 Km2, selected to be finer than the smallest home range reported for capercaillie, which varies from 0.5 to 10 Km^2 (Storch 1995a). The landscape of study resulted in an area of 8,092 Km^2, encompassing approximately the montane range over 650 m.a.s.l.

Under the assumption that human related variables, in terms of access to birds, are the main causes of mortality, while on the other hand variables related with habitat availability determine reproduction, two independent models were constructed, by relating each explanatory variable to one of the key demographic features survival and reproduction. In the natural (reproduction) model, proportion of forest (positive effect) was the most important factor, following by proportion of tall shrub species (positive), forest fragmentation in a radius of 2 Km (negative effect) and the length of ecotones between forest and shrubs (positive). In the human (survival) model, number of villages in an area of 1.5 Km around the cell was the most relevant variable (negative effect), together with elevation and slope (positive effect) which are indicators of human accessibility. The resulting best models describing the natural and human habitat quality indexes Q_N and Q_H, respectively, are shown in figure 3 of Chapter IV (with further information).

6.2.4. The Population model

The life-history of individuals is simulated as a succession of stochastically determined demographic processes (Figure 2 and Table 1). The succession of events takes place every year, which constitutes the time-step of the model. The model categorizes individuals into different sex and age classes, each being affected by some distinctive demographic processes. Those processes are, in this order: hunting for adult males (until the late 70's); reproduction, egg-laying and nest-incubation for reproductive (adult or subadult - one year old) females; hatching, feeding of chicks and dispersal for young birds (less than one year old); and annual survival for all classes. To describe the occurrence of demographic processes, we defined 17 model parameters, which are interpreted as probabilities for each bird individually.

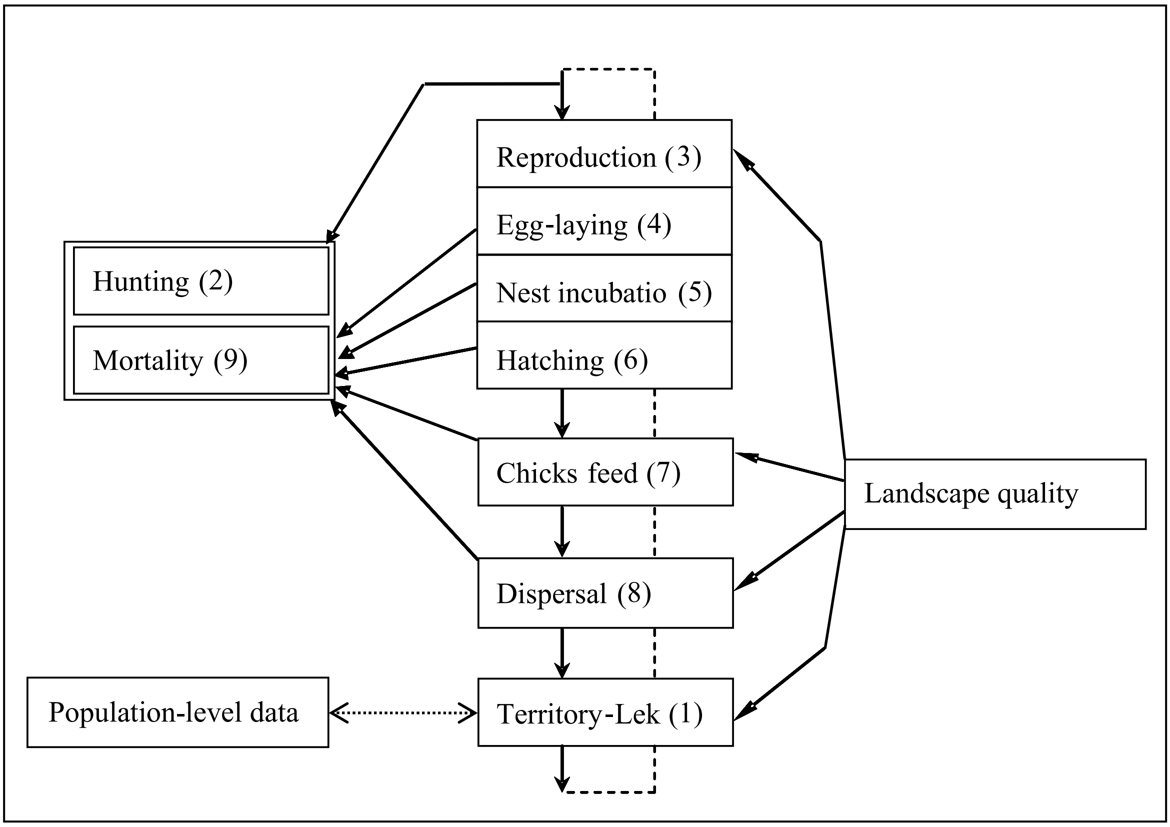

Figure 2. Succession of demographic processes during each annual cycle. The numbers in parentheses refer to the number of the model rules explained in the text.

Landscape quality

In our spatially explicit model, human and natural habitat quality affects several demographic processes. Individual habitat selection takes place on the natural habitat quality map, individual behaviour being affected only by the attractiveness of the habitat. Habitat selection during early chicks' period depends on a single variable from the natural map, the length of forest/scrubland ecotones ($Q_{ECOTONE}$). Natural habitat quality (i.e. the natural index Q_N) determines the capacity of territories (i.e. the maximal number of males and females that may reproduce at a given lek - see below) and dispersal movement. On the other hand, survival during each demographic process is determined by the total habitat quality (i.e. the average of natural and human indexes Q_N and Q_H).

Territory - Lek (1)

Capercaillie reproduction is based on displaying at leks. Males are site tenacious displaying on the same lek every spring, while females can visit several leks within their home range before copulating. In order to simplify our model, individuals are not provided with a home range, but they are included in a territory. Territories were defined, according to reported home range size (Storch 1995a), as the circular neighbourhood area of 2 Km radius surrounding a given lek. That way, the individuals reproducing at a given lek are those inhabiting the surrounding territory. Each territory possesses a capacity less or equal to a maximum capacity (*Capacity*) previously fixed. To define the capacity of a given territory, we look at the natural (Q_N) habitat quality of that territory and compare it with the quality of the best territory in order to proportionally assign a capacity. Each male will display at the lek in the centre of the territory where it inhabits. In the case of females, all the leks (up to three) inside the inhabited territory can be used during reproduction.

Maximum age in the model is 10 years. At the end of each annual cycle, annual survival of every bird is determined stochastically with a death probability that depends on the age class and the territory. Basic death probabilities are *mRate* for adults and *mRate*+*mRInc* for sub-adults (less than two years old). These values represent the death rate of the territory with the highest total (average of Q_H and Q_N) habitat quality, while for the others that value is increased proportionally to their relative habitat quality decrease, up to (*mRate*+)*mTerrit* for the territory with the lowest quality. This “annual survival” encompasses all the sources of mortality not considered by the rest of demographic rules.

Hunting (2)

Though capercaillie was not officially considered a game bird before the mid-twentieth century, its shooting had been practised from long before. Males used to be shot during the displaying period, mostly before fecundation took place (Castroviejo et al. 1974), until shooting became illegal at the late 70's. In our model, survival of adult males is assessed stochastically every year until 1977 before reproduction takes place, with a death-probability value of *mHunt*.

Reproduction (3)

Only after two years males are sexually mature and can reproduce (Cramp & Simmons 1980), the maximum number of males in each lek being determined by natural habitat quality of the surrounding territory.

Scenario a) FEMALES CAN REPRODUCE OR NOT

The probability for a female to reproduce in a given lek depends on the number of mature males that display on that lek, being higher in those leks with a bigger number of males. Females visit their correspondent leks in random order and reproduction success for a female in a lek is determined stochastically with a probability that increases linearly with the number of males present in that lek, being ensured when the number of cocks displaying reaches a threshold (*MaleThr*).

Scenario b) FEMALES ALWAYS REPRODUCE

For a female to reproduce in a given lek the only necessary condition is male presence, so females reproduce if any of their leks are occupied by mature males. When the reproduction season begins, females visit their correspondent leks randomly, and reproduction occurs when a lek with displaying males is visited. This scenario takes place when threshold *MaleThr* equals one.

Egg-laying (4)

The clutch size for a reproductive female is determined stochastically from a discrete probability distribution, ranging from 4 to 7 eggs for sub-adult hens and 5-9 eggs for completely adult hens (Lindström et al. 1997; Grimm & Storch 2000). Probability for chicks of being males or females is the same.

Nest-incubation (5)

Survival of the entire clutch for every reproductive hen is assessed in a similar way to aforementioned annual death rate of territories (1). Basic probability for an adult hen inhabiting the best territory to lose its entire clutch is *mClutch*, while this value is increased to *mClutch+mCInc* for sub-adult hens. Those values increase in *mTerrit* for the territory with the lowest quality, and proportionally to that value for the rest of the territories.

Hatching (6)

We assess survival of every egg, being *mEggs* the probability for each egg of failing to hutch.

Feeding of chicks (7)

In the first month of their life, chicks are highly dependent on *Vaccinium* and particularly on the larvae of arthropods that feed on their leaves (Storch 1993; Wegge et al. 2005). To provide the chicks with that food, hens limit the habitat used during chick-rearing period to those zones rich in *Vaccinium*, which are mainly placed in internal clearings and forest edges; we call that effective habitat the “core area”. We also hypothesize that the size of the core area could have been increased in the last decades due to heavy competition from ungulates, whose abundance has grown enormously (Pollo et al. 2003). It is known that high herbivory levels on Vaccinium cause a decrease in fruit production in the following years (Tolvanen et al. 1993), and this could have had a detrimental effect on the quality and availability of bilberry for capercaillie (Fernández-Calvo and Obeso 2004), forcing the hen to enlarge the area needed to fulfil food requirements for the chicks. Apart from that, forest edges are the place where chicks are most vulnerable to predation, as capercaillie predators are generalist species and their efficiency is increased in these ecotones. All this factors bring about the first month of chicks as the most critical period for survival (Hannon & Martin 2006) and may cause, at bigger scales, a decrease in breeding productivity in populations inhabiting highly fragmented forests with respect to populations occupying more continuous forests.

We define the "core area" where the young chicks feed as the percentage of the total territory containing the highest total length of forest/scrubland ecotones. The percentage is given by the sum of *FArea*, which is applied every year, and *UngArea*, which we applied only in the last decades to take into account the growing competition with ungulates (we suppose that the more the competitors, the larger the core area needed to fulfil the food requirements). Then, for assessing survival during early chick-rearing we first look at the percentage (*FArea+UngArea*) of territory used as core area, and determine its total habitat quality. Mortality is calculated as the sum of two factors, basal mortality *mFeed* (which is entirely applied), plus a proportion of habitat-mediated mortality *mCore* (the proportion increases linearly as the quality of the core area decreases). If *mCore* = 0 there is no impact of ecotones on chick survival.

<u>Dispersal</u> (8)

After independence at the end of summer, young birds disperse in autumn from their natal area until they settle in a territory (Moss 1985; Moss et al. 2006). Then the central lek (and those inside the territory if the bird is a female) is assigned to that bird. Here, natural habitat quality is introduced in the model as thresholds (*dQN*, *dSTOP*) to determine different types of movement behaviour. Dispersal habitat (i.e. the preferred habitat during dispersal) is defined as the cells with a natural habitat quality higher than *dQN*. Matrix is defined as the cells with a value of natural habitat quality less than *dQN* but higher than *dSTOP*, and the cells with a value lower than *dSTOP* are dispersal barriers. The value of *dSTOP* is 0.03, which was fixed in a dispersal model previously developed (see Chapter VI).

According to the results of the aforementioned dispersal model (Chapter VI), we divided the dispersal season into a fixed maximum number of dispersal events, which we called "days" (*MaxDays*). Each dispersal event birds move linearly a certain distance (i.e. a certain number of cells) determined stochastically from a sex-distinctive Poisson probability function (mean values for the number of cells moved per day were λ_m =1 for males and λ_f =3 for females). The birds move the entire daily distance at once in a straight line. The cells surrounding the bird were divided into 8 sectors corresponding to the directions south, south-east, east, north-east, etc., and every day we stochastically obtain a sector and a distance. Birds will move the given distance through the selected sector if there is dispersal habitat (Q_N > *dQN*) available at the selected distance, even when matrix occupies the intermediate habitat. If there is not dispersal habitat at the given distance, a new distance is drawn from the Poisson distribution. In the very rare case that there is not dispersal habitat at all inside the selected sector (note that the sector comprises almost 20 Km^2), birds are forced to turn back to the initial cell and we count for this day a default distance of 2 cells for calculation of dispersal mortality.

We introduced a parameter for reproducing the observed behaviour of subadults of different species that often wander prolonged periods over large areas of suitable habitat before they settle (Forsman et al. 1984; Wiegand et al. 2004). At the beginning of the dispersal season, juveniles are not allowed to settle until a wandering period comprising *Wander* days finishes. Dispersal stops if the bird encounters a lek or if it dies. Assuming that birds moving larger distances (Hannon & Martin 2006) and visiting areas of lower habitat quality should have higher risk of mortality, survival of dispersing birds was stochastically determined on a daily basis depending on the distance covered (*mmov* - mortality associated with movement) and on the quality of the visited cells (*mhab* – mortality associated with habitat). See Chapter VI for further information on dispersal rules and behaviour.

<u>Mortality</u> (9)

There are five periods in the model in which mortality is increased with respect to the rest of the annual cycle, four of them operating over the eggs and the young birds with less than one year of life:

a) During reproduction season of the years when hunting was legal (until 1977 in the model), adult males were shot. Probability for each male of being shooting (*mHunt*) is stochastically determined.
b) During reproduction season, it is not unusual that hens loss all their brood. We determine stochastically if a given hen losses the nest, the probability being greater for first-year reproductive hens (*mClutch*+*mCInc*) than for adults (*mClutch*). The mortality of each territory (*mTerrit*) modifies those values to obtain the final probability of losing the nest.
c) A proportion (*mEggs*) of eggs may fail to hatch.
d) For the first month of chicks, death probability is computed as the sum of basal mortality (*mFeed*) and habitat-mediated mortality (*mCore*), which depends on the length of ecotones in the core area.
e) Survival of dispersing birds is determined daily, basing on the distance moved (*mmov*), and the average of the natural and human quality of the cells visited (*mhab*).

Annual survival is determined stochastically with a death probability that depends on the age class and the territory. Death probability for adults (mRate) is lower than for subadults (mRate+mRInc). The mortality of each territory (mTerrit) modifies those values to obtain the final death probability.

One simulation step

The cycle in Figure 2 represents one year. Firstly, initial individuals are allocated in territories (1). At the beginning of the reproduction season, cocks are shot (2, 9). Later on, each hen decides where to reproduce (3), and the size of her brood is determined (4), as well as the possible loss of the entire brood (5, 9) and the hatching success of each egg individually (6). During the first month of life, the model describes habitat use of chicks (7), and their consequent limited survival is assessed (7, 9). During dispersal, habitat use (8) is also described, together with associated mortality (8, 9), and finally young surviving males and females are assigned to their territories (1). Before the time-step ends, survivorship of each bird is assessed (1, 9), and then we update individuals' age for the next year.

6.2.5. Model parameterizations and outputs

Some dispersal parameters were fixed previously to the bulk model simulations. The length of the dispersal season (*MaxDays*=60 days) and the habitat quality threshold for a cell to be considered a dispersal barrier (*dSTOP*=0.03) were selected, respectively, to be large enough and small enough to maintain individual behaviour temporally and spatially unrestricted (almost all juveniles should reach a territory in absence of mortality). The mean number of female and male steps per day (λ_f =3 and λ_m =1), were determined so that simulated dispersal distance fitted the published data on dispersal distance (see Storch and Segelbacher 2000 and Sachot 2002 for a review of available data). The determination of these four parameters is further explained in Chapter VI.

Table 1. Variables and parameters of the model, and their range of values.

Description	**Symbol**	**Range**
Habitat variables		
Human habitat quality index	Q_H	0 - 1
Natural habitat quality index	Q_N	0 - 1
Ecotone abundance index	$Q_{ECOTONE}$	0 - 1
Demographic parameters		
Maximum influence of habitat quality (Q_H+Q_N) in mortality	*mTerrit*	0 - 0.72
Maximum capacity of a territory (separately for each sex)	*Capacity*	3 - 12
Basic probability of mortality	*mRate*	0.1 - 0.55
Incremented probability of mortality for sub-adults	*mRInc*	0 - 0.45
Additional probability of mortality for cocks due to hunting	*mHunt*	0 - 0.2
Number of cocks in a lek to ensure reproduction of hens	*MaleThr*	1 - 5
Probability of nest-losing for adult hens	*mClutch*	0.06 - 0.6
Incremented probability of nest-losing for sub-adult hens	*mCInc*	0.04 - 0.4
Probability of hatch-failing	*mEggs*	0.04 - 0.4
Basic percentage of territory used for chick-feeding	*FArea*	0.05 - 0.14
Incremented percentage due to abundance of competitors	*UngArea*	0 - 0.81
Basic chick mortality	*mFeed*	0.25 - 0.7
Maximum additional chick mortality due to habitat ($Q_{ECOTONE}$)	*mCore*	0 - 0.72
Days of wandering behaviour	*Wander*	3 - 12
Lower limit of dispersal habitat (Q_N)	*dQN*	0.05 - 0.5
Maximum daily dispersal mortality due to habitat (Q_H+Q_N)	*mhab*	0.05 - 0.14
Daily per step (i.e. per cell moved) dispersal mortality	*mmov*	0.0014 - 0.0079

We varied the four remaining dispersal parameters (Table 1) approximately within the ranges obtained in the previously developed dispersal model (Chapter VI). We varied daily per step mortality (*mmov*) between 0.0014 and 0.0074, and maximum daily habitat mortality (*mhab*) between 0.05 and 0.14 (note that mortality is applied every day). The threshold of natural habitat quality dividing matrix and dispersal habitat (*dQN*) was varied between 0.05 and 0.50. The period of wandering behaviour, when dispersers move but do not settle (*Wander*), ranged from 3 to 12 days. Variation of the outstanding parameters (Table 1) was made over a broad range of values, because of our scarce knowledge of capercaillie ecology in the Cantabrian Mountains. The mean values adopted were mostly based on the literature for other European populations (Rajala 1974; Lindén 1981; Storch 1993, 1995a, b, Grimm & Storch 2000; Moss et al. 2001; Sachot 2002; Summers et al. 2004).

We generated, through independent variation of the 17 model parameters, 10,000 model parameterizations (i.e. 10,000 sets of parameter values) with uniform distribution of parameter values between the minimum and the maximum showed in Table 1. For each model parameterization, model run consisted in simulating, as a first step, the dynamic of the population from 1957 (when all displaying areas showed acceptable abundance of capercaillie) to 1982 and, when predicted occupancy complied with 1982-census, simulating the dynamic between years 1982 and 2000. The purpose of the first step of 25 years (before the first census in 1982) was to give a stable demographic structure to the simulated population, obviating the stochastic and unpredictable functioning during the first years due to possible incongruities in the attributes and the spatial distribution of initial individuals. As the main model output for assessing plausibility of parameterizations, we obtained the simulated occupancy of each territory year by year.

6.2.6. Population patterns and Model adjustment

Pattern 1: Overall occupancy.— Gross accordance between model predictions and the population-level data was assessed by comparing the global simulated occupancy of territories with the observed lek occupancy pattern over the entire study area.

Pattern 2: Overall spatial structure of occupancy.— Observed and simulated occupancy patterns were compared looking at each territory individually. Spatial agreement was measured as the percentage of territories correctly assigned to their correspondent occupied-unoccupied category.

Pattern 3: Regional spatial structure of occupancy.— Pattern 1 and 2 evaluated the relation between simulated and observed occupancy simultaneously over the entire study area. Here, we categorized the study area into five sub-regions, as the result of one latitudinal (north and south facing slopes) and two longitudinal divisions of the Cantabrian range; the result is five and not six sub-regions because the south-facing slopes are deforested in the central area. This way, we evaluated the accordance between observed and simulated spatial structure of occupancy (pattern 2) separately for each sub-region, obtaining five sub-patterns. The sub-regions are, from 1 to 5, Western Asturias, Western Leon, Eastern Leon, Eastern Asturias and Central Asturias.

Parameter adjustment.— We defined four successive filters of increasing accuracy according to the fulfilment of the three described patterns for selecting plausible model parameterizations. The parameterizations complying simultaneously with filters 1, 2, 3 and 4 represent the remaining process and parameter uncertainty after model calibration and are used for deriving model predictions.

Filter 1. Gross compliance: We grossly tested the fulfilment of pattern 1 in 1982. The census in 1982 was presumably biased to the visit of suspected occupied leks, with 93% of visited leks showing presence of capercaillie but otherwise only half of the leks being visited.

For a parameterization to be in compliance with our expectations, we demanded that simulated global occupancy of territories over the entire study area in 1982 was larger than 40%. With this filter we just discarded extremely implausible parameterizations.

Filter 2. Moderate compliance in 1982: Parameterizations satisfying filter 1 were reset and simulated again 10 times from 1957 to 1982. The ongoing parameterization was demanded to comply with the observed patterns 1 to 3: This time, when testing fulfilment of pattern 1 we demanded simulated global occupancy to be larger than 50%. Regarding pattern 2, global spatial agreement between simulated and observed lek occupancy should be at least 70% (at least 70% of leks occupied in 1982 should appear as occupied in the model). However, global spatial agreement could show large differences among sub-regions. In order to deal with these possible regional errors, we demanded that spatial agreement should be larger than 60% in each of the five sub-regions individually (pattern 3).

Filter 3. Moderate compliance in 2000: For a given parameterization satisfying filter 2, the dynamic of the population was simulated repeatedly 100 times between 1982 and 2000. This filter is tested in two different ways for fulfilment of pattern 1: First, simulated global occupancy of territories over the entire study area in 2000 must be at most 75% of that in 1982 (i.e., population declining at least 25% in occupancy). Second, simulated global occupancy must be equal to observed occupancy in 2000 plus or minus 20% (i.e., between 32% and 48%).

Filter 4. Accurate compliance in 2000: This filter consisted in testing the relative accuracy of a given parameterization in reproducing the observed spatial structure of occupancy (pattern 2 and 3) in comparison to the accuracy obtained for a random distribution of occupancy. We destroyed the spatial structure of simulated occupancy pattern with independent randomizations of the distribution of occupied and unoccupied territories while maintaining the observed overall occupancy (40%). After 5000 randomizations, relative accuracy of our parameterization was measured as the percentage of random spatial structures that performed worst than simulated spatial structure in reproducing the observed population pattern of lek occupancy. We tested spatial accordance for all territories together, as well as for occupied and extinct territories separately. In relation to pattern 2, relative spatial accordance should be larger than 95% in all cases (occupied, extinct, and both). In relation to pattern 3, relative spatial accordance should reach 90% at least in four of the five sub-regions when all territories are tested together and in three sub-regions when occupied or extinct territories are separately tested.

6.2.7. Model predictions and their sensitivity to model parameters

We recorded 19 different variables (model predictions, Table 2) in order to examine population dynamics. We performed a pseudo-sensitivity analysis to investigate the impact of the different model parameters on the predictions, executing multiple linear regressions with the 17 parameters (i) as independent variables and the model predictions (k) as dependent variables. We also performed principal component analysis to test for multicollinearity between the independent variables, which could appear as a result of compensatory effects between model parameters producing unstable estimates of the regression coefficients $\beta_{k,i}$.

To investigate the relative impact of parameters on predictions we calculated the statistic $T_{k,i} = \beta_{k,i}/\mathrm{SD}_i$, that is expressed by the ratio of coefficient to its standard deviation, for balancing both effects; this statistic allowed us to rank the parameters according to their relative impact on a given model prediction. We also constructed, for each model parameter i, a vector $v_i = (T_{1,i}, \ldots, T_{18,i})$, and calculated correlation coefficients between all vectors v_i and v_j to investigate whether different parameters impact predictions in a similar way.

Table 2. Description of the 18 selected model predictions.

Symbol	**Description**
N_{tot}	Mean total population size (adult birds) in the whole study area in year 2000
N_j	Mean number of adult birds in the five sub-regions ($j = 1,..., 5$) in year 2000
Brood	Mean number of chicks per hen in year 2000
mChick	Mean chick mortality (before dispersal) in year 2000
mDisp	Mean dispersal mortality in year 2000
$Disp_{M,j}$	Mean number of dispersing males that settle in each of the 5 sub-regions in year 2000
$Disp_{F,j}$	Mean number of dispersing females that settle in each of the 5 sub-regions in year 2000

6.2.8. Stochasticity effects on predictions

To obtain an estimate of the impact of stochasticity on model predictions, the procedure for determining model predictions was repeated 100 times with each model parameterization. Then, we calculated the resulting mean (mean) and standard deviation (SD) of the 100 replicate estimations of each model prediction. We used the average of the coefficients of variation CV = SD/mean of the five best model parameterizations to reflect variation in each model prediction due to stochasticity.

6.2.9. Population viability

Finally, we projected the dynamic of the population for the next fifty years. In order to construct the “actual” population, we employed again the results of the same five best parameterizations. Model was then applied 1000 times repeatedly during fifty years, and population numbers were recorded year by year.

6.3. RESULTS

6.3.1. Model adjustment (Parameter uncertainty)

Sixty seven per cent of model parameterizations fulfilled the observed overall population pattern with the conditions required (filter 1). This was relatively easy to fulfil, acting as a very gross filter to discard very implausible parameterizations. However, when testing for more detailed spatial and temporal patterns extracted from the occupancy data, the filter became much more restrictive. Filter 2 was satisfied by 23% of model parameterizations, and 9.12% of parameterizations satisfied filter 3. Finally, only 1.03% of all tested parameterizations fulfilled the strictest filter 4 being so considered in good accordance with the observed population pattern of lek occupancy.

6.3.2. Impact of parameters on predictions

Model predictions, as expected from the large parameter uncertainty, varied over wide ranges (Table 3), this high uncertainty in model output being also reflected in their high standard deviation.

Principal components analysis showed multicollinearity in the independent variables, a problem that was overcome by removing two parameters (*UngArea* and *mmov*) from the regression functions. We found that the multiple linear regression functions, with the parameters and predictions as independent and dependent variables, respectively, were significant at a high degree ($p<0.01$) for most predictions, showing also high R^2 values (Table 3). The main exception came from one of the sub-regions (identified by the sub-index 5 in table 3), where the model parameters had little effect on the dynamics of the population.

The averages of the absolute value of the coefficients in table 3 ranked the parameters according to their sensitivity, the most sensitivity ones pointing to the ecological processes whose lack of information is contributing to the uncertainty in model predictions to a greater extent. The parameter with a stronger impact on model predictions was the hunting pressure (*mHunt*), followed by the capacity of territories (*Capacity*), nest losses of adult hens (*mClutch*) and the habitat-mediated mortality during dispersal (*mhab*). On the other side, the parameters with the lowest sensitivity were those associated to sub-adult increments in both mortality rate (*mRInc*) and probability of nest-losing (*mCInc*), followed by the two parameters determining chick mortality between hatching and dispersal (*mFeed* and *mCore*).

Correlation coefficients between the v_i vectors defined for the parameters showed that some a priori non-related parameters impacted predictions in a similar way. As an example, the vector of parameter *MaleThr* that gives the number of males displaying in a lek for ensuring reproduction of females showed a very strong relation (correlation coefficient = 0.84) with the vector of the parameter *mCore*, which controls the probability of mortality for chicks influenced by the habitat quality. Another example was the strong negative relation between the vector of the parameter controlling the percentage *FArea* of territory used for chick-feeding and the vector of the probability *mEggs* of hatch-failing (correlation coefficient = 0.95). We found also a positive correlation between the vectors of the parameters giving the maximum influence of habitat quality in basal mortality (*mTerrit*) and the maximum influence of habitat quality in chick mortality (*mCore*), with a correlation coefficient of 0.74, between the vector of the percentage *FArea* of territory used for chick-feeding and the vector of the parameter *dQN* that defines the threshold for a habitat unit to be considered dispersal habitat, and between the vectors of basal annual mortality rate *mRate* and habitat-mediated mortality *mhab* during dispersal.

Table 3. Obtained mean value of predictions (model outputs) based on the model parameterizations whose obtained pattern of territory occupancy was in accordance with observed pattern of lek occupancy at all steps. The table shows the mean ± the standard deviation, the minimum and maximum values of the predictions, the R^2 and p-value of the multiple linear regressions relating the parameters as independent variables to the model predictions as dependent variables, and the relative weights of parameters in predictions.

Prediction	Mean±SD	Min	Max	R^2	p	Impact coefficients of parameters on predictions ($T_{k,i} = \beta_{k,i}/\mathrm{SD}_i$)														
						mTerrit	*Capacity*	*mRate*	*mRInc*	*mHunt*	*MaleThr*	*mClutch*	*mCInc*	*mEggs*	*FArea*	*mFeed*	*mCore*	*Wander*	*dQN*	*mhab*
N_{tot}	911±135	683	1231	0.82	0.001	1.63	3.69	-1.43	-0.65	-3.93	1.46	-1.37	1.06	-1.10	0.44	-0.07	2.08	0.49	1.21	-0.03
N_1	288±100	148	488	0.76	0.010	1.79	1.23	-1.48	-1.35	-2.89	1.14	-0.58	1.27	-0.35	-0.41	-1.32	1.47	-0.68	1.99	0.61
N_2	70.1±37.5	16	157	0.74	0.019	-0.08	1.13	-2.58	-0.05	-2.44	-0.35	0.37	-1.72	1.39	-2.35	0.23	0.20	2.17	1.23	2.95
N_3	238±48	150	329	0.68	0.056	-0.50	2.68	-0.35	0.25	-1.46	-0.07	-0.49	0.02	-0.14	0.32	0.29	0.14	1.17	-0.06	-0.20
N_4	237±60	131	389	0.74	0.016	0.92	3.08	0.65	0.26	-1.68	0.85	-1.40	0.93	-2.07	2.16	1.42	1.51	0.24	-1.00	-2.16
N_5	51.1±24.7	15	116	0.34	0.868	0.54	0.10	0.71	0.42	0.59	1.33	-0.79	0.69	-0.87	1.03	0.21	0.81	-0.71	-0.32	-0.85
Brood	2.27±0.41	1.84	3.35	0.98	0.000	1.94	-2.64	1.32	1.94	-1.15	-2.20	2.48	-0.42	2.21	-2.04	-0.14	-0.60	0.88	2.58	2.19
mChick	0.376±0.060	0.32	0.52	0.99	0.000	-0.81	1.75	-0.32	1.36	0.14	-0.89	9.28	-0.38	-0.11	-0.99	1.49	-0.41	3.37	0.37	-0.51
mDisp	0.489±0.065	0.31	0.59	0.74	0.000	0.06	-5.37	1.78	-0.07	0.63	0.01	-0.06	-0.01	0.01	-0.14	0.09	-0.01	0.11	-0.05	0.10
$Disp_{M,1}$	38.1±34.3	4	118	0.92	0.000	-1.10	0.31	-0.51	0.25	-2.22	-0.93	1.45	-0.53	1.20	-1.64	-0.58	-1.11	1.60	1.71	0.96
$Disp_{M,2}$	10.0±7.4	1	28	0.79	0.005	0.35	0.16	-1.88	0.32	-1.82	0.19	-0.06	-0.68	0.82	-1.66	-0.85	0.63	1.08	1.41	2.51
$Disp_{M,3}$	25.2±19.4	1	67	0.96	0.000	-0.07	0.61	-0.70	0.36	-3.57	-0.59	1.01	0.15	0.88	-1.49	-1.02	0.01	0.84	1.90	1.50
$Disp_{M,4}$	28.2±25.8	1	91	0.80	0.003	-0.39	0.44	-0.01	0.63	-1.39	-0.50	0.86	-0.56	0.30	-0.40	0.29	-0.54	0.97	0.52	-0.06
$Disp_{M,5}$	6.3±4.6	0	18	0.41	0.703	0.59	0.08	1.02	1.30	0.70	0.60	-0.69	0.29	-0.82	0.91	0.67	0.52	-0.39	-0.68	-0.90

Table 3. (continued)

Prediction	Mean±SD	Min	Max	R^2	p	Impact coefficients of parameters on predictions ($\beta_{k,i}$)														
						mTerrit	*Capacity*	*mRate*	*mRInc*	*mHunt*	*MaleThr*	*mClutch*	*mCInc*	*mEggs*	*FArea*	*mFeed*	*mCore*	*Wander*	*dQN*	*mhab*
$Disp_{F,1}$	56.7±32.9	12	142	0.82	0.002	2.93	0.38	-1.12	-1.23	-1.68	2.14	-1.89	1.95	-0.87	0.11	-1.96	2.37	-2.17	1.97	0.65
$Disp_{F,2}$	10.4±8.5	1	41	0.84	0.001	1.65	1.01	-1.99	0.89	-2.02	-0.64	-0.23	-2.25	1.32	-2.33	1.17	0.51	1.85	0.23	3.34
$Disp_{F,3}$	53.7±19.1	22	105	0.79	0.005	-0.01	1.37	-0.45	0.92	-0.40	0.50	-1.16	0.14	0.21	-0.25	-0.95	0.15	0.55	0.53	0.61
$Disp_{F,4}$	48.6±16.7	17	84	0.74	0.018	2.14	2.78	1.89	1.26	-0.19	1.24	-2.75	1.03	-2.50	2.87	1.71	1.43	-0.71	-2.34	-2.32
$Disp_{F,5}$	8.8±6.0	0	25	0.40	0.746	0.89	-0.26	0.14	0.11	0.18	1.32	-0.34	0.21	-0.09	0.23	-0.15	0.27	-0.73	0.21	-0.04

6.3.3. Stochasticity effects

A small population size is a known cause of demographic stochasticity. In our model, however, the variation in the predictions due to parameter uncertainty (Table 3) was roughly one order of magnitude larger than the uncertainty in model predictions due to stochasticity. Indeed, the average of the coefficients of variation CV for half the predictions was less than 0.05, and only three predictions showed a CV>0.2.

6.3.4. Model predictions

Our model predicts a total population size of 911 birds in the Cantabrian Mountains at year 2000 (Figure 3), which is some higher than actual estimates of approximately 500 birds (Obeso & Bañuelos 2003). Model estimation of population size depended mainly on the parameter *mHunt* defining the hunting pressure until the late 70's and the maximum capacity (*Capacity*) of territories. Each of these two parameters also affected the uncertainty in predicting population size in two of the sub-regions alternatively. Thus, hunting pressure *mHunt* affected bird numbers in Western Asturias and Western Leon (sub-regions 1 and 2, respectively), while *Capacity* affected Eastern Asturias and Eastern Leon (sub-regions 3 and 4). Besides, in spite of the importance of mentioned parameters, uncertainty in the prediction of bird numbers in the area located in the south-western part (Western Leon, sub-region 2) depended primarily on basal annual mortality rate (mRate) and mortality associated to habitat quality during dispersal (mhab).

The model predicts a mean value of 2.27 chicks per reproductive female, and a subsequent mortality rate of 0.38 during early chick period prior to dispersal, these two predictions depending mainly on the parameter controlling the probability (*mClutch*) of nest-losing for adult hens. In the case of the number of chicks per hen other two parameters (*Capacity* and the threshold *dQN* for dispersal habitat) are also of close importance.

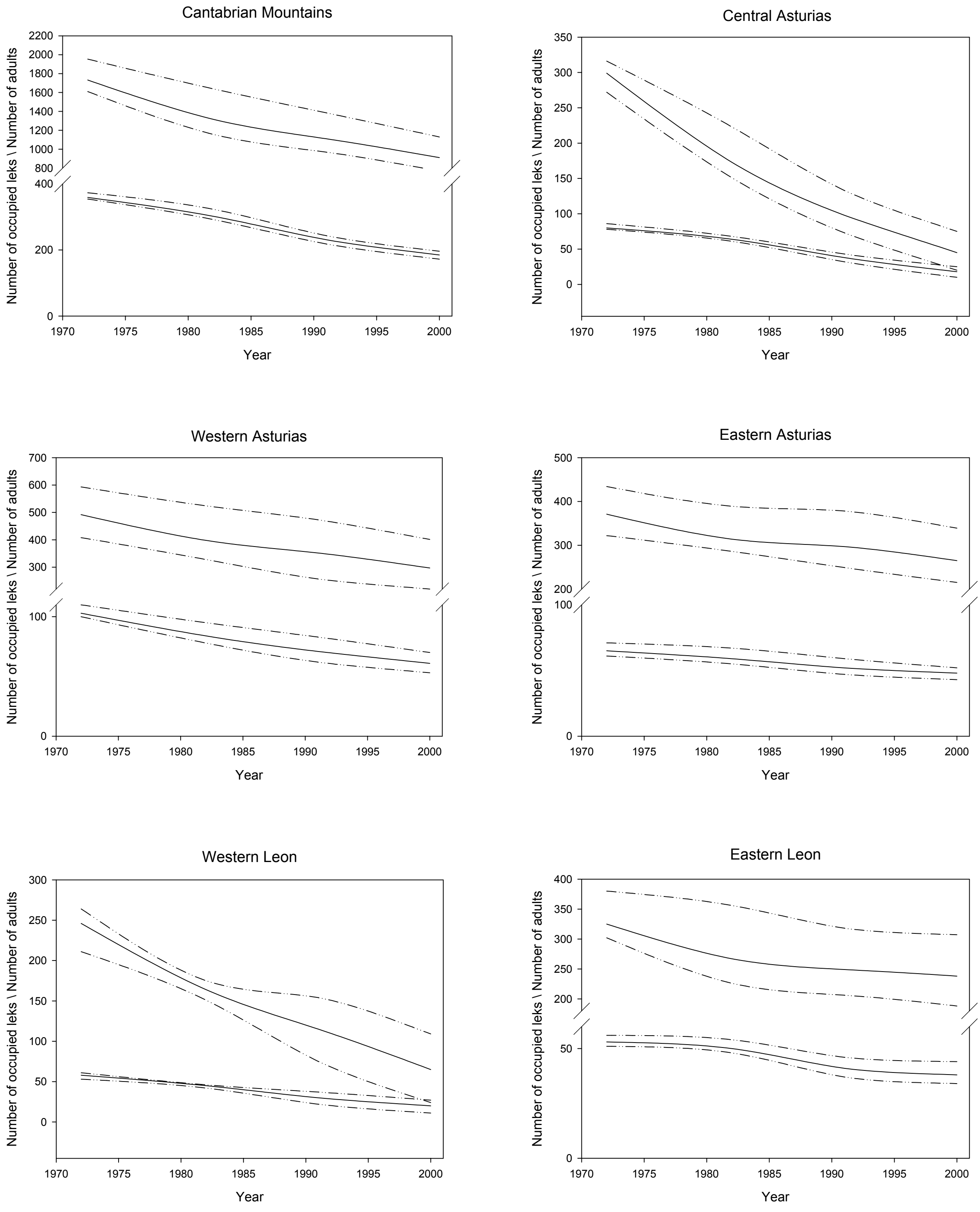

Figure 3. Time series of population size and lek occupancy for the whole Cantabrian range and the five sub-regions. In each plot, the three lines located above represent the number of adults in the population, while the three lines below are the number of occupied leks. Solid lines are the mean values, and surrounding dash-dot lines represent percentiles 10 and 90.

According to the model predictions, males and females performed very similarly in accomplishing the dispersal process; mortality rate equalled 0.49 during that period, depending mainly on the *Capacity* of territories. For both sexes the model predicts that the area where most birds successfully complete dispersal is sub-region 1. Depending on the sex and the sub-region, however, the parameters leading dispersal predictions varied. Looking at the differences between sexes, uncertainty in dispersal predictions for females mainly came from the parameter defining the influence of habitat quality in annual mortality (*mTerrit*), followed by the maximum capacity of territories (*Capacity*), while in the case of males the parameters with the biggest influence were hunting pressure (*mHunt*) and the threshold defining dispersal habitat (*dQN*). Apart from those sex-related variables, uncertainty related to dispersal for both sexes in sub-region 2 depended on the parameter *mhab*, which determines the daily habitat-mediated mortality during dispersal.

6.3.5. Population viability

Similarly to the dispersal model (Chapter V), the dynamic of the population in the area located south-east (Eastern Leon, sub-region 3) was not adequately modelled. In this area, the model predicted a very slow decline in population size and occupancy during recent years, while the most recent census in year 2006 showed a very acute regression with only 5 or 6 remaining occupied leks. Therefore, we assumed that zone as virtually extinct and excluded it from predictions of bird numbers when population viability was tested.

For the four remaining sub-regions, the model predicts a population decline of 79% in bird numbers for the next 50 years, predicted population size in 2050 being about 142 adults (Figure 4). Fourteen per cent of all replicates resulted in global extinctions. When we looked at the spatial pattern of the process with more detail, differences between sub-regions appeared. Central Asturias and Western Leon were the regions where extinctions occurred with a higher percentage of cases. Particularly Central Asturias showed a high probability of extinction of 87%.

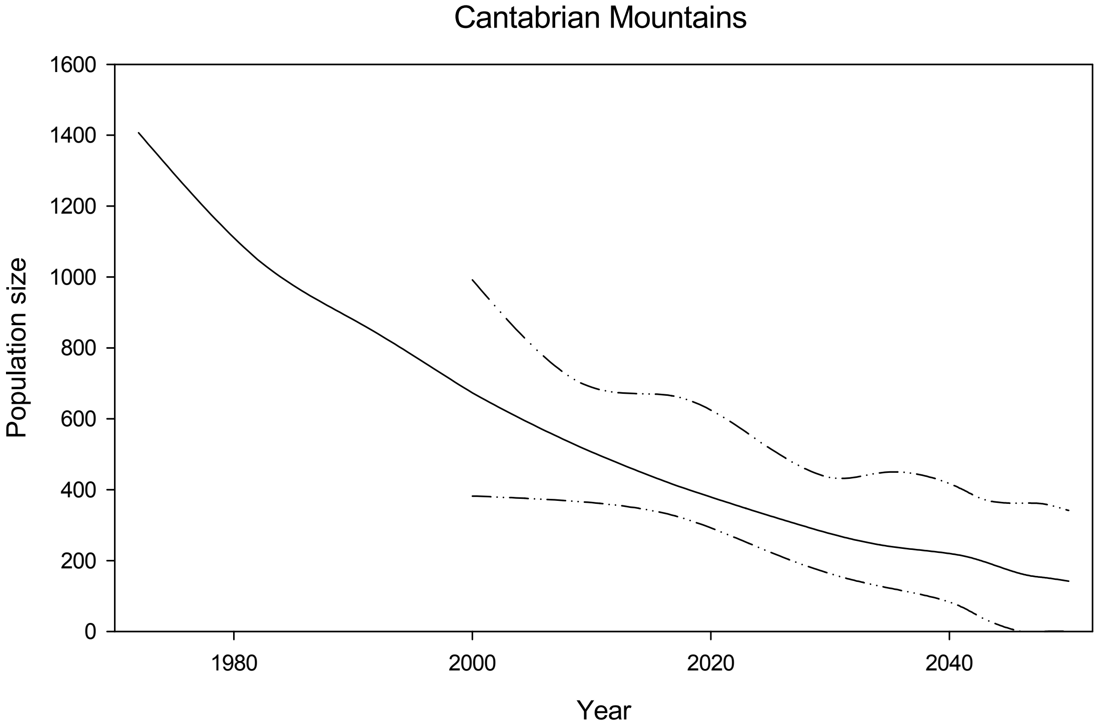

Figure 4. Population size of projected population over the whole Cantabrian range between years 2000 and 2050. Solid lines represent the mean values of number of adults, lower and upper dash-dot lines representing percentiles 10 and 90, respectively.

6.4. DISCUSSION

Our model allowed us to identify some of the ecological processes and demographic features with a higher impact on the metapopulation dynamics. Indeed, we found evidence that the hunting pressure on displaying cocks, an activity that we simulated to take place from the 50s to the late 70's, is the parameter with the highest overall impact on the predictions of current population dynamics and numbers still in year 2000, followed by the carrying capacity of territories and the losses of the entire clutch by adult reproductive hens.

6.4.1. Gains of our approach

The lack of ecological information is a major handicap in ecological modelling, as it generates uncertainty of model parameters and processes that translates into model reliability problems (Wennergren et al. 1995; Beissinger and Westphal 1998). However, this problem could be overcome by the use of methodological approaches that take into account the relationships between the species and their habitats efficiently. Inverse pattern-oriented modelling allows us to access valuable information hidden in observed population patterns. This population-level data is used for an indirectly estimation of model parameters and for selecting an appropriate process structure, acting as a filter to discriminate between probable and improbable model variants and parameterizations, and so diminishing both sources of uncertainty (Wiegand et al. 2003; Grimm et al. 2005).

Our capercaillie data consisted in information about presence-absence of the species at 444 leks distributed over most of the Cantabrian range obtained from two temporally separated surveys of the displaying areas in years 1982 and 2000. From these population-level data, we extracted several patterns of increasing detail, beginning with the observed percentage of occupancy over the entire study area (pattern 1), following by the observed global spatial structure of occupancy (pattern 2), and finally the observed five sub-patterns of spatial structure of occupancy, separately for each sub-region (pattern 3). Application of these patterns allowed us to select plausible model parameterizations in a rational way, furthermore reducing the standard error of model predictions in approximately one order of magnitude less than that obtained when the entire parameterization space was analyzed.

The accepted model parameterizations and their predictions in response to the internal model relations represent the state and the uncertainty of our current knowledge, given our habitat model, our model structure and parameters, and the observed population data.

6.4.2. The state of the population

The parameter with a stronger impact on current model predictions was the hunting pressure during the mid-twentieth century (*mHunt*, see Table 3). This result suggests that the ongoing decrease in the metapopulation size might have its origins in the strong human pressure before hunting became illegal in the late 70's. After that, the population may have remained relatively stable or declined slightly for some time, but eventually collapsed after a transient time. Landscape fragmentation and low bird numbers may have interacted then resulting in intensification in the population decline mediated by density dependent phenomena such as the Allee effect (Stephens and Sutherland 1999). This is in accordance with the results of our previously developed dispersal model (Chapter V), which pointed to the only recent increasing in the importance of dispersal process on the dynamic of the metapopulation.

The total population size of 911 birds predicted by the model (Table 3) is almost twice the currently accepted estimate of 500 adults in year 2000 (Obeso & Bañuelos 2003). This difference might reflect the still remaining uncertainty of our model structure and parameters, mainly in relation to the carrying capacity of the habitat (*Capacity*) and the increased mortality in the past due to hunting pressure (*mHunt*).

After applying mortality rate during early-chicks season, the model predicts a mean value of productivity of 1.40 birds per reproductive female with the parameter controlling the probability of nest-losing (*mClutch*) showing the highest sensitivity. However, the unique up-to-date published study that provides recent demographic estimations of Cantabrian Capercaillie from field data (Obeso and Bañuelos 2003) estimated a mean productivity of 0.47 for Asturias and Leon between years 1997-99, and that value approximates to 0.5 for the whole Cantabrian Mountains when the period 1997-2006 is considered. Our prediction is then near three times larger than those values, and twice the average productivity of a well studied Scottish forest where capercaillie is also rapidly declining (Summers et al. 2004 with field data from 1989 to 1999). According to our sensitivity analysis, this discrepancy demands further investigation of the causes and rates of nest losses as the most adequate working action for improving our model estimates of productivity.

Nevertheless, the more significant result regarding productivity is that the value predicted by the model corresponds to a declining population. For illustrating this, it lies clearly below the value of 1.8 registered in Scotland between years 1975-83 (Moss & Oswald 1985), which was considered a stable population (but see Moss et al. 2000 for a lower estimation of productivity maintaining a steady population). Besides, our mean value would have fallen into the category of “middling breeding success” inside a period of clear decline of capercaillie according to the results of another Scottish study between years 1975-99 (Moss et al. 2001). Hence, although predicted productivity still needs to be estimated with more detail, at a broad scale the model seems to perform well in reproducing this population feature of a declining population.

Mean dispersal mortality predicted by the model equalled 0.49, which results in a mean value of recruitment of 0.71 birds per reproductive female after dispersal, with the habitat capacity (*Capacity*) as the parameter with the highest sensitivity. To our view, the relatively high predicted values of mortality during early-chick season and dispersal is another meaningful result of the model. Indeed, both early chick survival and dispersal are, as already appointed by some authors (Hannon & Martin 2006; Sachot et al. 2006), main processes determining the maintenance of capercaillie populations in highly fragmented habitats.

Even though the predicted population trend (Figure 4) points to a clear decline, if we compare model predictions to the pessimistic view that field surveys offers, probability of extinction in the next fifty years is still not very high according to the model, with 14% of simulations resulting in the population becoming extinct. We consider, however, that the relatively low predicted extinction risk is consistent with the rest of model predictions. It seems that, at this stage of model adjustment and regarding the declining rate, our predictions draw a more optimistic scenario than that described from observational data. Indeed, we have already mentioned that our model actually predicts a population size in year 2000 which is close to double the size estimated from field data, and differences in estimations of productivity from model outputs and from field surveys follow the same pattern as well.

However, apart from the clear but relatively slow decline, there are some aspects of the predicted future dynamic of the population that rapidly persuade us that there are not positive expectations to wait for. The most meaningful one is the constraint of the spatial distribution of the population. We easily see this phenomenon when we analyze the future dynamics separately for the five sub-regions. The capercaillie territories of Central Asturias comes to be completely unoccupied in 87% of the cases, generating a vacuum that divides the actual population in two completely unconnected ones situated eastwards and westwards, respectively.

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CAPÍTULO 7. Discusión general y conclusiones

Esta Tesis constituye una aproximación multi-escalar a la ecología y la dinámica de la población de urogallo cantábrico. Los modelos desarrollados en ella nos han permitido profundizar en el conocimiento de las relaciones entre el urogallo y su hábitat y obtener información sobre la dinámica de la población y las causas de su declive, así como predecir correctamente la distribución espacial de la especie y sus requerimientos de hábitat a diferentes escalas. Estos conocimientos suministran herramientas de gestión que pueden contribuir a su conservación en la Cordillera Cantábrica.

Selección de hábitat

La selección de hábitat es un proceso espacialmente jerarquizado que, de modo esquemático, comprende al menos tres escalas de análisis, desde la selección del área de campeo en función de los patrones del paisaje, pasando por la búsqueda de los mejores lugares de anidamiento y alimentación en función de la disponibilidad de comida y refugio dentro del área de campeo, hasta la elección concreta de los elementos de la dieta dentro de los lugares de alimentación (Hildén 1965; Verner 1975; Schaefer & Messier 1995; Rolstad et al. 2000). Los modelos de selección de hábitat incluidos en esta tesis comprenden las dos escalas superiores, con el área de campeo como nexo de unión entre ambas.

Nuestro análisis de selección de hábitat a escala local (Capítulo 3) es el primero en estudiar el uso del hábitat por el urogallo cantábrico en unas escalas espaciales y temporales que abarcan la totalidad del área vital de la especie y de su ciclo anual, respectivamente. Hasta la fecha, los únicos estudios realizados se restringieron temporalmente a la época de celo (Castroviejo 1975; Martinez 1993), o bien espacialmente a los cantaderos o sus inmediaciones (Quevedo et al. 2006b). La selección del hábitat a escala local por parte del urogallo cantábrico tiene lugar a nivel de asociaciones multi-específicas de vegetación, siendo los matorrales de ericáceas (*Erica* spp.) las formaciones que en mayor medida se asocian a la presencia de la especie. Estos resultados ponen de manifiesto las particularidades de la subespecie cantábrica con respecto a otras poblaciones europeas. Así, en la práctica totalidad de los trabajos del centro y norte de Europa se destaca la importancia casi exclusiva (mención aparte para el arándano) del bosque maduro con una moderada cobertura de copas como principal factor determinante de la presencia de urogallo (Gjerde & Wegge 1989; Picozzi et al. 1992; Storch 1993; Saniga 2003; Bollman et al. 2005). Por el contrario, sólo en uno de los escasos trabajos en que las formaciones de ericáceas (excluyendo de nuevo el arándano) son siquiera consideradas, se sugiere una relación positiva entre su presencia y la presencia de urogallo (Bollman et al. 2005 en los Alpes centrales); en el resto (ver por ejemplo Picozzi et al. 1992 en Escocia y Saniga 2003 en los Cárpatos), los autores descartan cualquier correlación.

En lo que respecta a la selección del hábitat a escala de paisaje (Capítulo 4), nuestro modelo ofrece una perspectiva más amplia que el resto de modelos de calidad de hábitat desarrollados hasta la fecha para distintas poblaciones de urogallo (Storch 2002; Jacquin et al. 2005; Graf et al. 2005, 2006; Quevedo et al. 2006a), al correlacionar las variables geográficas con características demográficas fundamentales de la población, como son la supervivencia y la reproducción. Como resultado de nuestra aproximación conceptual bidimensional, el hábitat del urogallo ha sido categorizado funcionalmente en cinco clases (matriz, sumidero, sumidero atractivo, refugio y fuente), permitiéndonos estructurar espacialmente el proceso de declive sufrido por la población y explicar el papel de las diferentes variables demográficas en dicho proceso. Según nuestro modelo, la falta de disponibilidad de hábitat fuente a escala de paisaje es un problema capital para el urogallo en la Cordillera Cantábrica, un resultado que apoya las conclusiones del único trabajo en esta materia publicado hasta la fecha (Quevedo et al. 2006a). La representación del hábitat obtenida de nuestro modelo demuestra que el urogallo cantábrico habita en un complejo entramado de unidades de hábitat de muy distinta calidad, pero abundando sobre todo las áreas de baja calidad. Esta es una característica común en muchas poblaciones periféricas de especies en peligro (Channell y Lomolino 2000). Los urogallos parecen estar confinados en pequeñas zonas de buena calidad no relacionadas entre sí y rodeadas por una proporción más grande de zonas que actúan como sumidero para la población. Además, las áreas no ocupadas de buena calidad parecen ser demasiado pequeñas y escasas como para permitir la persistencia estable de individuos después de una supuesta colonización.

Nuestros resultados también revelan algunas cuestiones significativas sobre las causas y el estado del proceso de extinción que la población está experimentando. En ese sentido, aunque el modelo de reproducción recrea más fielmente la distribución histórica de los cantaderos, es el modelo de mortalidad el que mejor reproduce el patrón observado de desocupación de los mismos. Estos resultados, junto con los de trabajos previos que muestran que los cantaderos ocupados actualmente soportan una menor presión humana (Suárez-Seoane & García-Roves 2004; Quevedo et al 2006a), apoyan a nuestro entender la aproximación conceptual adoptada en el modelo del Capítulo 4, que asume que las variables relacionadas con la disponibilidad de alimento determinan el éxito reproductor, mientras que las relacionadas con las actividades humanas son la principal causa de mortalidad. Además, nuestro estudio sugiere que el tamaño de la población es tan bajo que podría haber alcanzado un valor umbral por debajo del cual la estocasticidad demográfica pasaría a ser el factor que gobernase la dinámica de la población. Otros trabajos apoyan este extremo, confirmando a la estocasticidad demográfica como elemento a tener en cuenta en poblaciones en declive en paisajes altamente fragmentados (Sachot et al. 2006).

Modelo de población

En esta tesis también se señalan los procesos demográficos que podrían estar jugando un papel más destacado en la dinámica actual de la población. En este sentido, el modelo de dispersión demuestra que el patrón de extinción de cantaderos observado se explica en gran medida por la estructura espacial de la conectividad efectiva entre territorios, de modo que la desocupación reciente de cantaderos se halla determinada por una relativamente baja conectividad. Este resultado está en sintonía con otro modelo desarrollado para una población de urogallo amenazada en Suiza (Sachot et al. 2006), que sugiere especial atención al proceso de dispersión y su implicación en las extinciones locales. Conforme la fragmentación del hábitat divide a las poblaciones en pequeñas sub-poblaciones, aumenta la susceptibilidad a dichas extinciones y a las fluctuaciones de carácter estocástico (Akçakaya & Baur 1996).

El modelo demográfico apunta como una de las posibles causas del declive de la población a la elevada presión cinegética sobre la especie. Aunque la caza pasó a ser ilegal a finales de la década de los 70, los efectos de su desmesurada intensidad (Castroviejo et al. 1974) pudieron dejarse notar tiempo después. Es sabido que las poblaciones naturales presentan un largo periodo de retardo entre las perturbaciones y su respuesta visible a las mismas (Ovaskainen & Hanski 2002). Como consecuencia de ese retardo, la excesiva presión humana de mediados del siglo pasado pudo no haberse visto reflejada hasta varias décadas después, momento en el cual la población pudo disminuir por debajo de un determinado umbral. Después, la fragmentación del hábitat y la escasez de individuos pudieron interaccionar resultando en una intensificación del declive de la población debida a fenómenos denso-dependientes como el Efecto Allee (Stephens & Sutherland 1999).

Conservación y manejo del hábitat

La persistencia del urogallo cantábrico depende, en gran medida, de la conservación de su hábitat, que debe estar referida a todas las distintas escalas ecológicas en las que el urogallo y su hábitat se relacionan.

Los planes de conservación regionales para la subespecie están centrados casi exclusivamente en el mantenimiento de una adecuada cobertura de las especies arbóreas dominantes y del arándano. Si bien está clara la importancia del bosque maduro con una cubierta moderada de copas y la subsiguiente abundancia de arándano en la ecología del urogallo, nuestros resultados designan también a otras formaciones vegetales, principalmente brezales (*Erica* spp.) y prados de montaña, como elementos esenciales de su hábitat (Quevedo et al. 2006b; ver también Capítulo 3). Las políticas de gestión no deben obviar la importancia de mantener un tan complejo mosaico de micro-hábitats, necesario para que la especie vea satisfechos todos sus requerimientos de hábitat. Si, por el contrario, el manejo del hábitat se fundamenta exclusivamente en las medidas actualmente aplicadas, se corre el riesgo de practicar actuaciones contraproducentes, como aclareos de matorral o talas del piso subalpino en bosques actualmente ocupados por el urogallo, convirtiendo finalmente la supuesta mejora en una excesiva simplificación estructural del hábitat, y dando como resultado efectos negativos sobre la población.

En lugar de ello, la conservación debe centrarse sobre todo en realzar la protección eficaz de los bosques aún ocupados y de sus alrededores. La protección de áreas ocupadas se debe interpretar básicamente en términos de evitar las actividades humanas (como apertura de pistas nuevas a través del bosque o los ya mencionados aclareos) y el sobre-pastoreo por ungulados domésticos. En primer lugar, la especie ha demostrado ser altamente susceptible a la actividad humana; incluso los beneficios de una acción humana de supuesta mejora del hábitat se podrían ver sobrepasados por los daños causados a los urogallos por la actividad en sí misma. En segundo lugar, los altos niveles de herbivoría sobre *Vaccinium* causan una disminución de la producción de frutos en los años siguientes (Tolvanen et al. 1993), y ello podría tener un efecto perjudicial sobre la calidad y disponibilidad del arándano para el urogallo (Fernández-Calvo y Obeso 2004). La restricción del acceso a los ungulados domésticos, no solamente a las áreas actualmente ocupadas sino también a las áreas que actualmente están siendo manejadas, podría tener un efecto más positivo para favorecer el crecimiento del arándano (Klaus y Bergmann 1994; Côté et el al. 2004) que los mencionados aclareos de matorral (cuya eficacia no está probada), y evitaría las molestias humanas a la especie. El sentido común nos dice que cuando existen dos posibilidades para lograr el mismo propósito, será siempre mejor probar en primer lugar la solución conservadora, es decir, aquella en la cual menos factores actúan. La eliminación tanto de las actividades humanas como del sobre-pastoreo por ungulados domésticos deberían ser las primeras medidas a tomar en la gestión del hábitat de la especie.

Hipótesis de trabajo futuras

Existen aún muchos vacíos de conocimiento en la ecología del urogallo cantábrico, algunos de las cuales se han puesto de manifiesto con el desarrollo de esta Tesis. A continuación se resumen brevemente algunas posibles líneas de trabajo e investigación para resolverlos:

- Averiguar el impacto de la depredación de nidos en la baja tasa de reclutamiento observada. Desde una perspectiva teórica, nuestro modelo de población señala a esta variable como la que mayor incertidumbre genera en las predicciones de productividad de la población, por lo que se hace necesario acotar su valor si queremos aumentar la fiabilidad de los modelos. Desde una perspectiva aplicada, nos interesa conocer tanto la magnitud de la tasa de depredación como las especies causantes, para elaborar las posibles medidas paliativas de la actual situación.
- Mejorar el conocimiento sobre la competencia interespecífica con los ungulados por los recursos tróficos, especialmente el arándano, pieza clave en la alimentación tanto de los adultos como de los pollos. Desde las últimas décadas ha aumentado enormemente la cantidad de ungulados silvestres, así como el tiempo que los ungulados domésticos pastan libres en el monte. Debemos averiguar si se ve modificada la disponibilidad del recurso para el urogallo, y si ello constituye un factor limitante para la población.

- Una medida controvertida, dado el bajo número de individuos, sería la de radio-marcar individuos pre-dispersivos, para investigar el mecanismo, tiempo y distancia de dispersión, sin duda uno de los procesos menos conocidos y con un mayor peso en la dinámica de la población al estar ésta espacialmente estructurada.
- Analizar la condición fisiológica de los individuos mediante medida del nivel de metabolitos en las heces. Se trataría de obtener un indicador del estrés de los individuos que serviría, por un lado, como variable indicadora de presión humana, y por otro, para validar los modelos de hábitat bajo la hipótesis de una correspondencia entre mayor calidad del hábitat y mejor condición fisiológica de los individuos.
- Mejorar los inventarios forestales para que incorporen a sus bases de datos especies importantes para el urogallo, principalmente el arándano. Disponer de ese tipo de información sería muy útil para estudiar la selección de hábitat dentro del área de campeo.
- Avanzar en el empleo de imágenes de satélite que permitan identificar y clasificar el hábitat del urogallo a distintas escalas espaciales. El objetivo final sería fusionar eficazmente la escala local y de paisaje en un único modelo de hábitat que incorporase las imágenes de satélite y la cartografía digital actualmente disponible, con lo que aumentaría su poder predictivo.

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CONCLUSIONES

1. El paisaje forestal de la Cordillera Cantábrica está severamente fragmentado, formando un patrón espacialmente jerárquico de grano fino localmente agregado y con baja conectividad entre los distintos agregados.
2. Los bosques representan tan solo el 23% del paisaje forestal potencial de la cordillera. El tamaño del 55% de los fragmentos es menor de 1 hectárea, y sólo el 1.4% supera las 100 hectáreas. El valor de cobertura forestal se halla por debajo del umbral crítico que determina efectos negativos directos de la fragmentación en la biodiversidad.
3. A escala local, el urogallo selecciona su hábitat a un nivel mayor que el determinado por la presencia de cada especie vegetal individualmente. En general, el urogallo selecciona positivamente lugares con abundancia relativa de brezales. En la zona occidental los lugares preferidos por el urogallo son los brezales asociados a un dosel de abedul y serbal. En la zona oriental de la cordillera el urogallo muestra preferencia por zonas de brezal-pastizal.
4. La cobertura arbórea es, a escala de paisaje, la variable más importante para determinar la presencia de urogallo. El modelo logístico formado por esa variable, junto a la abundancia de matorral y la conectividad de ambos tipos de vegetación en su área de campeo, caracterizan la calidad del hábitat para la alimentación/reproducción.
5. La disponibilidad de hábitat adecuado para el urogallo a escala de paisaje es muy escasa. Solo alrededor del 5% del paisaje montano de la cordillera puede considerarse un hábitat adecuado para el urogallo.

6. La cantidad de asentamientos humanos en los alrededores del hábitat del urogallo es el factor más determinante para estimar la supervivencia de los urogallos a escala de paisaje, afectándola negativamente. El modelo logístico formado por esa variable, junto a la elevación y la pendiente, caracterizan la calidad del hábitat para la supervivencia.
7. El patrón espacial actual de ocupación de cantaderos se explica adecuadamente con el modelo de calidad del hábitat para la supervivencia, sin que el modelo de alimentación-reproducción tenga efecto significativo. El declive de la población estaría pues causado por una elevada tasa de mortalidad, en lugar de por una baja productividad.
8. La elevada presión cinegética ejercida sobre el urogallo hasta la década de los 70 produjo un impacto negativo determinante en la dinámica de la población, cuyos efectos continúan manifestándose en la actualidad.
9. La dispersión juega un papel fundamental en la dinámica de extinción reciente de la población. La interacción entre la estructura del paisaje, los bajos efectivos de la población y el comportamiento de los individuos durante la dispersión ha provocado que, durante las dos últimas décadas, los territorios peor conectados no hayan recibido aportes suficientes de individuos y se hayan desocupado.
10. La estocasticidad demográfica, mediada por el bajo número de individuos de la población y la estructura fragmentada del paisaje, es uno de los principales factores (si no el principal) que actualmente dirigen la dinámica de la población.