Cartografía predictiva de la distribución de aves terrestres: un estudio piloto en Andalucía occidental

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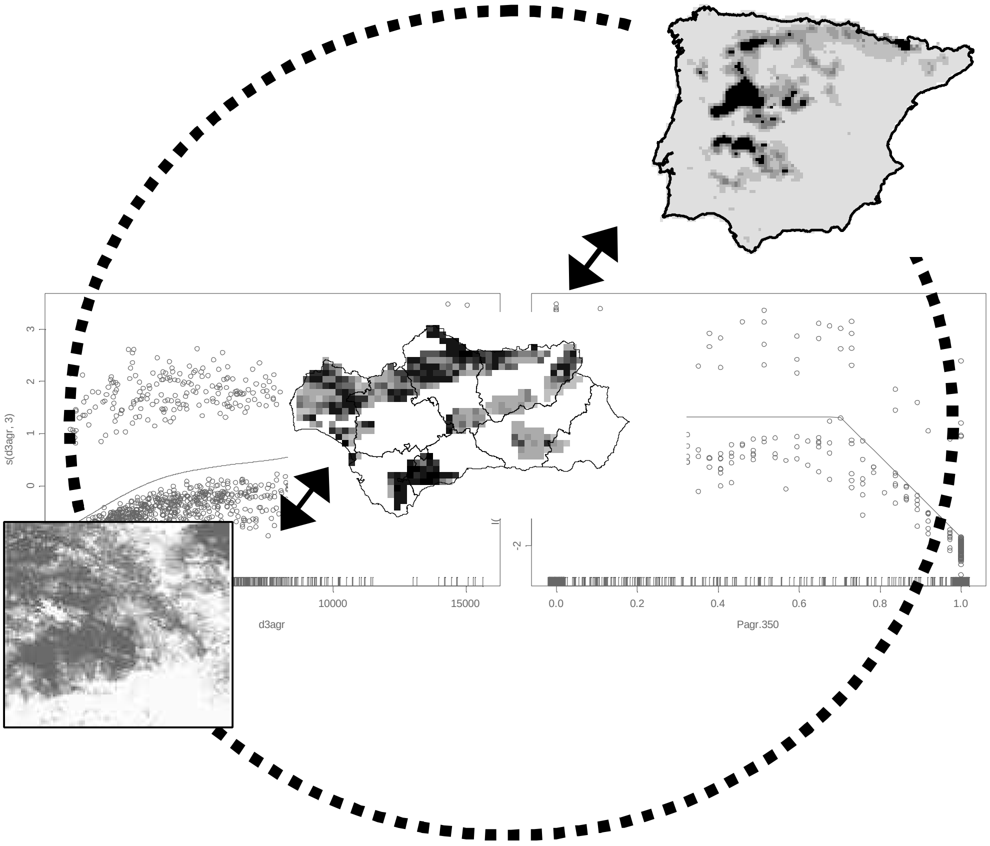

Tesis Doctoral
Universidad Autónoma de Madrid – 2002

DEPARTAMENTO DE ECOLOGÍA

FACULTAD DE CIENCIAS

UNIVERSIDAD AUTÓNOMA
DE MADRID

DEPARTAMENTO DE BIOLOGÍA
APLICADA

ESTACIÓN BIOLÓGICA DE DOÑANA

CONSEJO SUPERIOR DE
INVESTIGACIONES CIENTÍFICAS

CARTOGRAFÍA PREDICTIVA DE LA DISTRIBUCIÓN DE AVES TERRESTRES: UN ESTUDIO PILOTO EN ANDALUCÍA OCCIDENTAL

Memoria presentada por el Licenciado Javier Seoane Pinilla para optar al grado de Doctor en Biología por la Universidad Autónoma de Madrid

Sevilla, Noviembre de 2002

Carlos Montes del Olmo, Director del Departamento de Ecología de la Universidad Autónoma de Madrid

CERTIFICA

que la Tesis Doctoral que lleva por título *Cartografía predictiva de la distribución de aves terrestres: un estudio piloto en Andalucía occidental*, presentada por el Licenciado **Javier Seoane Pinilla** para optar al grado de Doctor en Biología, reúne los requisitos necesarios para su presentación y defensa pública, si procede, de acuerdo con la normativa vigente.

Y para que conste a los efectos oportunos, firmo la presente en Madrid, a 1 de octubre de 2002.

Fdo.: Carlos Montes del Olmo

Javier María Bustamante Díaz, investigador de la Estación Biológica de Doñana, centro perteneciente al Consejo Superior de Investigaciones Científicas (CSIC)

CERTIFICA

que la Tesis Doctoral que lleva por título *Cartografía predictiva de la distribución de aves terrestres: un estudio piloto en Andalucía occidental*, presentada por el Licenciado **Javier Seoane Pinilla**, ha sido realizada bajo mi dirección y cuenta con mi aprobación para su presentación y defensa pública, si procede, de acuerdo con la normativa vigente. Esta tesis supone, como aportación original al campo de la ecología, el primer estudio en detalle que aborda la elaboración y aplicación de modelos estadísticos de distribución de un conjunto numeroso de especies, a escalas local y regional, en España.

Y para que conste a los efectos oportunos, firmo la presente en Sevilla, a 25 de septiembre de 2002.

Fdo.: Javier M. Bustamante Díaz

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INTRODUCCIÓN Y OBJETIVOS

No sería exagerado afirmar que el hombre desde sus orígenes ha observado con interés los organismos que lo rodeaban y, muy probablemente, ha tratado de predecir dónde y en qué abundancia aparecerían aquellas especies que utilizaba como alimento, materias primas y medicina (Harris 1983). Este interés fundamentalmente utilitario se ha compaginado desde muy pronto en la historia de la humanidad con otro interés científico, motivado por la simple, aunque siempre provechosa, curiosidad de entender el mundo que nos rodea; así, por ejemplo, Aristóteles dejó escritas hace 2500 años algunas obras (como su *investigación sobre los animales*) en las que describía la relación entre diversas especies, muchas de las cuales no tenían una inmediata utilidad para el hombre, y el tipo de hábitats que ocupaban. Tales descripciones se hicieron muy frecuentes en los catálogos de especies que hicieron los naturalistas del siglo XIX (por ejemplo, Wilson y Audubon para la ornitología norteamericana, Block & Brennan 1993) y se correspondieron con un esfuerzo por sintetizar cualitativamente como los patrones de distribución espacial que se observaban podían deberse a procesos físicos (el *Essai sur la géographie des plantes* de Humboldt y Bonpland en 1807) o, más tarde, evolutivos (Grinell 1904 en Block & Brennan 1993, quienes resaltan con aparente asombro que la evaluación que Grinell hizo sobre la relación entre Parus rufescens y los hábitats en que se encontraba era capaz de explicar la expansión de esa especie en EEUU en la década de 1980). Por último, a mediados del siglo XX, los trabajos de Hutchinson (1978) y Mac Arthur (1958) impulsaron la estrategia moderna de análisis cuantitativo de las relaciones entre las especies y sus hábitats (ver Block & Brennan 1993).

Actualmente, el estudio de la distribución espacial de las especies tiene una gran importancia en ecología (Lawton 1996; Gaston & Blackburn 1999); tanto que para algunos autores la meta principal de esta ciencia es analizar las causas de que las especies aparezcan donde lo hacen con las abundancias en que lo hacen (Begon, Harper & Townsend 1995). Por otro lado, y desde un punto de vista aplicado, las sociedades industrializadas están demandando herramientas de planificación territorial que incluyan un tipo de valoración objetiva y repetible de los recursos naturales, entre los que se encuentra, en un capítulo destacado, la biodiversidad (Colwell & Coddington 1994; Díaz, Illera & Hedo 2001). Por este motivo, se han desarrollado en la última década algunos programas regionales que primero muestrean extensivamente distintos grupos animales y vegetales y después generan una cartografía de su distribución (como detallaré más abajo), cuya principal utilidad, desde una vertiente conservacionista, es la de servir como una guía de la adecuación del territorio para las distintas especies. Así, los distintos proyectos denominados “Gap” que se han realizado desde 1993 en EE.UU. (Scott *et al.* 1993; y ver Bojórquez-Tapia *et al.* 1995 para su aplicación en suramérica) tienen como objeto evaluar las necesidades de protección de fauna y flora mediante el examen de la cobertura de la red de espacios protegidos sobre los hábitats considerados adecuados para las distintas especies; los programas que se han llevado a cabo en Australia desde 1994 (Pearce, Ferrier & Scotts 2001), y en Suiza desde 2000 (Guisan & Harrell 2000, ver también http://www.wsl.ch/land/products/biomod/ewelcome.html) también pretendían identificar las áreas apropiadas para cada especie a una resolución espacial detallada (típicamente 40 hectáreas en los proyectos Gap, 4 ha en la cartografía australiana y 1 ha en el proyecto Landspot suizo). En España no tenemos un programa similar, aunque el interés en disponer de una cartografía general de la diversidad ha conducido al desarrollo de los atlas regionales de vertebrados referidos a cuadrículas de 100 km^2 (el de peces ya está finalizado, Doadrio 2001, y el resto estaban editándose mientras se elaboraba este texto).

La relevancia de la cartografía de especies en biología de la conservación se manifiesta al enumerar sus numerosas aplicaciones, que comprenden desde unas conceptualmente sencillas (pero necesarias) como, por ejemplo, el diseño de redes de espacios protegidos (mediante la localización de áreas susceptibles de protegerse: Kiester *et al.* 1996, y el ordenamiento en función de su interés conservacionista: Margules & Austin 1994; Bojórquez-Tapia *et al.*, 1995), y la generación eficaz de mapas de distribución en grandes territorios (e.g., Verlinden & Masogo 1997; Wright, Fielding & Wheater 2000; Osborne, Alonso & Bryant 2001, quienes aprovechan las herramientas de la teledetección), hasta otras más complejas como el manejo de especies amenazadas (e.g., Palma, Beja & Rodrigues 1999; Sánchez-Zapata & Calvo 1999, donde se identifican patrones de paisaje limitantes para la distribución de algunas especies y se prevén efectos de los cambios en los usos del suelo), la gestión de ecosistemas (He *et al.* 1998, quienes generan una proyección espacial y de estructura de la población de bosques multiespecíficos), la reintroducción y recolonización de especies (e.g., Mladenoff *et al.* 1997, 1999, donde se predicen las áreas de expansión y los tamaños poblacionales que podría alcanzar Canis lupus expansión por el oeste norteamericano; y Yáñez & Floater 2000, donde se describen las áreas adecuadas para la reintroducción de la tarántula Brachypelma klaasi), la comprobación de hipótesis biogeográficas (e.g., Mourell & Ezcurra 1996; Leathwick 1998; Manel, Buckton & Ormerod 2000), o los análisis poblacionales (e.g., Akçakaya, McCarthy & Pearce 1995; Akçakaya & Atwood 1997; donde se da una dimensión espacial a los análisis de viabilidad poblacional, y Dunning *et al.* 1995, quienes introducen los modelos poblacionales espacialmente explícitos). Además, otras áreas de biología aplicada se benefician del análisis de la distribución de especies y de la delimitación de áreas de distribución espacial, por ejemplo, los estudios de especies invasoras, plagas y vectores de enfermedades (e.g., Venier *et al.* 1998; Buchan & Padilla 2000, que estudian las áreas susceptibles de ser invadidas o afectadas por una plaga), otros en relación con indicadores biológicos (e.g., Utzinger, Roth & Peter 1998, donde el análisis de la distribución espacial de especies permite reconocer efectos de la contaminación sobre el pez Cottus gobio), o, por último, algunos con una perspectiva proxima al ordenamiento urbano (Le Lay, Clergeau & Hubert-Moi 2001, quienes tratan sobre la gestión de especies en un entorno antrópico). Otras posibilidades de la cartografía de especies y numerosas referencias se pueden encontrar en Guisan y Zimmerman (2000), Manel et al. (2001) y, con especial referencia a las limitaciones metodológicas, en el capítulo I de esta tesis doctoral.

Los modelos de adecuación del hábitat y los Sistemas de Información Geográfica

Se podría suponer que la adquisición experimental del conocimiento preciso de los factores que influyen en la aparición y la abundancia de las especies permitiría hacer predicciones exactas de dónde (y cuándo) aparecería cada especie en concreto, es decir, permitiría cartografiar sus distribuciones con exactitud. Sin embargo, el conocimiento de la distribución de una especie sólo puede ser de tipo probabilístico pues son varios los elementos estocásticos que influyen en que una especie esté presente en un área independientemente de lo adecuada que le resulte (Tyre, Possingham & Lindenmayer 2001). Además, los estudios experimentales resultan muy costosos y son imposibles de realizar para ámbitos amplios. Por tanto, son necesarias otras aproximaciones (un caso habitual y legítimo para algunos ecólogos, e.g. Lawton 1996, pero ver también Hairston 1989, cap.1 para una defensa apasionada de la experimentación). La alternativa es el uso de modelos, bien de tipo numérico (o simulación), en los que se resumen los factores más importantes de un proceso y sus efectos posibles; o bien de tipo estadístico, en los que se emplean variables descriptoras fáciles de medir y que se confía en que se correlacionen con los factores causales subyacentes. Aunque existe una previsible tendencia a la unión de ambos tipos de modelos en el mismo análisis de distribución de especies (Akçakaya, McCarthy & Pearce 1995; Akçakaya & Atwood 1997; Hirzel 2001), los primeros (modelos basados en el individuo y de autómatas celulares) generan predicciones generales y son más adecuados para la comprobación de hipótesis, mientras que los segundos tienen un ámbito de aplicación particular y son más apropiados para la cartografía de especies (Morrison, Marcot & Mannan 1998, cap.10). Son estos últimos los que se emplearán a lo largo de esta tesis doctoral con el nombre de modelos de distribución de especies (del inglés *predictive distribution modelling*) o de adecuación del hábitat (*habitat suitability modelling*).

La mayor parte de los ejemplos de aplicaciones que se han enumerado anteriormente utilizan *mapas de distribución potencial* que se elaboran en una secuencia de dos pasos. Primero, se construyen modelos estadísticos multivariantes que definen la respuesta de una especie a un conjunto de variables explicativas que resumen los aspectos físicos y biológicos a los que está expuesta la especie (es decir, se define la *adecuación del hábitat*). Segundo, se interpola ese resultado al conjunto del área de estudio mediante un Sistema de Información Geográfica (es decir, se genera un mapa de hábitat potencial, Guisan & Zimmermann 2000). Tal secuencia se empleará también en los diferentes capítulos de esta tesis doctoral, donde se introducen brevemente la estrategia de modelado así como los métodos estadísticos y los propios de un Sistema de Información Geográfica (en adelante SIG) que se utilizan. No obstante, es conveniente exponer de manera sucinta algunos fundamentos de los métodos estadísticos y de SIG que se emplearán, para ofrecer una visión de conjunto que centre al lector. Una exposición detallada de los métodos estadísticos puede encontrarse en McCullagh y Nelder (1989, capítulos 1,2 y 4), Hastie y Tibshirani (1990, capítulos 2 a 6), y en Chambers y Hastie (1993, capítulos

7 y 8), mientras que las referencia idóneas para los principales temas de GIS y teledetección tratados aquí son Lillesand y Kiefer (1994, capítulos 1 y 5 a 7), Burrough y McDonnell (1998, capítulos 1 a 4), y, Gutiérrez-Puebla y Gould (1994) como introducción en castellano.

Algunos rudimentos estadísticos

Los primeros análisis de la distribución de especies se basaban en técnicas de ajuste por mínimos cuadrados, generalmente regresiones múltiples lineares o análisis discriminante (p.e., los estudios que buscaban identificar las relaciones entre las especies y sus hábitats, wildlife-habitat relationships, ver referencias en Morrison, Marcot & Mannan 1998). Estos análisis relacionaban una variable respuesta que informaba sobre la presencia de una especie en un área, bien en términos de abundancia o bien según una variable dicotómica indicativa de la presencia o ausencia, y distintas variables explicativas (o predictoras) que describían el entorno ambiental de los puntos de muestreo. En estos casos el modelo que se usa es del tipo:

$$Y_i = \alpha + \sum_{j=1}^{p} \beta_j \; X_{ij} \; + \varepsilon_i$$

donde, siguiendo la terminología tradicional, Y es la variable respuesta que debe ser contínua y cuya relación con los predictores se asume lineal, B_j los coeficientes que multiplican a cada variable predictora X; y e_i los errores, que se suponen que siguen una distribución normal y se cancelan unos a otros. Tanto la variable respuesta como las predictoras habían de ser transformadas frecuentemente para acercarlas a una distribución normal, lo que podría no resultar fácil (ni razonable), especialmente en el caso habitual de analizar una respuesta binaria indicativa de la presencia o ausencia de una especie en un punto. En los últimos 20 años estos modelos lineares se han incorporado a un marco más amplio de análisis, el de los *modelos lineares generalizados* (o GLM, del inglés Generalized Linear Models, Nelder & Wedderburn 1972; McCullagh & Nelder 1989) donde la variable respuesta puede seguir cualquiera de las distribuciones de la familia exponencial (normal, Poisson, binomial, gamma o normal inversa), y los ajustes del modelo ya no se estiman mediante mínimos cuadrados, sino mediante estadísticos de máxima verosimilitud. En contraste con el funcionamiento de las técnicas de mínimos cuadrados, donde *los datos se ajustan a un modelo* determinado (las desviaciones se solucionan transformando los datos), el paradigma de la estadística de máxima verosimilitud es el *ajuste del modelo a los datos* mediante la búsqueda de los valores de los parámetros del modelo (B_j) que hacen más probable el conjunto de datos observado (McCullagh & Nelder 1989; capítulo 2, y Harrell 2001, para una introducción a la estadística de máxima verosimilitud). En los GLM la variable respuesta no se modela directamente, sino a través de una transformación denominada *función vínculo* (g(Y)) y una *distribución de los errores* adecuada a la naturaleza de tal respuesta:

$$g(Y_i) = \alpha + \sum_{j=1}^{p} f_j(X_{ij}) \; + \varepsilon_i$$

Así, en el modelo adecuado para una variable respuesta binaria (el equivalente a la regresión logística) no se estima directamente la probabilidad de que la variable adquiera uno de los dos estados posibles, sino que se usa la función logit:

$$E(\text{logit}(Y)) = E(p/q) = \frac{e^{\sum \beta X}}{1 - e^{\sum \beta X}} + \varepsilon$$

donde p es la probabilidad asociada a uno de los estados de la variable dicotómica (en nuestro caso la presencia de una especie en un punto de muestreo) y q la probabilidad complementaria (en nuestro caso la ausencia de tal especie en el mismo punto); los errores siguen aquí una distribución binomial. La linearidad del modelo se mantiene en el denominado *predictor lineal* ($\eta=\Sigma\beta X$) que ya no informa sobre la variable respuesta directamente, como en la regresión gaussiana tradicional, sino sobre la función que se haya usado (el logit(Y) en el modelo equivalente a la regresión logística), por lo que ha de ser transformado para que resulte más interpretable.

Una limitación de los GLM es que las relaciones que se modelan son lineales, es decir, los predictores X influyen sobre la variable respuesta Y de una manera constante determinada por sus coeficientes β; por ejemplo, un incremento de n unidades en un predictor X influye en $\beta(X_1-X_n)$ unidades en la respuesta Y. Aunque esta limitación puede modificarse en alguna medida mediante el uso de transformaciones polinómicas de las variables (por ejemplo usando $X+X^2$ en lugar de X), se han desarrollado recientemente modelos aún más generales de los que los GLM pueden considerarse un caso particular. Se trata de los modelos aditivos generalizados (GAM, del inglés Generalized Additive Models, Hastie & Tibshirani 1990), que difieren fundamentalmente de los GLM en que la relación entre la respuesta y los predictores se estima mediante una función de suavizado gráfico como las regresiones locales o los “splines” (término para el que no conozco su traducción al castellano):

$$g(Y_i) = \alpha + \sum\nolimits_{j=1}^{p} f_j(X_{ij}) \; + \varepsilon_i$$

donde los valores de Y_i se estiman con un procedimiento doblemente iterativo considerando los valores de los predictores X en un entorno próximo al punto i. Tal mecanismo incluye la estima iterativa de mínimos cuadrados baremados, *iterated reweighted least squares* o IRLS, y del modelado iterativo de los residuos parciales, conocido como *backfitting* (este no es el lugar para entrar en más detalles estadísticos, pero el lector interesado en ellos puede dirigirse a los breves e ilustrativos capítulos 3 y 6 de la estupenda monografía de Fox 2000).

El uso de GLM está muy establecido en ecología (Crawley 1993; Crawley 2002) y se han usado con frecuencia para modelar la distribución de especies y la selección de hábitat (p.e.: Austin *et al.* 1996; Bustamante 1997; Bustamante *et al.* 1997). Su cálculo es relativamente rápido y, al poderse expresar de forma analítica, son fáciles de transportar a un entorno de SIG (Guisan, Theurillat & Kienast 1998). Por el contario, los GAM son aún raros en ecología en general y en los estudios de ditribución de especies en particular (Franklin 1998; Elith 2000; Fewster *et al.* 2000; Forney 2000). Su mayor flexibilidad tiene como contrapartida una mayor lentitud (debido al proceso doblemente iterativo que se requiere para su cálculo) y la carencia de una fórmula analítica para resolverlos que dificulta implementarlos en un entorno SIG. Por estos motivos los GAM se usan con frecuencia de manera exploratoria, para detectar qué transformaciones de los predictores puede ser adecuada (como se sugiere en Hastie & Tibshirani 1990; Brown 1994; y se aplica en una situación práctica en Franklin 1998).

El siguiente esquema resume las características de las técnicas estadísticas que se han introducido en los párrafos precedentes, y muestra una explicación que ayudará a interpretarlas en el contexto de la modelización del hábitat potencial que se empleará más adelante:

- en los modelos lineares (lm):

$E(Y) = f(y) = \Sigma\beta X = \beta_1 X_1 + ... + \beta_p X_p$,

es decir, la probabilidad de que una especie esté presente en un punto de muestreo depende de una combinación lineal de las variables predictoras

- en los modelos lineares generalizados (glm):

$E(Y) = g[f(y)] = \beta_1 X_1 + ... + \beta_p X_p$,

es decir, el cociente entre la probabilidad de presencia y la probabilidad de ausencia de una especie en un punto de muestreo (el "logit" de Y) depende de una combinación lineal de las variables predictoras

- en los modelos aditivos generalizados (gam):

$E(Y) = g[f(y)] = \Sigma f(X) = f_1(X_1) + ... + f_p(X_p)$,

es decir, el cociente entre la probabilidad de presencia y la probabilidad de ausencia de una especie en un punto de muestreo (el "logit" de Y) depende de una combinación no necesariamente lineal de las variables predictoras

La evaluación de este tipo de modelos se enfrenta con dos problemas fundamentales que pueden hacer que se sobreestime su éxito: la autocorrelación espacial de los datos (detallado en el capítulo I) y la consideración de múltiples modelos alternativos. En primer lugar, estos modelos suponen que los errores son independientes entre sí, es decir, asumen que un punto de muestreo no ofrece información respecto sus vecinos. Sin embargo los procesos ecológicos, y en particular la distribución y abundancia de las especies, muestran con gran frecuencia autocorrelación espacial por la que los puntos geográficamente próximos tienden a parecerse (Legendre 1993; Augustin, Mugglestone & Buckland 1996). En esta tesis doctoral se ha optado por obviar el análisis de la dependencia espacial cuando se hacían comparaciones *relativas* entre modelos generados con los mismos datos (capítulos II a VI donde las conclusiones de los análisis son inmunes a los posibles sesgos de construción de lo modelos por basarse en comparaciones relativas), y se han usado regresiones de las coordenadas geográficas y autocovariables cuando se pretendía ofrecer una valoración *absoluta* de los modelos (ver capítulos VII y VIII). En segundo lugar (y con un desarrollo más detallado porque no se hace mención a este asunto en el capítulo I), un comportamiento típico entre quienes practican la estadística o entre los propios estadísticos profesionales es realizar inferencias a partir de un modelo como si éste se hubiera especificado a priori (Chatfield 1995), es decir, ignorando el hecho de que fue escogido entre un conjunto de modelos alternativos (lo que se ha considerado un escándalo oculto, *a quiet scandal*, en la literatura estadística (Breiman, 1992 en Chatfield 1995). Se trata de un problema general que comprende, por ejemplo, los problemas bien conocidos derivados de realizar predicciones con modelos generados mediante regresión por pasos, que se ha demostrado que pueden incorporar variables espúreas y sobreestimarse sus capacidades predictivas (Flack & Chang 1987; Buckland, Burnham & Augustin 1997; en el campo de la estadística y Mac Nally 2000, en ecología). Además, recientemente están apareciendo críticas a tal paradigma que abogan por tener en cuenta la incertidumbre en la especificación de un modelo, bien mediante la consideración simultánea de varios modelos, cuyas predicciones se promediarían de forma que se daría más peso a aquellas que se dedujeran de modelos más creíbles (Burnham & Anderson 1998; ver la propuesta basada en la teoría de la información: Anderson, Burnham & Thompson 2000; y otra que se fundamenta en un método de partición jerárquica: Mac Nally 2000); o bien mediante la preespecificación de la complejidad de los modelos y la incorporación de tal incertidumbre de selección de un modelo a los coeficientes de regresión (lo que Harrell 2001, denomina shrinking y podría traducirse como “encogido de los coeficientes”). A pesar de estas críticas (que han aparecido fuera de la literatura estadística especializada con posterioridad al comienzo de esta tesis doctoral), en los capítulos siguientes se seguirá el procedimiento común de construcción de modelos mediante una selección de variables predictoras paso a paso. Existe un motivo triple para no seguir las nuevas propuestas: (i) se carece de la información básica necesaria para diseñar un modelo (es decir, para especificar sus variables predictoras a priori) para la mayor parte de las especies que se tratarán aquí, (ii) los predictores usados son groseros y fueron diseñados con objetivos diferentes a la investigación de las relaciones entre las especies y sus hábitats, y (iii) el número de especies que se considera en los análisis es alto por lo que se precisan métodos automáticos para analizarlas eficazmente. La desventaja principal del método de selección por pasos es, en el caso que ocupa a este trabajo, la sobreestimación de la capacidad predictiva de los modelos resultantes mediante los estadísticos habituales (el porcentaje de absorción de varianza o devianza) y, en menor medida, la incorporación de variables espúreas a los modelos. Sin embargo, el primer problema es irrelevante en las comparaciones *relativas* entre modelos (como las que se usan en la mayoría de los capítulos de esta tesis doctoral) y ambos problemas pueden paliarse mediante técnicas de remuestreo (p.e., bootstraping y jackknife) y de validación cruzada (Verbyla & Litvaitis 1989), así como por el uso pragmático de medidas empíricas de capacidad predictiva (Kapa y AUC, que estiman el porcentaje de aciertos independientes del azar, ver Pearce & Ferrier 2000; Manel, Williams & Ormerod 2001). Todas estas técnicas se usan extensivamente en los capítulos que siguen.

Algunos rudimentos de los Sistemas de Información Geográfica

Los Sistemas de Información Geográfica o SIG son bases de datos relacionados espacialmente cuyo diseño tiene como objetivos: (i) almacenar y mantener datos espacialmente explícitos, (ii) mostrarlos y analizarlos, (iii) realizar operaciones espaciales complejas con ellos y (iv) comunicar eficazmente los resultados a los gestores y al público en general (ver Hirzel 2001, capítulo 1). Para ello, los datos se almacenan en las llamadas *capas de información* según dos tipos de estructura: vectorial y en rejilla (o “ráster”). En el primer tipo los datos se adjuntan a objetos cuyas coordenadas espaciales se definen con precisión. Estos objetos pueden ser puntos, o tener forma de líneas o polígonos según las características de la información que incorporen. Así, los puntos suelen servir para almacenar datos con dimensiones espaciales muy reducidas o sin ellas (p.e., el lugar donde se hizo un muestreo), las líneas son adecuadas para formas monodimensionales como cauces o carreteras, y los polígonos para estructuras bidimensionales como parcelas de cultivo o de un tipo de vegetación. Los datos que incorporen puede ser de cualquier tipo: numéricos contínuos como la temperatura, numéricos discretos como el número de aves detectadas o bien categóricos, como el tipo de vegetación. La estructura vectorial es muy adecuada para almacenar y manejar datos cualitativos como son las coberturas de usos del suelo que sirven de base para las variables predictoras que se usarán a lo largo de esta tesis. En la segunda clase de estructura de almacenamiento, de tipo rejilla, los datos se adjuntan a las celdas (o "píxeles") de tamaño homogéneo en que se divide el área de estudio. Este tipo de almacenamiento es más adecuado para datos cuantitativos que muestren una variación espacial gradual, como puede ser la temperatura, humedad, altitud, etc (cada uno de los cuales es una capa de información distinta plasmada en una imagen o mapa). Además, el sistema de rejilla incorpora fácilmente la información generada mediante teledetección por satélite (que se emplea ampliamente en los capítulos que siguen), pues estos sensores almacenan los registros según una misma estructura en celdas isométricas. En esta tesis doctoral la mayor parte de los datos se almacenaron y gestionaron en forma de rejilla. Los programas que utilizamos fueron IDRISI (Eastman 1997; Eastman 1999) y MIRAMON (Pons 2000) debido a sus relativos bajos costos y facilidad de uso.

Así pues, el esquema de funcionamiento general de un GIS es conceptualmente sencillo y aborda problemas para cuya resolución satisfactoria es necesario considerar simultáneamente distintas características del territorio que tienen una expresión espacial. Cada una de tales características (frecuentemente usos y coberturas del suelo, y factores climatológicos y topográficos) se representa en imágenes (o mapas) que pueden superponerse para obtener información sobre un punto localizado del territorio (correspondiente en nuestro caso a los puntos de censo) o sobre un entorno arbitrario determinado por el analista (ver figura 2 del capítulo V). Este modo de proceder sólo difiere de los trabajos que, hasta hace poco, debían realizarse a mano (como, por ejemplo, los que se aprenden en las prácticas de la asignatura de ecología en la UAM) en su mayor rapidez y en la posibilidad de llevar a cabo operaciones muy complejas.

Una de las principales fuentes de información para un SIG es la teledetección, que puede definirse como la adquisición de información remota, es decir, alejada del sensor que la recibe. Nuestros ojos, por ejemplo, son un magnífico sensor de la luz reflejada por los objetos que nos rodean. Los satélites que orbitan la tierra reciben información de la radiación electromagnética reflejada por la cubierta terrestre siguiendo el mismo principio (un emisor de energía –generalmente el sol–, un cuerpo que la refleja y un sensor que la recibe), pero de manera no limitada a las radiaciones de longitudes de onda visibles por el ojo humano. Así, el hombre no puede percibir la radiación infrarroja que, recogida por sensores electrónicos, permite distinguir fácilmente entre cuerpos con distinta temperatura o grado de humedad, lo que resulta de enorme utilidad para la elaboración de pronósticos meteorológicos, el seguimiento del estado fitosanitario de masas vegetales o la generación de cartografía, entre otras aplicaciones. Los satélites comerciales cuya información más se usa en los SIG transportan sensores, denominados multiespectrales, que son capaces de medir la energía en distintas partes del espectro electromagnético. La cantidad y calidad de los datos que aportan (y la utilidad que se les pueda dar) dependen fundamentalmente de su resolución espacial, es decir, del tamaño del área sobre el terreno para el que el sensor obtiene un valor, y de su resolución espectral, es decir, de la magnitud del espectro electromagnético a la que el satélite es sensible. En este trabajo se ha utilizado información procedente de los sensores TM (“Thematic Mapper”) de los satélites Landsat, del sensor LISS-III del satélite IRS, y del sensor AVHRR (“Advanced Very High Resolution Radiometer”) de los satélites gestionados por el NOAA (“U.S. National Oceanic and Atmospheric Administration”). Los sensores TM son sensibles a siete longitudes de onda que cubren el espectro electromagnético en el segmento correspondiente a la luz visible, y en partes del infrarrojo cercano, medio y térmico. Cada imagen cubre 185 km y tiene una resolución espacial de 30 metros (900 m^2) que es muy próxima al detalle de la cartografía temática de que dispusimos (50 metros para los mapas del SinambA), lo que facilitó usar tales datos para modificarla (especialmente para distinguir pequeñas formaciones de ribera que no aparecían reflejadas en los mapas temáticos). El IRS tiene características similares (625 m^2 de resolución espacial) y lo utilizamos con el mismo objetivo. En contraste, el sensor AVHRR tiene unas menores resolución espectral y espacial pues sólo recoge información en cinco bandas del espectro electromagnético en unidades de 1.1 km (ca. 1 km^2) de área. Por tanto, resulta más adecuado para evaluaciones en superficies extensas: nosotros lo utilizamos para calcular un índice de superficie riparia en Andalucía (ver capítulo VII), y un índice de vegetación de la península Ibérica (ver capítulo VIII).

Objetivos, sujetos de estudio y estructura de la tesis

El objetivo inmediato de este trabajo es explorar las posibilidades del modelado de la distribución de especies en un entorno antropizado y heterogéneo, con la intención de sugerir pautas generales para el desarrollo de una estrategia eficaz de cartografía de especies. Por este motivo se han probado distintas técnicas y estrategias a cada una de las cuales se dedica uno de los capítulos que forman esta tesis doctoral, como se detalla en los últimos párrafos de este apartado. En consecuencia, gran parte de este trabajo tiene una notable, pero ineludible, componente técnica que se ha pretendido compensar con la puesta en práctica de los modelos en la Sección Tercera.

El objeto de estudio han sido las aves, y dentro de ellas las ligadas a medios terrestres. Tal selección se hizo atendiendo a que, por un lado, este grupo de organismos comprende un conjunto numeroso y variado de especies, lo que permite ensayar modelos bajo distintas características de abundancia y selección de hábitat, y, por otro, las aves se muestrean de manera relativamente sencilla, lo que facilita la adquisición de datos de campo para construir los modelos. Las aves ligadas a medios acuáticos como marismas, lagunas y, en general, áreas de aguas libres, no se consideraron en este trabajo porque requieren una metodología de muestreo de campo y de análisis en un entorno de SIG muy diferente al resto (sí se analizaron, sin embargo, las especies propias de los sotos de ribera). En un trabajo de comparación de estrategias de modelado (Pearce & Ferrier 2000) mostraron que los distintos grupos de organismos pueden diferir en cuanto a las estrategias de modelado que les resultan óptimas. Sin embargo, creemos que los resultados generales de esta tesis doctoral podrían ser extensibles a otros grupos de organismos distintos de las aves terrestres porque la principal disimilitud que encontraron Pearce y Ferrier (op.cit) se debió a la complejidad de las relaciones que se modelaban (p.e., los modelos de los reptiles incorporaron los predictores como polinomios de un grado superior al del resto de organismos), y en los capítulos que siguen los modelos que se prueban son muy flexibles (modelos GAM y polinomios que pueden ser de alto grado).

Esta tesis doctoral está dividida en cuatro secciones de distinta extensión. La mayoría de los capítulos que la componen se han escrito en inglés con el estilo y formato de un artículo científico y muchos de ellos ya están enviados a distintas revistas de difusión internacional para publicarse. Esta situación se aleja del procedimiento habitual en las tesis tradicionales en las que un manuscrito totalmente inédito se defendía ante un tribunal y después se extraían los artículos que hubieran lugar, pero se acerca a una opción más moderna que evita grandes dilaciones entre la realización de un trabajo y su publicación (un ejemplo de esta práctica en biología de la conservación son estas dos excelentes tesis doctorales defendidas recientemente en Europa : Guyonne 2001; Hirzel 2001). La ventaja más relevante para el lector es que la lectura de los capítulos se agiliza, pues aquéllos son breves y están centrados en un problema particular; en contra debe admitirse que se hallará una cierta repetición en los apartados metodológicos, alguna heterogeneidad en los análisis que se siguen (fruto del aprendizaje durante la elaboración de la tesis), y, quizás, la ausencia de una mayor descripción de detalles muy técnicos de interés principalmente para quien se embarcara en una empresa similar.

La Sección Primera (Reflexiones preliminares: utilidad y limitaciones de los modelos de distribución de especies) está compuesta por sólo un capítulo (Capítulo I) donde se detalla la utilidad y limitaciones de los modelos de distribución de especies en ecología. El Capítulo I complementa esta introducción general justificando el interés de la cartografía de especies y detallando sus limitaciones técnicas y conceptuales.

La Sección Segunda (Aspectos metodológicos: Técnicas y estrategias del modelado de la distribución de especies), que forma la mayor parte de la tesis y tiene un importante componente metodológico, comprende los capítulos II a VI, que exploran distintas técnicas y estrategias de modelado analizadas para valorar su utilidad en la definición general de un protocolo de modelización. Así, el Capítulo II describe una técnica de optimización del tiempo dedicado a los muestreos de aves que se fundamenta en el teorema del valor marginal: las distintas especies tendrán un tiempo óptimo de muestreo diferente y predecible según sus características de tamaño, abundancia y tipo de hábitat preferido.En el Capítulo III se comparan modelos generados mediante un procedimiento estadístico automático con otros construidos mediante un protocolo supervisado paso a paso, y se concluye que los modelos automáticos tienen una capacidad predictiva similar a la de los modelos supervisados. El capítulo IV analiza las fuentes de datos de donde se extraen los predictores que se prueban en los modelos y muestra que la cartografía temática digital existente (que se ha elaborado con propósitos diferentes a las necesidades de la cartografía de especies) permite crear modelos a gran resolución de alta capacidad predictiva, igual o mayor que la que se alcanza con información de satélite (los resultados sugieren, además, que existe un límite máximo a la capacidad predictiva que se puede alcanzar con estos modelos). Los modelos que se aplicarán más adelante y, en particular, en el capítulo VII de la Sección Tercera, se desarrollarán mediante un procedimiento automático de selección de predictores derivados en su mayor parte de la cartografía temática digital preexistente. El capítulo V aborda la selección del grado de detalle espacial de los predictores para cada especie que haga mayor la capacidad predictiva de sus modelos, y concluye que las variables ambientales que se usan como predictores deben medirse en un radio muy amplio en torno al punto de muestreo, lo que muestra de forma indirecta un efecto de la configuración del paisaje sobre la probabilidad de encontrar a una especie en concreto en un área. Por fín, el capítulo VI explora qué conjunto de variables explicativas (topo-climático y descriptivas de la vegetación y el paisaje) genera modelos más predictivos, y determina que los mejores modelos se construyen con un conjunto mixto de variables e identifica a los descriptores del paisaje como las más importantes.

En la Sección Tercera (Puesta en práctica: aplicaciones de la cartografía de especies) se exploran dos aplicaciones típicas del modelado de la distribución de especies. En primer lugar (capítulos VII y VIII) se utilizan datos referidos a una malla de 10x10 kilómetros, que es la forma que tradicionalmente se ha usado en los esfuerzos de cartografiado regional de especies. En estos ejemplos se usa la modelización para detectar algunas áreas geográficas adecuadas para distintas especies de rapaces e identificar zonas con problemas de conservación. En segundo lugar (Capítulo IX), se estudia hasta qué punto difieren los modelos empíricos estadísticos que se desarrollan en esta tesis doctoral con los que podrían crearse basándose en el criterio de expertos aplicado a la cartografía de especies existente (i.e., datos de atlas y mapas de distribución).

La Sección Cuarta (Conclusiones: esperanzas y desesperanzas de los modelos) comprende sólo un capítulo (Capítulo X) en el que se ofrecen unas conclusiones generales y una valoración de los resultados obtenidos.

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SECCIÓN PRIMERA

Reflexiones preliminares

Models are like politicians: support them, use them, but don't unquestioningly trust them.

—M.L. Morrison, B. Marcot y R. William Mannan, WILDLIFE-HABITAT RELATIONSHIPS. University of Wisconsin Press. 1998.

CAPÍTULO I: Modelos predictivos de la distribución de especies: una revisión de sus limitaciones

RESUMEN

En las últimas dos décadas se ha despertado un enorme interés en el modelado de la relación entre las especies y sus hábitats, que responde tanto a la demanda de información aplicable a la gestión del territorio y a la conservación como al fundamento básico de la ecología en estudiar la distribución y abundancia de los organismos. Sin embargo, los modelos predictivos de distribución de especies descansan en ciertas presunciones y tienen unas limitaciones que conviene conocer antes de desarrollarlos. En este trabajo se ofrece primero un breve sumario de los tipos de modelado que pueden encontrarse en estudios de ecología, centrándose en los modelos monoespecíficos de distribución, es decir, en aquellos que relacionan las características del hábitat con la presencia de una especie en particular. Posteriormente, se presenta una síntesis comentada de las limitaciones de carácter biológico y estadístico de los modelos predictivos, analizando en detalle las presunciones en que se sostienen y los problemas metodológicos que dificultan su aplicación. Se concluye que los modelos de distribución de especies están sujetos a numerosos defectos, pero su desarrollo puede ofrecer una interesante herramienta complementaria en la gestión del territorio.

CHAPTER I: Predictive models of species distribution: a review on their limitations

SUMMARY

In the last two decades there has been a growing interest in modelling wildlife-habitat relationships. This is due both to the necessity of basic information for land management and conservation, and to the fundamental interest of Ecology in studying the distribution and abundance of organisms. However, wildlife-habitat models relay on several asumptions, and have some limitations that must be known. This work offers first a brief summary of the type of models that can be found in ecological studies. The focus is on monoespecific models of species distribution, that is, in those that relate habitat characteristics with the presence/absence of a single species, but the discussion can be extended to other model types, in particular those which deal with several species at a time. Second, a commented synthesis on both statistical and biological limitations of the distribution models is given in detail, with an analysis of the underlying assumptions and methodological problems. In conclusion, distribution models have numerous shortcomings but their development may provide a worthy tool for land management.

INTRODUCCIÓN

En las últimas dos décadas se ha despertado un enorme interés en el análisis de la relación entre las especies y sus hábitats, extendiéndose los estudios de selección de hábitat a la realización de modelos que predicen la distribución y abundancia de especies. Esta tendencia es un producto del doble interés de estos modelos. Por una parte, existe una fuerte demanda de información en numerosos problemas de conservación en los que las relaciones de las especies con sus hábitats son primordiales y, por otra, la ecología tiene un interés primario en estudiar la distribución y abundancia de los organismos, lo que algunos autores han identificado como su objetivo principal (Begon, Harper & Townsend 1995, p.124). En consonancia con esta situación, recientemente han aparecido diversos trabajos realizados en la península Ibérica que desarrollan modelos de distribución de especies (González, Bustamante & Hiraldo 1990; González, Bustamante & Hiraldo 1992; Donázar, Hiraldo & Bustamante 1993; Bustamante 1996; Bustamante 1997; Brito, Crespo & Paulo 1999; Sánchez-Zapata & Calvo 1999; Franco, Brito & Almeida 2000; Martínez Palao *et al.* 2000; Suárez, Balbontín & Ferrer 2000), y es de esperar que su número siga aumentando en un futuro próximo, dadas las perspectivas optimistas de su posible uso en la gestión del medio natural.

La utilidad general de los modelos de distribución de especies radica en que permiten trabajar con muestras incompletas acerca de la distribución o abundancia de especies, lo que es especialmente importante en los estudios en áreas remotas o de difícil acceso, donde no resulta práctico llegar a la totalidad del territorio, o bien en trabajos en que los recursos sean insuficientes para ello (Osborne & Tigar 1992; Skov & Borchsenius 1997; Manel, Dias & Ormerod 1999). Los datos recogidos en un muestreo se extienden al conjunto del área de interés mediante la generación de mapas de carácter predictivo (ver p.ej.Mladenoff *et al.* 1995) entre cuyos valores principales se encuentra, en nuestra opinión, el que pueden ser una herramienta útil para los gestores del territorio. Finalmente, si las variables predictoras pueden derivarse de sensores remotos (fotografía aérea, imágenes de satélite) la información proporcionada por sensores remotos podría servir para crear mapas predictivos fácilmente actualizables (Palmeirim 1988; Avery & Haines-Young 1990; Miller & Conroy 1990; Andries, Gulinck & Herremans 1994; Paruelo & Golluscio 1994). Estos modelos han sido utilizados para evaluar las necesidades de protección en un territorio (Scott *et al.* 1993; Bojórquez-Tapia *et al.* 1995). La modelización por separado de un gran número de especies (o la modelización de la riqueza) permite identificar áreas de distinto interés conservacionista, como pueden áreas ricas en especies o en táxones amenazados, para tenerlas en cuenta en la creación de espacios protegidos. El ejemplo paradigmático de esta aproximación es el análisis GAP (Scott *et al.* 1993), actualmente muy desarrollado en EEUU aunque no está exento de críticas (Short & Hestbeck 1995; Conroy & Noon 1996). En particular, no hay un acuerdo sobre si existe una coincidencia geográfica de la riqueza, rareza o grado de amenaza entre diferentes táxones (ver p.ej.Williams & Gaston 1994; Castro *et* *al.* 1996; Prendergast 1997). Por último, otra extendida aplicación de los modelos de las relaciones entre las especies y sus hábitats es la predicción de impactos, ya sean naturales, como en los estudios que sugieren posibles modificaciones en la distribución de especies relacionados con el cambio climático o incendios (Box, Crumpacker & Hardin 1993; He & Mladenoff 1999); ya sean impactos artificiales, como los provocados por infraestructuras, actividades extractivas o cambios en el uso del territorio (Avery & Haines-Young 1990; Lavers & Haines-Young 1996). En estos casos los modelos son herramientas que permiten decidir entre alternativas de gestión del territorio (Turner *et al.* 1995).

A pesar de las numerosas aplicaciones de los modelos de las relaciones entre las especies y sus hábitats, éstos son una representación incompleta de la realidad y, por tanto, tienen limitaciones de las que deben ser conscientes quienes los desarrollan y quienes los utilizan. En este trabajo se ofrece primero un breve sumario de los tipos de modelado que pueden encontrarse en estudios de ecología, centrándose en los modelos monoespecíficos de distribución, es decir, en aquellos que relacionan las características del hábitat con la presencia de una sola especie (aunque el razonamiento puede extenderse fácilmente a otro tipo de modelos, en particular los multiespecíficos). Posteriormente, se presenta una síntesis comentada de las limitaciones de carácter biológico y estadístico de los modelos predictivos, analizando en detalle las presunciones en que se sostienen y los problemas metodológicos que dificultan su aplicación.

Una versión resumida de este trabajo fue presentada en el I Congreso Ibérico de Ecología, celebrado en Santiago de Compostela (La Coruña) entre el 25 y 28 de septiembre de 2000 y organizado por la Asociación Española de Ecología Terrestre y la Sociedade Portuguesa de Ecología.

Tipos de modelos

En lo que sigue se considerarán sólo los modelos empíricos que relacionan la distribución de una sola especie (es decir, su existencia y/o abundancia en un área, lo que denominaremos *variable respuesta*) con un conjunto de variables del medio que describen aspectos bióticos, físicos o humanos a través de una formulación matemática o lógica (lo que denominaremos *variables predictoras*). Como modelo empírico se entenderá en este trabajo aquellos que se basan en datos reales, como es común en la mayor parte de los trabajos de campo, en oposición a los modelos teóricos (sensu Morrison, Marcot & Mannan 1998) cuya formulación parte de supuestos de funcionamiento de un hipotético sistema u organismo. Por tanto, no se tendrán en cuenta los modelos multiespecíficos (p.ej. análisis GAP Scott *et al.* 1993), los que usan como variables predictoras rasgos vitales de los organismos (Lawton 1993), ni los que se basan exclusivamente en técnicas de interpolación espacial (Cressie 1993; Maurer 1994). La discusión se centrará en modelos de tipo correlativo, definidos aquí como los que se basan en correlaciones, no necesariamente causales, entre variables, aunque gran parte de lo que se expone puede aplicarse a la mayoría de los modelos de las relaciones entre las especies y sus hábitats (Morrison, Marcot & Mannan 1998).

Los modelos que se más se han usado en ecología para predecir la distribución de especies podrían dividirse en tres grandes grupos atendiendo a su funcionamiento: los que estiman el rango de tolerancia ecológica, los modelos de tipo correlativo y ordenación multivariante, y redes neuronales artificiales.

Dentro del primer tipo de modelos se encuentran los llamados de análisis de superposición (Brito, Crespo & Paulo 1999) y los de envuelta climática (Austin, Nicholls & Margules 1990; Box, Crumpacker & Hardin 1993), que podrían considerarse extensiones de análisis típicos de los Sistemas de Información Geográfica. El funcionamiento de estos modelos es como sigue. Primero se identifican los lugares en las que una especie está presente y se calculan los valores mínimos y máximos de las variables ambientales que se considera *a priori* que afectan a su distribución (generalmente variables descriptoras del clima, la altitud, etc.). La extensión de los resultados al conjunto del área de estudio se hace suponiendo que los lugares adecuados para la especie son aquellos cuyos valores de todas las variables predictoras estén dentro de los rangos en los que se la ha observado. Estos modelos dependen de una selección adecuada de las variables ambientales y normalmente tienden a sobreestimar la extensión areal ocupada (pueden subestimarla si se seleccionan demasiadas variables de escasa relevancia para la especie). La utilidad que se les suele reconocer es la de aportar un primer análisis orientativo, que es particularmente valioso en áreas extensas o escasamente prospectadas (Skov & Borchsenius 1997).

Al segundo grupo pertenece una gran variedad de modelos cuyo patrón común es que tratan de relacionar la presencia o la abundancia de una especie con distintas variables predictoras a través de una función matemática. Esta función permite establecer el tipo de relación que existe entre la variable respuesta y las predictoras. En general, el uso de técnicas como análisis discriminante (González, Bustamante & Hiraldo 1990; González, Bustamante & Hiraldo 1992) y regresiones lineares múltiples (Donázar, Ceballos & Fernández 1989; Carrascal, Bautista & Lázaro 1993) han ido dejando paso a otras enmarcadas dentro de los Modelos Lineares Generalizados ("Generalized Linear Models" o GLM, de las que las anteriores pueden considerarse casos particulares) pues permiten una mayor flexibilidad al tratar los datos (Nicholls 1989; Austin, Nicholls & Margules 1990; Donázar, Hiraldo & Bustamante 1993; Bustamante *et al.* 1997). Una mención especial merece la regresión logística, que es la técnica más usada pues utiliza variables binomiales (p.ej. aquellas cuyas respuestas son 1 y 0) fácilmente entendibles en el contexto de análisis de presencia/ausencia. En cuanto a las técnicas de ordenación multivariante, éstas son utilizadas generalmente como paso previo a la modelización (Carrascal, Bautista & Lázaro 1993) para resumir un conjunto numeroso de variables en unas pocas variables sintéticas, pero pueden usarse por sí mismas para crear mapas predictivos de la distribución (análisis factorial del nicho ecológico,Hausser 1995; Hirzel, Hausser & Perrin 2000). Por último, existen técnicas de ajuste no paramétrico como regresiones locales o modelos aditivos generalizados (Generalized Additive Models o GAM,Hastie & Tibshirani 1990) que se han utilizado para aspectos similares a los que aquí se tratan y son el horizonte hacia el que probablemente irán tendiendo los próximos trabajos

(Thomas & Neil 1991; Fewster *et al.* 2000).

Un último tipo de modelos, que se separa en esta revisión por sus peculiaridades, es el de redes neuronales artificiales, denominadas así porque están basados en un modelo conceptual del funcionamiento del cerebro. En este caso los efectos de las distintas variables predictoras sobre la respuesta se transforman y se combinan en grupos denominados *neuronas* cuyo número se determina subjetivamente. Estas combinaciones y el peso relativo de cada neurona en la respuesta final se modifican iterativamente (a través de los denominados "algoritmos de entrenamiento") hasta dar con un ajuste a los datos que se considere apropiado (StatSoft 1999). Se argumenta en favor de su utilización que pueden modelar relaciones no lineares muy complejas (Lek *et al.* 1996) y en su contra que no permiten reconocer fácilmente posibles relaciones causales entre los predictores y la respuesta (originan modelos de tipo "caja negra") y que requieren mayor tiempo de computación (Manel, Dias & Ormerod 1999). El modelado de la distribución de especies a través de redes neuronales se ha emprendido recientemente y sus ejemplos son todavía escasos (Mastrorillo *et al.* 1997; Manel, Dias & Ormerod 1999).

LIMITACIONES DE LOS MODELOS

Presunciones

El modelado de la abundancia o presencia de especies en función de variables del hábitat reposa sobre dos presunciones básicas: (i) que la variable respuesta es independiente entre localidades y (ii) que todas las variables predictoras importantes se incluyen en el modelo (Lennon 1999). Puesto que habitualmente no se sabe a priori cuáles son las importantes, es necesario hacer una selección a través de tests estadísticos de manera que el modelo final retiene sólo las variables que se consideran significativas, de acuerdo con el principio de parsimonia por el que se prefieren modelos sencillos con pocas variables a otros más complejos que expliquen lo mismo. Sin embargo, la primera de las presunciones es probablemente falsa en la mayoría de los trabajos ya que las condiciones ambientales en un punto de estudio tenderán a ser similares en un área próxima y, por tanto, las especies ligadas a tales condiciones tenderán a presentarse también en los puntos vecinos. Además, no es raro que las especies aparezcan distribuidas de forma agregada puesto que los individuos establecidos en un área pueden ejercer un efecto de atracción hacia nuevos colonizadores o condicionar la dispersión de los descendientes, de forma que la probabilidad de encontrar a una especie en un lugar podría no ser independiente de la probabilidad de encontrarla en lugares vecinos (Legendre & Troussellier 1988; Augustin, Mugglestone & Buckland 1996). Estos dos aspectos originan lo que se conoce como autocorrelación espacial de la variable respuesta. Cuando esta existe, los tests estadísticos que seleccionan las variables predictoras tienden a incorporar en los modelos aquellas variables que cambien espacialmente de una forma gradual, lo cual impide hacer una interpretación biológica del modelo y perjudica su capacidad de ser aplicado a otros lugares, aunque puede resultar conveniente si el objetivo es explicar una distribución en un área determinada (Augustin, Mugglestone & Buckland 1996; Lennon 1999). El método más comúnmente utilizado para tener en cuenta la autocorrelación espacial se basa en incorporar a los modelos una o distintas variables predictoras que informen del estado de la variable respuesta en un área vecina cuya extensión se decide empíricamente. Por tanto, en estos modelos, denominados autologísticos por ser un refinamiento de la regresión logística, las relaciones de vecindad se analizan como una variable predictora más (Preisler 1993; Smith 1994; Augustin, Mugglestone & Buckland 1996; Chou & Soret 1996; Wu & Huffer 1997).

Por otro lado, los modelos de la distribución de especies asumen implícitamente que los hábitats están saturados, es decir, que todo hábitat adecuado para una especie estará ocupado por ella. Sin embargo, si un organismo cuya selección de hábitat se pretende modelar muestra una dinámica poblacional en la que hay efectos de fuente-sumidero, un área adecuada podría estar vacía si aún no hubiera sido colonizada o si la población existente se hubiera extinguido por causas naturales o provocadas por el hombre (Días 1996). Además, puede haber interacciones entre especies (p.ej., predación o competencia) que hagan que un hábitat en otro caso adecuado no esté ocupado (Lawton & Woodroffe 1991). Esta situación origina los tipos de error por comisión, en los que se predice erróneamente la presencia de una especie en un lugar (Fielding & Bell 1997).

Otra presunción fundamental es que la probabilidad de detección de una especie será mayor en sus hábitats óptimos. En los modelos de distribución se mide generalmente la abundancia de una especie en distintas áreas caracterizadas por un conjunto de variables y se equipara la abundancia con la calidad del hábitat para esa especie. No obstante, existen ciertos procesos naturales que hacen que esta presunción pueda ser falsa en algunos casos (Van Horne 1983). Por un lado, la distribución actual de una especie podría reflejar situaciones pasadas, si existen cambios en la densidad de los individuos de frecuencia plurianual que sigan variaciones a escala local en factores que influyan en la demografía, como la intensidad de depredación o la cantidad de alimento. Por otro lado, en poblaciones animales que desarrollen jerarquía social, los individuos desfavorecidos (subadultos inexpertos, ejemplares enfermos, etc...) pueden ser desplazados a ambientes subóptimos en los que podrían adquirir gran abundancia (Días 1996). Finalmente, los índices de selección de hábitat pueden estar afectados por el tamaño poblacional de manera que, por ejemplo, un hábitat de elevados recursos podría usarse mucho hasta que la población creciera tanto que la presión de competencia intraespecífica condujera a ocupar hábitats subóptimos con menor competencia (Hobbs & Hanley 1990). En esta línea de razonamiento se ha destacado que una población más numerosa no significa que esté en mejores condiciones; así se ha mostrado (Hobbs & Swift 1985) que un área con abundantes recursos de baja calidad puede mantener a una gran población infraalimentada, mientras que otro área de escasos recursos de alta calidad soporta a pocos individuos de, probablemente, mayor eficacia biológica (“fitness”). Por último, existen simulaciones en las que se recrea un hábitat fragmentado y revelan que el tamaño medio poblacional de los fragmentos está influido principalmente por la dispersión de individuos entre ellos y no por su capacidad de carga (Fahrig & Paloheimo 1988). Por estos motivos se ha propuesto que la adecuación de un hábitat se mida baremando la abundancia de las especies con la eficacia biológica de los individuos que lo ocupan (Van Horne 1983).

Si los modelos trabajan sobre un muestreo de áreas disponibles ((o unidades de recursos disponibles en la terminología deManly, McDonald & Thomas 1993), se asume que éstas han sido escogidas independientemente y al azar, y que todos los individuos tienen las mismas probabilidades de acceso a ellas (Boyce & McDonald 1999). Además, el significado que en cada caso se dé al concepto de "disponibilidad" se ha identificado también como un problema importante en estudios de selección de hábitat (Mac Clean *et al.* 1998; Wilson, Shackleton & Campbell 1998) que cabe extender al contexto de modelos de ditribución. Así, en un modelo de regresión logística típico se comparan las variables predictoras de un conjunto de localidades en el que se ha observado a una especie con otro en la que se la supone ausente, de manera que, a efectos analíticos, el área disponible es la suma de las áreas de los dos conjuntos de localidades: a mayor área en que se midieron los predictores en torno a cada localidad, mayor área disponible y, según los trabajos anteriores, mayor probabilidad de cometer error de tipo I al incorporar variables espúreas a los modelos.

Limitaciones

Unas de carácter biológico ...

Existen varias razones para esperar que los modelos no funcionen correctamente. Las dos primeras que se subrayan aquí son producidas por el propio fenómeno que se quiere modelar.

Por un lado cabría esperar que, hasta cierto punto, la distribución actual de una especie estuviera afectada por acontecimientos pasados (Días 1996; Fielding & Bell 1997) lo cual podría ser especialmente relevante en organismos sésiles de larga vida, como muchos táxones vegetales. Así por ejemplo, una especie podría habitar un área que colonizó hace tiempo y que hoy en día carece de las condiciones que le son más favorables; tal especie podría estar sufriendo un lento declive en esa zona pero los modelos (que generalmente se desarrollan en un intervalo de tiempo breve) no lo detectarían.

.

		Observado	
		Presencia	Ausencia
Predicho	Presencia	a	b
	Ausencia	c	d

Figura I. Matriz de confusión. **a**: presencias predichas correctamente; **b**: falsos positivos; **c**: falsos negativos; **d**: ausencias predichas correctamente.

Figure I. Confusion matrix. **a**: presences correctly predicted; **b**: false positives; **c**: false negatives; **d**: abscences correctly predicted

Por otro lado, clases distintas de individuos de una población podrían mostrar una selección de hábitat diferente, dependiendo por ejemplo de sus estatus social (pero no por una simple expulsión de individuos subordinados a hábitats subóptimos sino por una selección activa de hábitats diferentes con distinta oferta de recursos, ver Ardia & Bildstein 1997) Esta situación se ha encontrado en aves rapaces (Cade 1955; Koplin 1973; Smallwood 1987; Bustamante *et al.* 1997) y podría ser típica de organismos animales que exhiban una jerarquía social cuyos distintos grupos fueran dimórficos (p.ej., en las rapaces diurnas las hembras suelen ser mayores que los machos y los tamaños de las presas que les suponen un beneficio óptimo son diferentes).

Las predicciones de los modelos de la distribución que tratan con datos de presencia/ausencia se analizan con una matriz de confusión (figura I) y pueden estar erradas de dos formas: en las presencias (falsos positivos) y en las ausencias (falsos negativos). Las distintas medidas de error (tabla I) tienen características diferentes y, en particular, algunas están influidas por la prevalencia. Por ejemplo, suponiendo que se realizó un muestreo de 100 lugares y en sólo 10 apareció la especie objeto del estudio (N=100, a+c=10, b+d=90), un modelo trivial sería suponer que ninguno de los lugares es apto para ella (a+b=0, c+d=100) lo que daría una tasa de clasificación correcta del 90% ((a+d)/N=0+90/100, ver tabla I).

Además, los modelos dan generalmente valores continuos para las predicciones dentro del intervalo (0,1) pero los valores de la matriz de confusión que se utiliza para compararlos son valores discretos 0 ó 1. Esto hace que los valores de probabilidad de aparición hayan de ser convertidos, de manera que se adjudique la presencia de la especie a todas las áreas cuya probabilidad de aparición supere un umbral. El problema reside en la elección de este punto umbral, al que son sensibles las medidas de error (ver figura I yBrito, Crespo & Paulo 1999; Franco, Brito & Almeida 2000, para ejemplos reales). La elección de 0,5 como umbral en el ejemplo de la figura II conduciría a un bajo poder predictivo positivo (aproximadamente la mitad de las presencias predichas serían reales). La adopción de un umbral más bajo, por ejemplo 0,3, aumentaría el poder predictivo para las presencias (hasta 0,85), mientras que un umbral mayor, como 0,8, aseguraría un elevado poder predictivo para las ausencias (cerca del 0,9). Cada estrategia se adecuaría a distintos escenarios, por ejemplo, la primera en la selección de espacios que albergaran a una especie a proteger y la segunda en la selección de áreas alternativas para la ubicación de actividades humanas de gran impacto para cierta especie.

Por último, los modelos de distribución se limitan implícitamente a poblaciones en equilibrio cuya relación con el hábitat no cambia (Boyce & McDonald 1999), de otra manera sería necesario hacer un modelo para cada situación (Arthur *et al.* 1996).

... y otras de corte metodológico.

Existen además varios problemas metodológicos en el tipo de modelización que aquí se trata que impiden que los modelos sean perfectos. Estos se refieren a la comparación de modelos mediante medidas de error de la predicción, a la conversión de probabilidades dadas por los modelos a valores de presencia o ausencia y a la naturaleza correlativa de las relaciones que se establecen entre la variable respuesta y las predictoras.

Medida	***Cálculo***
Prevalencia *¿en qué fracción de puntos ha aparecido una especie?*	(a+c)/N
Tasa de clasificación correcta total *¿qué fracción de puntos se predijo correctamente?*	(a+d)/N
Tasa de clasificación incorrecta *¿qué fracción de puntos se predijo incorrectamente?*	(b+c)/N
Sensibilidad *¿qué fracción de las presencias se predijeron correctamente?*	a/(a+c)
Especificidad *¿qué fracción de ausencias se predijeron correctamente?*	d/(b+d)
Poder predictivo positivo *de las presencias predichas ¿qué fracción es correcta?*	a/(a+b)
Poder predictivo negativo *de las ausencias predichas ¿qué fracción es correcta?*	d/(c+d)
Kappa *¿qué fracción de puntos se predijo correctamente teniendo en cuenta la prevalencia?*	[(a+d)-(((a+c)(a+b)+(b+d)(c+d))/N] / [N-(((a+c)(a+b)+(b+d)(c+d))/N)]

Tabla I. Medidas de error (modificado de Fielding & Bell 1997) y preguntas a las que responden.

Table I. Error measures (modified fromFielding & Bell 1997) and questions that they address.

Se ha descrito un método de comparación de modelos que evita el problema de la influencia del punto de corte sobre las medidas de error. Se trata de los diagramas ROC (de "Receiver Operating Characteristic", Zweig & Campbell 1993) en los que se representa la sensibilidad de un modelo, en ordenadas, contra su especificidad, en abcisas, para todos los puntos umbral de forma que el modelo que esté por encima en el diagrama tendrá una mayor exactitud relativa. Los diagramas ROC no informan de cuál es el punto umbral óptimo, pero existen métodos por los que pueden ser utilizados para conseguir esta información (referencias enFielding & Bell 1997). Sin embargo, existen pocos ejemplos prácticos en ecología del uso de los diagramas ROC (Manel *et al.* 1999).

Como corolario cabe decir que tanto la elección de las medidas de error con las que se comparen los modelos como, si procede, la elección del punto de corte han de ser escogidos con especial atención a las preguntas más relevantes en el contexto de la investigación que se esté realizando (Fielding & Bell 1997; Morrison, Marcot & Mannan 1998).

Las relaciones entre las variables respuesta y explicativas que se modelan suelen tener una naturaleza correlativa por lo que no revelan necesariamente pautas de causa y efecto. Esto hace que los modelos de distribución puedan fracasar en su aplicación a otras áreas (o tiempos). La solución sería utilizar variables predictoras causales en los modelos, pero esto excede nuestro conocimiento actual sobre la mayor parte de las especies. Además, el desarrollo de modelos causales

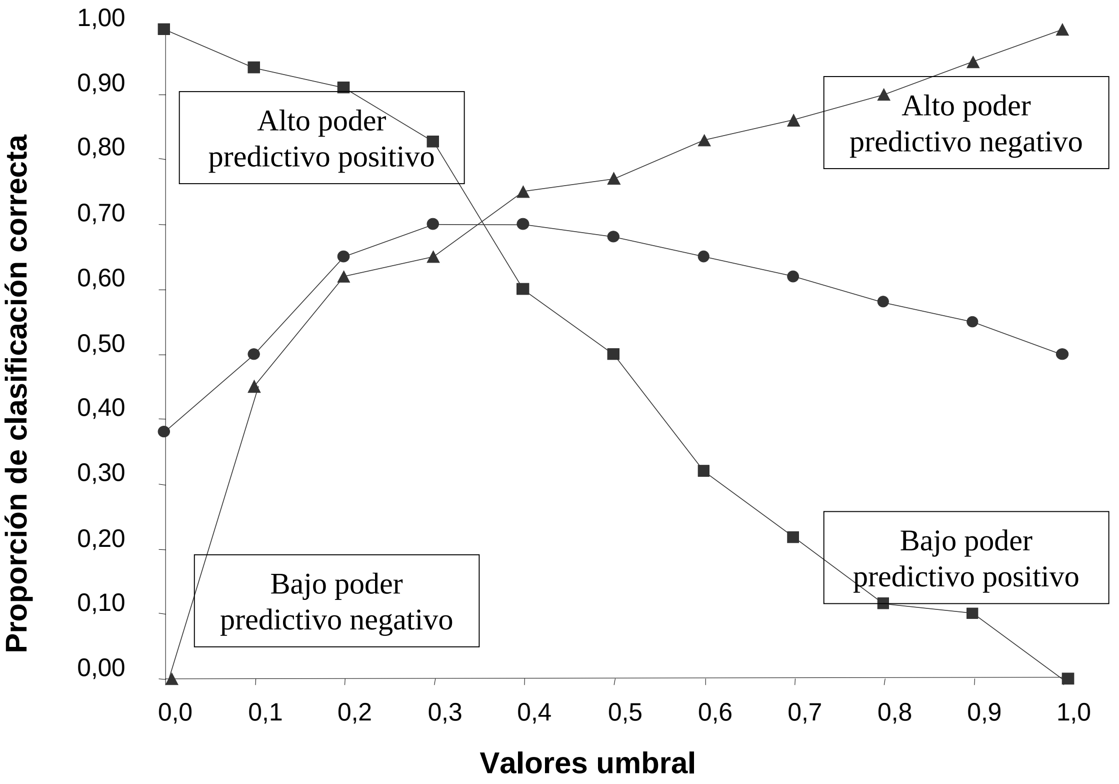

Figura II. Ejemplo de diagrama de la relación entre la tasa de clasificación correcta (cuadrados para las presencias, triángulos para las ausencias y círculos para el total) y el punto umbral para convertir los valores de probabilidad en valores de presencia/ausencia.

Figure II. Example of plot of the relation between correct classification rate (squares for presences, triangles for absences and circles for the overall) and the threshold used to convert probability values on presence/absence.

probablemente exigiría más tiempo del que permiten las necesidades de conservación que conducen a la modelización (en particular, ¿cómo se identifican a que variables del medio realmente responde una especie?; y una vez hecho esto, ¿cómo conocer la distribución espacial de esas variables predictoras, pues la cartografía disponible se ha creado con otro propósito?). Sin embargo, algunos autores han sugerido que la única solución posible reside en el uso de variables causales, pues la concatenación de presunciones podría conducir necesariamente a un bajo poder predictivo (Beutel, Beeton & Baxter 1999).

Por otro lado, los modelos suelen desarrollarse en un contexto multivariante, donde las correlaciones entre las variables (colinearidad) son muy probables. La multicolinearidad hace que puedan incorporarse a los modelos variables espúreas, y que queden fuera otras más próximas a la causales (Flack & Chang 1987). De nuevo, este problema reduce la capacidad de extrapolación de los modelos (es decir, la fiabilidad con que pueden ser aplicados en otras áreas distintas a aquellas en que se generaron) y hace que las distintas técnicas de modelado produzcan resultados diferentes (Mac Nally 2000). Una solución interesante a este problema es calcular todos los modelos posibles con las variables de que se dispone y escoger entre ellos según criterios que promedian la información recogida por el modelo y su complejidad (Akaike 1978; Schwarz 1978). Se ha propuesto además que la incertidumbre asociada a la selección de los modelos, es decir a la elección tanto de las variables predictoras como de la forma en que estas varían con la variable respuesta, se tenga en cuenta en las predicciones, ponderando los resultados procedentes de distintos modelos (Buckland, Burnham & Augustin 1997). Sin embargo, estas aproximaciones no son muy frecuentes en ecología (Toner & Keddy 1997). Finalmente, un método diseñado para identificar variables causales--pero no para generar modelos predictivos--reduciendo los problemas de multicolinearidad es la partición jerárquica (Chevan & Sutherland 1991; Christensen 1992), mediante la cual se calcula la influencia relativa de una variable en todos los modelos en los que aparece. Sus resultados pueden compararse con los modelos seleccionados mediante un criterio de información para ilustrar su grado de causalidad (Mac Nally 2000).

Cabe hacer un último comentario acerca de la posibilidad de validar los modelos de distribución. La verificación de modelos numéricos de sistemas naturales, si se entiende como tal la demostración de su certeza, es imposible porque tales sistemas no son cerrados y los resultados no son singulares (es decir, varios modelos pueden originar los mismos resultados). Según Oreskes *et al.* (1994) el término validación se emplea con dos significados erróneos; el primero es el de que las predicciones son consistentes con las observaciones, y el segundo el de que el modelo refleja con precisión la realidad. Estos autores afirman que los modelos sólo se pueden confirmar, entendiendo este término como la comprobación de que las observaciones coinciden con las predicciones; y subrayan que la confirmación no demuestra la hipótesis (el modelo), sólo apoya su probabilidad (Oreskes, Shrader-Frechette & Belitz 1994).

CONCLUSIÓN

Enfrentados a las limitaciones que se han expuesto, y ante un éxito muy variable al extrapolar modelos entre zonas geográficas distintas, algunos autores han recomendado cautela en la aplicación de los modelos a problemas de conservación, llegando a sugerir que la distribución de las especies podría ser impredecible (Fielding & Haworth 1995).

Sin embargo, los modelos de la relación especies-hábitat han mostrado su utilidad en distintas áreas y proporcionan una herramienta de, al menos, interés heurístico. La incorporación de variables causales y la atención a medidas de eficacia biológica aumentarían probablemente su valor. En cualquier caso merece la pena citar aquí a Morrison (1999, p.313) que da una perspectiva práctica a la utilización de modelos "Models are like politicians: support them, use them, but don`t unquestioningly trust them.".

AGRADECIMIENTOS

Este trabajo es una contribución al proyecto "Cartografía predictiva de la distribución de aves terrestres: un estudio piloto en Andalucía Occidental", financiado por la Dirección General de Enseñanza Superior e Investigación Científica (Ministerio de Ciencia y Tecnología) y fondos FEDER de la UE (proyecto # 1DF-97-0648). J.S. disfruta de una beca predoctoral del Ministerio de Educación y Cultura. Los autores desean agradecer los comentarios de dos revisores anónimos que contribuyeron a mejorar el trabajo.

NOTAS

Este trabajo ha aparecido publicado a principios de 2002 en *Ecología*, 15:9-21 (2001), con Javier Bustamante como coautor.

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SECCIÓN SEGUNDA

Aspectos metodológicos: técnicas y estrategias del modelado de la distribución de especies

Caminante no hay camino, se hace camino al andar.

—Antonio Machado
(en POESÍAS COMPLETAS. Residencia de Estudiantes, Madrid. 1917)

CAPÍTULO II: El muestreo de la presencia/ausencia para construir modelos predictivos: una aproximación de optimalidad usando el teorema del valor marginal

RESUMEN

En este estudio damos una solución basada en el teorema del valor marginal al problema de la asignación óptima de esfuerzo de muestreo (número de estaciones frente a tiempo empleado en cada estación) para estudios que utilicen estaciones de escucha, teniendo en cuenta el tiempo perdido por el observador en desplazarse entre estaciones. El trabajo se centra en obtener datos de presencia/ausencia para una especie de interés que puedan usarse para construir un modelo predictivo de su distribución. Las especies que son más grandes, raras o habitan tipos de vegetación estructuralmente más complejos se benefician de prospecciones proporcionalmente más largas en cada estación de muestreo. Las especies comunes y pequeñas que habitan áreas abiertas no necesitan que las prospecciones se prolonguen más de 5 minutos (en este tiempo una especie pratense de 10 g que tuviera una frecuencia total del 60% se detectaría en un 93% de los puntos), mientras que una especie más forestal, más grande o más rara precisaría de un tiempo de conteo más largo (una especie de 100 g cuya frecuencia total fuera del 10% sólo se detectaría en el 60% de los puntos durante los primeros 5 min). En este trabajo se proporcionan modelos de la duración óptima de la prospección en cada estación considerando varios tiempos de desplazamiento entre estaciones que pueden servir de ayuda en el diseño del muestreo.

CHAPTER II: Sampling bird presence/absence to build predictive models: an optimality approach using the marginal value theorem

SUMMARY

In this study we offer a solution based in the marginal value theorem to the problem of allocating sampling effort (number of stations versus time employed at each station) in point survey sampling schemes, taking into account the time wasted travelling between stations. We focus in obtaining presence/absence data for a bird species of interest that can be used to build a predictive model of its distribution. Species that are larger, rarer, or inhabit vegetation types that are structurally more complex benefit from proportionally longer surveys at each station. Common and small species inhabiting open areas do not need more than a 5-min survey (in this period a 10-g grassland species with a total frequency of 60% would have been recorded as present in 93% of the points in which it was present), while a larger and rarer forest species would benefit from a longer survey (a 100-g forest species with a total frequency of 10% would only be recorded as present in 60% of the points during the first 5 min). We provide models for optimal survey duration for a variety of travelling times to serve as an aid in sampling design.

INTRODUCCIÓN

Data on species presence/absence at point sampling stations are frequently used to build predictive models of bird distribution (Green, Osborne & Sears 1994; Bolger, Scott & Rotenberry 1997; Beard, Hengartner & Skelly 1999; Pearce & Ferrier 2001). Presence/absence data, although apparently with less information content than point-count stations, in which all bird individuals present at the census area are counted, have certain advantages for modelling: (1) Errors of presence/absence data follow a binomial distribution while bird counts rarely follow a Poisson distribution and need to be transformed for modelling. (2) Presence/absence data are not biased by double counting or by birds entering or leaving the census area as bird counts are. (3) There is less variability among observers when using presence/absence than when bird counts are used (personal observation). Empirical data show that models developed with presence/absence data to assess habitat suitability tend to perform at least as good as those developed with bird density data (Pearce & Ferrier 2001).

One may think of recorded presence/absence at a single point sample station as an asymmetrically biased estimate of true presence/absence of the species. Recorded presences indicate true presences of the species (apart from identification errors), while recorded absences may result because of actual absences or due to the species passing unnoticed to the observer. With this view in mind, one would have to remain a very long time at each sample station so that recorded presence/absence tended to coincide with true presence/absence.This would be specially true for rare and criptic species. An alternative way is to think of recorded presence/absence in statistical terms. The probability that a species will be recorded as present at a point sample station during a certain time will be proportional to its abundance in the area times its detectability to the observer. If dectability is similar or varies randomly among sampling stations, and abundance varies among habitats it will be possible to fit an environmental model predicting the probability of recording a presence and assume that those predicted probabilities will be proportional to abundances.

When obtaining field data to build these predictive models there exists a trade-off between the number of point sampling stations that can be done by an observer in a day and the duration of the survey at each point (Gutzwiller 1991; Gutzwiller 1993; Drapeau, Leduc & McNeil 1999). In general, the empirical work shows that most of the species are detected within the firsts min of sampling, so when talking about point-count stations there seems to be an agreement by experts in recommending short counts (5 to 10 min) (Fuller & Langslow 1984; Hutto, Pletschet & Hendricks 1986; Jiménez 2000). However, counts of short duration (5-10 min) have the disadvantage that most of the time could be wasted travelling between counting points and, besides this, a high proportion of species really present at the point may not be detected (Drapeau, Leduc & McNeil 1999). Moreover, some of these studies suggest that rates of detection are species-specific, therefore the optimal duration of the survey at a point may be affected by characteristics of the species that influence the probability of detection.

In the context of obtaining presence/absence data to model particular bird species the longer the time at the sample station the greater the probability of detecting a rare or criptic species that inhabits the area. On the other hand, short censuses give the opportunity of exploring more places, which may be crucial when studying large or heterogeneous areas, specially considering the need of a large sample of point surveys for modelling (Harrell 2001). In this context, a plot of cumulated recorded presences (divided by the total number of presences) at the sample station versus time would form a curve of cumulated relative frequency. The shape of this curve would show an increase towards an asymptote with a value equal to the mean frequency of the species in the study area, thus resembling a curve of diminishing returns. We can apply then the marginal value theorem (Charnov 1976) to the trade-off between number of survey stations and time spent at each station, reckoning the similarity between the curve of cumulative energy gain in a plot where an animal gradually depletes a resource, and the curve of cumulated relative frequency in an area of study where an observer gradually approximates the mean frequency of a particular species in the area. According to the marginal value theorem, the quantity to be maximised is the rate of energy gain: $E(t)/(t+\tau)$, where $E(t)$ is the cumulated energy up to time t, t is the time spent feeding in a plot, and τ is the time spent in travelling between plots. Equivalently, the analysis of optimal survey duration to sample presence/absence can be performed by substitution of $E(t)$ for $RF(t)$, the cumulated relative frequency at time t, and t being time spent at the sample station. Given a certain travelling time (τ), that we assume the observer can roughly fix in advance, the aim is to find the value of t that maximised $RF(t)$. Optimality theory predicts that the time spent in a plot should increase with increasing average travelling time between plots (Mac Nair 1982).

The aim of our study is to find an optimal solution, by applying the marginal value theorem, to the trade-off between the number of survey stations and time spent at each station to obtain presence/absence data adequate for predictive modelling of a particular bird species. We will take into consideration the time wasted by the observer travelling between sampling stations, and biological and ecological factors that may affect the detection probability: species abundance, body size and habitat type. Our focus is on obtaining comparable samples so the observer will have to remain a fixed time at each station. We think that our models can be usefull when planing preliminary surveys for a single species with time and man-power constrains.

METHODS

We recorded bird species presence/absence at point stations surveyed for 15 min. A total of 1118 stations were surveyed between April and June in 1999 and 2000, in two areas of 70 x 70 km in Western Andalusia, Spain (area centers were: 6° 21’ W 37° 39’ N, and 5° 28’ W 36° 44’ N). Each year, about 75% of the point stations were separated by more than 1000 m, the rest being 250-300 m apart (although then stations were in very different habitats). The observer started to record species about three min after reaching the survey station, so allowing birds to eventually return to normal behaviour. Two bands were considered at each survey station: an internal circular band within 50 m of the observer and an external band from 50 m to unlimited distance. First detection of a bird species in each band was recorded to the second. The reason for using two bands, one with fixed radius an the other with unlimited radius, is that fixed census radius has the advantage of sampling an area of known size but has the disadvantage that many species, specially the larger ones, are rarely recorded. The unlimited radius has the advantage or recording more presences but the disadvantage that the efective survey radius is unknown and varies between species. Sampling was performed throughout the day, avoiding only the hottest hours (generally, 1300 to 1600). Surveying outside of the optimal period of the day (Drapeau, Leduc & McNeil 1999) may confer more variability to data, but as points in different habitats were sampled at random times there is no reason to expect a bias due to this fact.

Vegetation types (Hall, Krausman & Morrison 1997) varied from cattle pastures with little or no presence of short camephytes (mainly *Lavandula stoechas* and *Thymus* spp.) and herbaceous dry cultures (mainly barley, wheat, and sunflower), Mediterranean scrub formations 50-250 centimeters tall, to Evergreen Oak *Quercus ilex* subsp. *ballota* and Cork Oak *Quercus suber* forests and “dehesas”, olive groves, and pine and eucalyptus (*Eucalyptus* spp.) plantations. These habitats were classified, respectively, as herbaceous (299 survey stations), scrub (94), and forest (751), on the grounds of presumed differences in richness and detectability of birds among habitats with different structure.

STATISTICAL ANALYSES

We divided the total duration of each point survey in periods of 30 seconds and calculated the proportion of points in which each species was detected in each time interval (what we call "relative frequency" hereafter). The result is a cumulative curve of probability of detection with time from survey start (RF(t)), which is our approximation to obtain an equivalent to the curve of cumulated energy gain (E(t)) of the marginal value theorem. Data were considered separately for a) detections in the 50-m internal band and b) for first detection in any of both the internal and external bands (that is, considering time of the first detection wherever it was recorded). The first curve is the result of a 50-m fixed-radius point survey while the second corresponds to an unlimited-distance point survey. We considered only species that appeared in more than 5% of the points surveys in adequate habitats, and used only point surveys in relevant vegetation types for each species (34 species for fixed-radius and 43 species for unlimited-distance point surveys). Following the optimization criterion used in the marginal value theorem (Mac Nair 1982), the maximum for $RF(t)/(t+\tau)$ was calculated, $RF(t)$ being the relative frequency at a time t, and τ being the travelling time between point stations. We consider that a field biologist is able to estimate mean travelling time in advance (at least to a certain degree) during the sampling design, accounting for accessibility of terrain, total area that wants to cover and the desired separation between point stations. The optimal survey duration was estimated for travelling times (τ) between 2.5 and 30 min at 2.5 min intervals. The upper limit for survey duration considered here is 15 min (the total duration of the survey we performed); consequently, if the estimate of optimal duration for a particular species was 15 min for a travelling time X, then optimal survey duration would be 15 minutes for all travelling times greater than X.

We analysed the effect of body size, regional abundance, and vegetation type on the shape of the cumulated curves of relative frequency and on the optimal duration of a survey for several travelling times between stations. Most bird species are registered mainly during the first min of the survey (thus having curves of cumulated relative frequency that soon approach an asymptote) while others may need a long survey to be detected (do not show a flattening tendency after 15 min). To summarise the shape of the curve for a particular species with a number, we used the ratio between relative frequency at 5 min and relative frequency at 15 min: ratios close to 1 indicate that in most points where the species was present it was recorded in the first 5 min, while low ratios indicate that at many points where the species was present it was not detected during the first 5 min but during the subsequent 10 min. We selected 5 min to compute the ratio because most curves of relative frequency showed an inflection point at around this duration (Fig.1), and several authors have suggested 5 min as an optimal survey duration (Fuller & Langslow 1984; Hutto, Pletschet & Hendricks 1986; Jiménez 2000). To explore which factors may affect the shape of this curve for each species we built a Generalized Linear Model of the ratio of relative frequencies in 5 and 15 min using the following as predictors: body weight (log-transformed), frequency in the total sampled points (pooling all vegetation types; this is a surrogate for regional abundance), and vegetation structure type. *P*-values for individual terms were calculated by analyzing the change in deviance associated with the deletion of each term from the saturated model; similarly, *P*-values for the saturated model were calculated by comparison with the null model. Weights were taken from the *Handbook of the Birds of Europe, the Middle East and North Africa* (Cramp et al. 1977-1994), choosing data for the spring season (both sexes combined), the appropriate subspecies, and the closest recording places whenever possible. Weights ranged from 5.3 g (Firecrest *Regulus ignicapillus*) to 508 g (Red-legged Partridge *Alectoris rufa*). Total frequency in the sample ranged from 0.02 (Yellow Wagtail *Motacilla flava*) to 0.53 (Goldfinch *Carduelis carduelis*)

Finally, we attempted a predictive model of optimal survey duration for fixed travelling times known in advance. To this end we performed generalised linear modelling of optimal survey duration for travelling times of 5, 10, 15 and 20 min and both census methods (fixed radius and unlimited distance). Explanatory variables tested were body weight (log-transformed), total frequency (presences divided by total number of sampling points irrespective of vegetation type), and vegetation structure type.

For illustration purposes we selected the following subset of species: Sardinian Warbler *Sylvia melanocephala* and Blackbird *Turdus merula* in scrub, Crested Lark *Galerida cristata* and Calandra Lark *Melanocorypha calandra* in herbaceous vegetation, and Wren *Troglodytes troglodytes* and Common Chaffinch *Fringilla coelebs* in forest. These species were selected to cover a reasonable variety of breeding habitats and frequency in the samples (percentage of points with presence of a species varies between 21% of forest points for the Wren to 81% of scrub points for the Sardinian Warbler).

RESULTS

As expected, curves of cumulated relative frequency for the selected species were higher for the unlimited-distance point surveys. Curves show, for most of the selected species, a very slow increase after 5-7 min of survey duration, almost reaching an asymptote in the case of the Sardinian Warbler. The exceptions are the Blackbird, for which the curve is still increasing steadily at 15 min and, to a much lesser extent, the Wren (Fig.1).

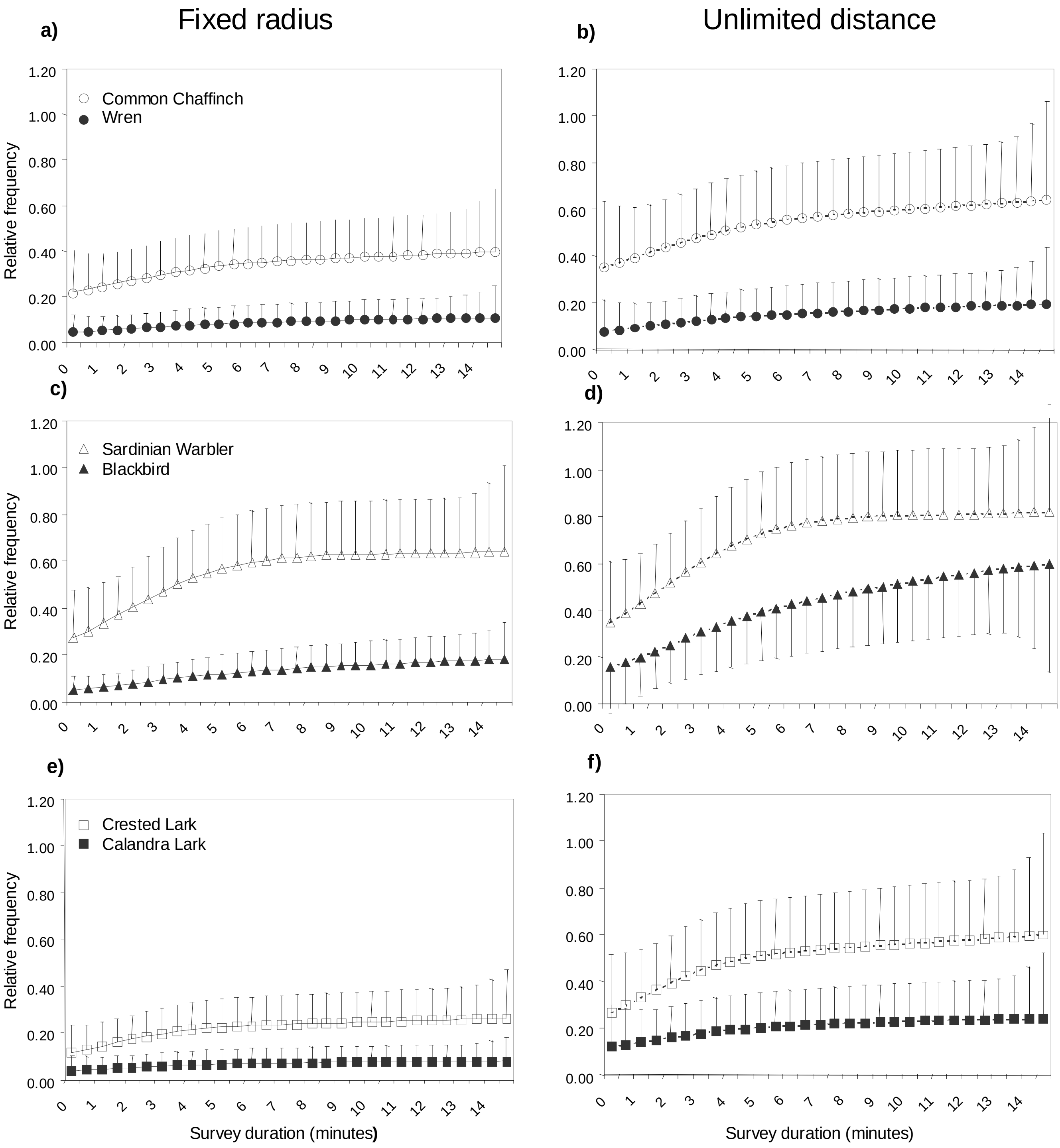

Fig. 1. Predicted cumulative frequency (presences/number of sampled points) for an example of forest (a, b), scrub (c, d), and herbaceous vegetation species (e, f), for 50-m fixed radius surveys and unlimited-distance surveys. Bars are one SE.

In unlimited radius point surveys, the shape of the curves of cumulated relative frequency for each species (as estimated by the ratio of relative frequencies at 5 and 15 min) is significantly affected by species body weight, total frequency, and vegetation structure (Table 1a), that explain altogether 40% of the deviance. Body weight has a negative effect, total frequency a positive effect and vegetation type an effect that decreases with vegetation structural complexity (Fig. 2). However, for the 50-m fixed radius surveys only body weight seems to have a significant negative effect on the ratio of relative frequency (Table 1b).

Optimal survey durations for the whole set of individual species showed, in general, a pattern of increase towards an asymptote when plotted against travelling time between points (graphs not shown), indicating that there was a maximum optimal survey duration not affected by travelling time

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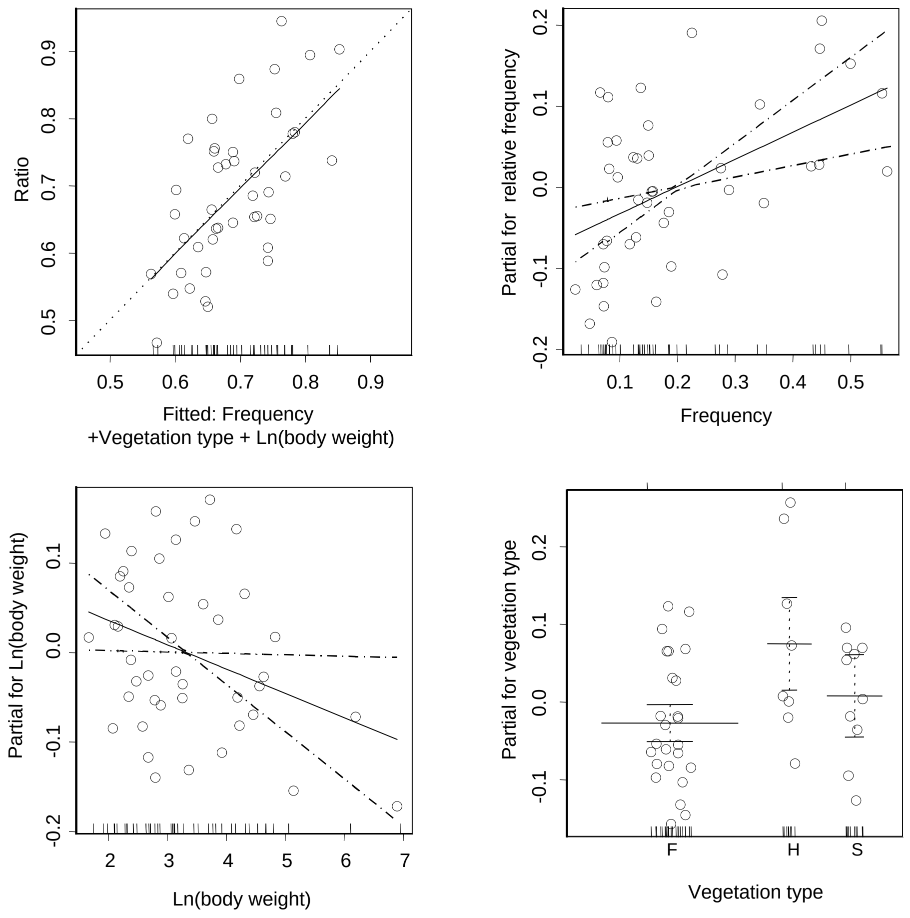


Fig. 2. Diagnostic plots for the model for the ratio of relative frequencies at 5 and 15 min (unlimited-distance survey): fitted model and partial effects of terms. Vegetation types are classified as herbaceous vegetation (H) , scrub (S) and forest (F), on the basis of presumed differences of detectability; Total frequency: frequency in the total sampled points (pooling all vegetation types). Body weight was log-transformed (natural logarithms) before the analysis.

TABLE 1. Analysis of deviance table for the model of relative frequency ratio in 5 and 15 min
Deviance analysis tables for the GLM of ratio of species relative frequencies in 5 and 15 min. P-values for individual terms are calculated by deleting each term from the saturated model; P-values for the saturated model is calculated by comparison with the null model. **a)** Results for the unlimited-distance point surveys. **b)** Results for the fixed-radius point surveys. In both a) and b) rounded treatment coefficients for the vegetation types -- modelled as dummy variables -- are: herbaceous vegetation, 0.10, and scrub, 0.04 (forest is taken as the reference, so entering the linear predictor as 0).

TABLE 1A. Unlimited-distance point surveys

Term	Coefficient	SE	Residual df	Change in df	Residual deviance	Change in deviance	F	P-value
Null			42		0.5214			
Saturated				4		0.2073	6.27	<0.001
Intercept	0.687	0.050						
Total frequency	0.335	0.097		1		0.0980	11.86	0.001
Vegetation type	-	-		2		0.0632	3.82	0.03
Ln(weight)	-0.027	0.013		1		0.0373	4.51	0.04

TABLE 1B. Fixed-radius point surveys

Term	Coefficient	SE	Residual df	Change in df	Residual deviance	Change in deviance	F	P-value
Null			33		0.4584			
Saturated				4		0.0958	1.92	0.14
Intercept	0.773	0.082						
Total frequency	0.117	0.215		1		0.0037	0.30	0.60
Vegetation type	-	-		2		0.0404	1.62	0.22
Ln(weight)	-0.059	0.026		1		0.0671	5.36	0.03

TABLE 2. Summary of models of optimal survey duration (T, in min) for a series of travelling times (5, 10, 15 and 20 min) in fixed radius and unlimited-distance point surveys. The complete model includes natural logarithm of body weight (LW), total frequency (TF), and vegetation types: herbaceous (H), scrub (S) and forest. The minimum adequate model contains significant terms only.

Census type	Travelling time (min) τ	P-value Complete model	Minimum adequate model	P-value	R^2(%)	P-value individual terms
Fixed radius	5	ns	T= 0.813+1.35 *LW	0.029	13	-
	10	ns	T= 3.79+1.4 *LW	0.053	11	-
	15	ns	T= 9.24	-	-	-
	20	ns	T= 11.63– 2.53*H – 3.43*S	0.028	21	-
Unlimited distance	5	0.037	T= 3.93	-	-	-
	10	0.001	T= 4.53+1.13*LW – 8.08*TF	0.002	24	LW: P=0.013 TF: P=0.014
	15	0.009	T= 7.60+0.915*LW – 9.31*TF	0.006	21	LW: P=0.005 TF: P=0.017
	20	0.010	T= 12.01 –9.91 *TF	0.010	14	-

In models for optimal survey duration and 50-m fixed radius designs the complete model that included body weight, total frequency and habitat was non significant in all cases (Table 2). Only body weight affected optimal survey duration and the effect was significant in two models (for 5 and 10 min of travelling time, Fig. 3). In unlimited distance point surveys the complete model for optimal survey duration was significant in all cases, indicating a positive relation with body weight, a negative relation with frequency and suggesting a positive relation with vegetation structural complexity (coefficients for scrub and herbaceous vegetation were negative and the latter had generally much higher absolute values). Simplification of the models indicated very significant effect of body weight and total frequency for 10 and 15 min, and 10, 15 and 20 min of travelling time respectively. The effect of habitat was not significant in all cases and only for 20 min travelling time was marginally significant. R-square of the final models were rather low, ranging from 13% to 27%.

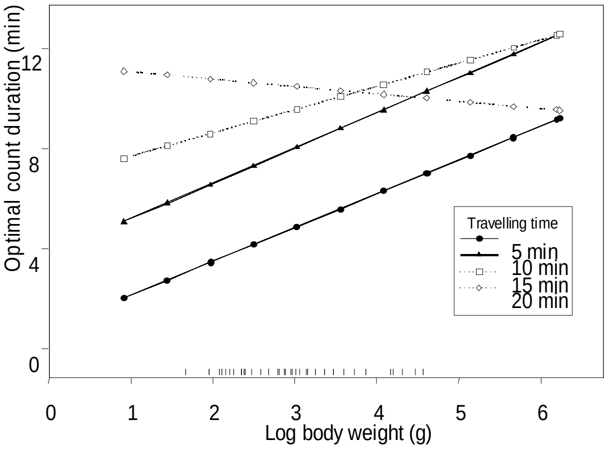
DISCUSSION

Optimal survey duration for individual species is inversely proportional to its ratio of relative frequencies at 5 and 15 min. A ratio of 1 for a species indicates that all points with a recorded presence at 15 min had that contact in the first 5 min of the survey, whereas a ratio of 0.5 indicates that only half of the points with a recorded presence after 15 min had the contact in the first 5 min. The GLM model built for the ratios shows a negative correlation with species weight, a positive correlation with total frequency (a surrogate for regional abundance), and a negative correlation with structural complexity of vegetation (the vegetation mean effects follow the order herbaceous>scrub>forest, Table 1).

Consequently, if the aim of a study is to register presence/absence in as many points as possible where a particular species could be present, our results indicate that survey duration at a each point should increase with species body size, decrease with expected regional abundance (longer surveys for rare species), and increase with habitat structural complexity. This pattern is only apparent if the method used is point surveys with unlimited distance, while only body weight needs to be considered for surveys with 50-m fixed radius design. Previous studies have shown different cumulative curves of percentage of total individuals counted with increasing count duration for different species (Scott & Ramsey 1981; Jiménez 2000). Fuller and Langslow (1984) suggest that cumulative curves, and therefore adequate sampling schemes (Barker, Sauer & Link 1993), might be species specific. Our analysis indicates that body size, regional abundance, and vegetation structure explain some of the differences in shape of these curves of relative frequency (about 40% of the variance), and consequently influence the estimate of optimal survey duration for a particular species (when we are only interested in presence/absence data). For example, our model predicts, for the unlimited-distance method, that a small and frequent grassland species (weighing 10 g and appearing in 60% of the total points) will have a ratio of relative frequency of 0.93, which means that in a 5-min survey this species would be detected in 93% of the points in which it was present after 15 min. On the other hand, a larger and rarer forest species (100 g and frequency equal to 10%) is predicted by the model to have a ratio of relative frequency of 0.60, that is, only in 60% of the points where the species is recorded as present after 15 min would it have been detected during the first 5 min.

A similar pattern was found when we tried to model the optimal survey duration for fixed values of travelling time between sample stations using body weight, total frequency and vegetation type as explanatory variables (Table 2). In general, the effect of body weight is positive (the larger the species the larger the optimal survey duration) and the effect of total frequency is negative (shorter optimal times for common species, see Figs. 3 and 4). We did not find a significant effect of vegetation type, although results suggest a positive effect of vegetation structural complexity (longer optimal times for forest and shorter for the more open vegetation types) and we think that differences among vegetation types may be masked by the variability of our data. For example, using our models for unlimited radius surveys, the predicted optimal survey duration for 10 min travelling time for the Goldfinch, a very common species of 13.2 g body weight, is 3 min, while for the Red-legged Partridge, less common and heavier (508 g), is around 10 min (Fig. 4) .

To summarize the analyses, only body weight affects the shape of the prevalence curve and consequently the optimal survey duration for a species when using 50-m fixed radius point surveys, while body weight, regional abundance, and vegetation structure affect the prevalence curve of a species and its optimal survey duration for designs with unlimited radius.



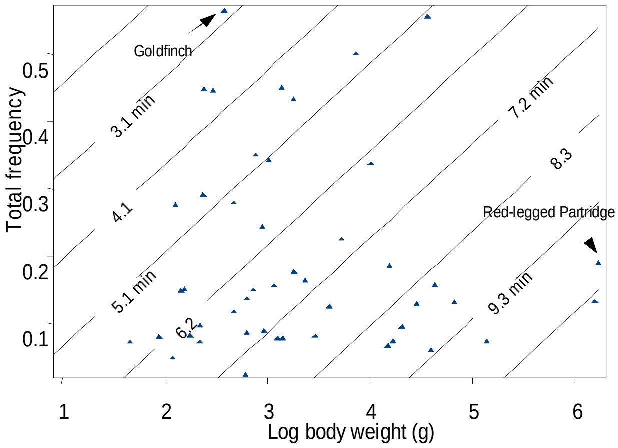


Fig. 3 (left). Models for optimal survey duration in relation to species body weight for 50-m radius point surveys for fixed travelling times between sampling stations (5, 10, 15, and 20 min). Non significant trends are indicated with point lines and open symbols. Bars above the x-axes indicate the body weights of the species used in the models.

Fig. 4 (right). Isolines of optimal survey duration in relation to species body weight and species total frequency in the study area (a proxy for regional abundance) for unlimited radius point surveys and 10 min travelling time between sampling points. Triangles indicate the total frequency and body weight of the species used in the model.

Larger species have greater mobility, larger home ranges, lower average densities (Peters 1983), and songs that can be heard from a greater distance (Calder III 1990), all of which increase the probability that they will enter the effective survey area the longer the observer stays in a point. Rare species (those with low abundance or low detectability for the observer, once these are corrected for body size) benefit from longer surveys only in the unlimited-distance method. This is probably because, when having a larger surveyed area, the observer requires more time to cover the whole area, and a longer time benefits more the inconspicuous species, those at low abundances, or those to which the observer is less habituated. Comparatively, rare species, if close to the observer (50-m fixed-radius method), do not require more time to be detected than common ones. Structurally complex vegetation types seem also benefit from longer survey durations the larger the census radius, but our analyses were not totally confirmatory in this regard.

Two limitations of this work must be noted. First, we performed census of 15 min and considered this time as the upper limit for optimal survey duration in the statistical analysis. That is, if we estimated an optimal survey duration of 15 minutes for a particular species at a given travelling time, all estimates of optimal survey duration for longer travelling times were necessarily also 15 min, but had we surveyed for a longer time a longer optimal time might have been estimated. This is probably the reason why body weight did not enter the models for 20 min of travelling time, since larger species have longer optimal survey duration, and so they reach the upper limit of 15 min for shorter travelling times. The second limitation is that we were to build simple models with few easily measurable variables, and so we did not add to the analysis behavioral variables that affects detectability of species (for example, foraging and singing behavior), and this is probably the reason why final models explained a rather low variability of data.

As a conclusion, the choice of a point survey duration to record presence/absence data for individual species should take into account, at least, the regional abundance and the body size of the species, and probably also the structural complexity of the vegetation in the area where the survey is planned to be carried. The models we offer could help in the sampling design to select an appropriate survey duration to record presence/absence data at point stations.

ACKNOWLEDGEMENTS

This work is a contribution to the project "Predictive cartography of land birds: A pilot study in Western Andalusia", funded by the *Dirección General de Enseñanza Superior e Investigación Científica* (Ministry of Science and Technology) and FEDER funds from the EU, project # 1DF-97-0648. J.S. had a predoctoral fellowship from the Ministry of Education and Culture. The extensive field work presented in this work could not have been done without the help and sense of humour of Daniel López Huertas, Luis M. Carrascal, and Mario Díaz who also brought intellectual insight to the project

NOTES

A version of this chapter is being prepared for submittion to *Ibis* (with J.Bustamante)

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CAPÍTULO III: ¿Incrementa la opinión de experto la habilidad predictiva de los modelos de la distribución de aves?

RESUMEN

El modelado predictivo del hábitat para la conservación y gestión resulta facilitado por procedimientos automáticos de selección y transformación de variables explicativas. Se ha argumentado que los modelos empíricos predictivos se beneficiarían si incluyeran una opinión de experto en las diferentes fases de la modelización, pero esto supone una elevada inversión de tiempo y es difícil de estandarizar. Los procedimientos automáticos, que son más rápidos y fáciles de integrar en un Sistema de Información Geográfica, pueden producir modelos altamente explicativos que ajustan bien los datos usados en la construcción del modelo, pero no predicen necesariamente mejor en un conjunto independiente de observaciones. Por el contrario, los modelos supervisados pueden incluir más frecuentemente relaciones causales y, por tanto, podrían extrapolarse mejor a otras áreas. En este trabajo generamos modelos predictivos del hábitat para la presencia/ausencia de 10 especies de aves en dos áreas de Andalucía (SO España), con el fin de comparar tres procedimientos de selección de predictores, que van desde uno automático a otro completamente supervisado (tipos de modelos), y comprobamos su capacidad discriminativa en tres escenarios de evaluación: (1) en el mismo conjunto de datos usado para construir los modelos, (2) en un conjunto de datos diferente (remuestreado) y (3) en datos de un área geográfica diferente. Los modelos automáticos alcanzaron una capacidad discriminativa significativamente mayor, según AUC y Kapa, sólo cuando se evaluaron con los datos de construcción. El resto de combinaciones entre tipo de modelos y escenarios de evaluación no mostraron diferencias significativas, aunque los modelos automáticos tendieron a resultar ligera pero no significativamente peores que los supervisados cuando se evaluaron con datos de un área geográfica diferente. Destaca el hecho de que la capacidad predictiva, medida a través de las estimas de discriminación en datos remuestreados, no difirió entre los distintos tipos de modelo. En conclusión, la incorporación de opinión de experto en la modelización (al menos en la forma que empleamos) no genera modelos con mayor capacidad predictiva. Por tanto, los procedimientos automáticos para construir modelos predictivos del hábitat parecen un medio eficaz y rentable para crear mapas de adecuación del hábitat en un contexto regional.

CHAPTER III: Does expert opinion increase the predictive ability of environmental models of bird distribution?

ABSTRACT

Predictive habitat modeling for conservation and planning is facilitated by automatic procedures for the selection and transformation of variables to be included into the models. Empirical predictive models have been claimed to potentially benefit from the inclusion of expert opinion in different stages of the model-building procedure, although this is a time-consuming task difficult to standardize. Automated procedures, faster and easier to integrate into a Geographic Information System, may render highly explanatory models that fit well the data used to build the model but not necessarily predict so well independent observations. On the contrary, supervised models may include more frequently causal relationships and, therefore, they may extrapolate better to other areas.

We built predictive habitat models for the presence/absence of 10 bird species in two areas of Andalusia (SW Spain) to compare three different kinds of procedures for predictor selection, ranging from a completely unsupervised to a fully supervised method (model types), and tested their discrimination ability in three evaluation scenarios: (1) on the same data used to build the models, (2) on a different (resampled) evaluation data set and (3) on data from a different geographic area. Unsupervised models had a significantly greater discrimination ability, in terms of both AUC and Kappa, only when evaluated with building data. Other model type-evaluation scenario combinations did not show significant differences, though unsupervised models tended to perform slightly but not significantly worse than supervised models when evaluated with data from a different geographic area. Notably, predictive ability, as measured by discrimination estimates on resampled data sets, did not differed between model types. To conclude, incorporating expert opinion in the model building, in the way we have done, does not render better models measured by their predictive ability. Therefore, unsupervised fitting procedures for building predictive habitat models seems an adequate cost-effective way to proceed when aiming to generate habitat suitability maps in a regional context.

INTRODUCTION

Predictive habitat models are increasingly being used to assess species distribution in both conservation and regional planning (Guisan & Zimmermann 2000; Pearce *et al.* 2001). This is mainly because statistical models of distributional data allow to benefit the most from wildlife surveys (Nicholls 1989), which is particularly relevant when distribution data are scarce or when areas are remote (Osborne & Tigar 1992; Bustamante *et al.* 1997; Manel *et al.* 1999). These models can be built with many different purposes. When the aim is generating distribution or habitat suitability maps for a big number of species that can be used for reserve selection or conservation planning, the predictive accuracy of the models is the most relevant indicator of model success, while standarization and automated model building are frequently desired because of time constrains and the need of implementing easily the models into a GIS to generate final maps (Guisan, Weiss & Weiss 1999).

Predictive habitat modeling is habitually tackled with regression-like approaches, among which logistic regression outstands due to its suitability to model a binary variable such as presence/absence (see a review in Guisan and Zimmermann 2000). In these common cases, a response variable —say the presence/absence of the species in an area— is related to a number of predictors with some suspected discrimination ability, and selection is done among them (however, some authors advocate to prespecify model complexity so avoiding this second part, see Steyerberg *et al.* 2000; Harrell 2001). In regression modeling, on one hand, the choice of predictors may be automated by full forward or backward algorithms designed to satisfy statistical criteria. Automated procedures are desirable because of both their quickness and easiness to standardize, but they are argued to incorporate spurious variables to the model when predictors are not totally independent —a very likely situation— (James & McCulloch 1990; Mac Nally 2000). On the other hand, supervised procedures to select among predictors may lead to models that are more credible, for example, by excluding or modifying relationships that do not meet some biological criteria; unfortunately this can be a tedious task and may result in overoptimistic estimates of model performance (Harrell 2001). Therefore, choosing one of the two selection procedures outlined above raises a possible conflict between the easiness to built a model and its credibility; a conflict which address is of prime importance in conservation and planning. Currently, the limited work on comparing models built with the two procedures of predictors selection suggests that pure statistical models, without supervision, can be as good as those built with expert opinion (Pearce *et al.* 2001). However, it can be expected that the relative performance of both kind of models changes in different scenarios of application. For instance, if automated models rely to a greater extent on casual correlations particular to a certain area (or, in a extreme example, if they rely on spureous correlations with unsound predictors), then they should fail when applied to independent data, though they might explain a great amount of the variation observed in the data that were used to build the model (Verbyla & Litvaitis 1989). The reverse may be true for supervised models (Lezzoni 1999). If they rely more on causal relationships (or intended to be causal) they may be expected to apply in a wider arrange of circumstances.

In this work we address the comparison between three different kinds of procedures for predictor selection in predictive species distribution modeling, ranging from a completely unsupervised (automatic stepwise variable selection by statistical software) to a fully supervised method (in which an expert onithologist decided whether statistical significant relations made sense in relation to the ecology of the species). We test the predictive ability of models in three scenarios: (1) on the same data used to build the models, (2) on a different evaluation data set and (3) on data from a different geographic area. The main aim is to explore whether the inclusion of expert opinion in the building of models renders models with a higher predictive ability, or ones that extrapolate better to other areas.

STUDY AREA AND METHODS

The study areas are two 70x70 km squares in Western Andalusia, Southern Spain. We will refer to them as Aracena (center: 6° 21’ W 37° 39’ N) and Grazalema (center: 5° 28’ W 36° 44’ N; Fig. 1). Both areas have roughly the same proportion of cropland (mainly wheat, sunflower and olive groves), shrubland and forests (mainly Mediterranean shrubland, evergreen and cork oak forests and “dehesas”), and similar and numerous human settlements. The areas differ mainly in that Grazalema mountains reach higher altitudes compared to those in Aracena, ranging from 0 to 1622 m.a.s.l. in the first area and from 0 to 960 in the second, and in the soil type: mostly calcareous in Grazalema and mostly acidic in Aracena.

Figure 1. Areas of study

We performed 1144 unlimited distance point surveys during the springs of 1999 and 2000, 521 in Aracena and 623 in Grazalema. We selected 10 species from all registered (172) according to three criteria: (i) they are abundant in both study areas, (ii) they have a variable range of prevalences (defined as the frequency of presences in the sample), and (iii) they are representative of the main landcovers present (cropland, shrubland and forest). The selected species were red-legged partridge *Alectoris rufa* L. (148 presences in Aracena vs 285 presences in Grazalema), linnet *Carduelis cannabina* L. (228 vs 402), short-toed treecreeper *Certhia brachydactyla* C. L. Brehm (306 vs 318), robin *Erithacus rubecula* L. (74 vs 237), Thekla lark *Galerida theklae* C. L. Brehm (170 vs 114), calandra lark *Melanocorypha calandra* L. (64 vs 88), blue tit *Parus caeruleus* L. (352 vs 307), European nuthatch *Sitta europaea* L. (226 vs 124), Sardinian warbler *Sylvia melanocephala* Gmelin (368 vs 620) and wren *Troglodytes troglodytes* L. (76 vs 269). Absences outnumbered presences for every species in both study areas, so to avoid bias due to this fact (Fielding & Bell 1997; Cumming 2000) we randomly selected a number of absences equal to the number of presences for each species in each study area. Sample sizes were similar or higher to those reported in previous works to give reliable estimates of accuracy (Pearce & Ferrier 2000; Stockwell & Peterson 2002).

The predictive variables in the models were a large set of environmental predictors (Table 1) extracted and amalgamated from a GIS of each study area and aimed to summarize most relevant environmental gradients and some landscape features. These predictors included variables descriptive of vegetation, landuse, landscape, topography (resolution 50 meters) and climate (resolution 1 km) that were averaged in a circle of 350 meters diameter centered in survey points. Extraction of variables from the GIS was done using IDRISI 32 (Eastman 1999), IDRISI for Windows (Eastman 1997) and MIRAMON (Pons 2000).

We built a generalized additive model (GAM, Hastie & Tibshirani 1990) for the presence/absence of each species in each study area with binomial errors and logit link using as predictors the environmental variables (Table 1). We built for each species an automatic model with stepwise selection of predictors using exclusively statistical criteria (what we call hereafter *unsupervised model*). First we performed a forward-backward stepwise selection from all possible predictors (with the step.gam procedure of S-PLUS 2000, MathSoft 1999). We started from a null model and tested each predictor sequentially as a smoothing spline with 3 degrees of freedom. The predictor that reduced the most the residual deviance was included in the model and the procedure was repeated until no more predictors improved the model. Then, we tried to simplify the resulting model by decreasing the complexity of each of the predictors included (by means of a smoothing spline with 2 degrees of freedom and a linear term). The criteria to enter, remove or simplify a term was the Akaike's Information Criterion (AIC Sakamoto, Ishiguro & Kitagawa 1986), that takes into account the reduction both in residual deviance and in residual degrees of freedom due to a certain predictor.

Variable description	Species
Mean altitude [a]	1,2,3,4,5,6,7,8,9,10
Mean slope [a]	1,2,3,4,5,6,7,8,9,10
Mean annual temperature [b]	1,2,3,4,5,6,7,8,9,10
Mean annual rainfall [b]	1,2,3,4,5,6,7,8,9,10
Mean annual potential solar radiation [a]	1,2,3,4,5,6,7,8,9,10
Percentage of crop land (crops, olive groves, vineyards) [c]	1,2,5,6,9,10
Percentage of herbaceous vegetation (including cereal crops) [c]	1,6
Percentage of olive groves [c]	-
Percentage of forest (including "dehesas" and open forest) [c]	3,4,7,8,9,10
Percentage of dense forest [c]	3,4,7,8,10
Percentage of deciduous forest [c]	3,4,7,8
Percentage of coniferous forest [c]	3,4,7,8
Percentage of shrub [c]	1,2,4,5,9,10
Percentage of riparian vegetation [c]	4,7,10
Presence of sparse tree cover (for example, included in a heterogeneous crop land area) [c]	6
Presence of dense tree cover (for example, included in a heterogeneous crop land area) [c]	6
Presence of sparse srhub or sparse shrub-like structures (such as vineyards) [c]	5,9
Presence of dense shrub [c]	2,5,9
Length of boundaries between forested landcover categories and the rest of vegetation categories [c]	3,4,6,7,8,9
Length of boundaries between forest and shrubland [c]	2,3,4,7,8,9
Fractal dimension of NDVI values of a satellite image as an index of heterogeneity in croplands [d]	1,6
Compactness ratio of dense forest areas (an indirect estimate of surface-perimeter ratio) [c]	3,4,7,8
Distance to the nearest urban area smaller than 2 ha [c]	-
Distance to the nearest urban area sized between 2 and 10 ha [c]	-
Distance to the nearest urban area sized between 10 and 100 ha [c]	-
The same distances to nearest areas sized <2, 2-10 and 10-100 ha of crop land, herbaceous vegetation, olive groves, forest land, dense forest land, deciduous forest, coniferous forest, shrubland, and riparian vegetation [c]	The same as for percentage of each category

Table 1. Predictors tested in all unsupervised models. The number in the second column indicates for which species each predictor was selected *a priori* in semi- and supervised models: **1** Red-legged Partridge, **2** Linnet, **3** Short-toed treecreeper, **4** Robin, **5** Thekla Lark, **6** Calandra Lark, **7** Blue Tit, **8** European Nuthatch, **9** Sardinian Warbler and, **10** Wren. Sources: **a** Digital Elevation Model of Andalusia at 50 m resolution. **b** raw meteorological data provided by the Instituto Nacional de Meteorología and interpolated by regression models and kriging at resolution 1 km^2 (own data, unpublished), **c** 1995 land-use/land-cover cover digital map of Andalusia from the SinambA (Consejería de Medio Ambiente, Junta de Andalucía). **d** IRS satellite image, sensor LISS III (date: 19/07/99 Aracena, date: 16/07/99 Grazalema). Fractal dimension estimated with IDRISI 32 on a NDVI (Normalized Difference Vegetation Index) image.

We incorporated expert opinion in the building of models in two ways. In the first one we chose the predictors to be submitted to the forward stepwise algorithm for each species according to previous knowledge of habitat selection of the species (see Table 1). For example, we judged appropriate to include the percentage of crop land among the predictors to be tested with calandra lark (but not the percentage of forest). Final model for each species in each area was obtained using a procedure analogous to the one described previously. Predictors were first entered in a forward fashion (ordered by AIC), but then the model was checked after each inclusion dropping those predictors that did not reduce significantly the residual deviance as measured by a Chi-square test (α=0.05%). We call these *semi-supervised models*.

The second way of incorporating expert opinion started from the model resulting from the semi-supervised procedure. In each model we tested transforming one by one the predictors selected by the previous automatic procedure into parametric polynomials, or into linear (or piecewise linear) terms that were sensible, based on our previous knowledge of habitat selection by the species and visual inspection of partial residual plots (Brown 1994; Franklin 1998). Statistically significant relations with environmental predictors that made no sense with species habitat selection and others apparently spurious were excluded from the final model. As miscelaneous examples: curvilinear forms were transformed when possible to quadratic polynomials, in increasing or decreasing relationships with distance to a particular habitat we tested the inclusion of an asymptote (i.e. assuming a constant effect after a certain distance), and a negative relationship with forest for a forest species would have been excluded from the model even if statistically significant. These are called *supervised models*. Therefore for each species and study area we obtained three *model types* with increasing degree of expert opinion invested in their building: unsupervised, semi-supervised and supervised.

To assess the performance of models we used Cohen’s Kappa statistic (Titus, Mosher & Williams 1984) and the area under the curve (AUC) of a receiver operating characteristic plots (ROC, Hanley & McNeil 1982; Murtaugh 1996; Cumming 2000) as measures of discrimination ability. Kappa estimates the chance-corrected percentage of agreement between predictions and observations. To calculate Kappa it is necessary to define a threshold of predicted probability above which to consider presence (Fielding & Bell 1997), and this was selected to be the average between the mean of probabilities for absences and the mean for presences (Fielding & Haworth 1995). The AUC is a threshold-independent measure of discrimination ability (Zweig & Campbell 1993), and it is not affected by prevalence of presences in the sample (Manel, Williams & Ormerod 2001); thus, it is considered to be better than kappa. However, AUC has only been recently used in ecology (Fielding & Bell 1997; Cumming 2000; Pearce & Ferrier 2000; Bonn & Schröder 2001; Manel, Williams & Ormerod 2001) and it is more complicated to estimate than Kappa, which has been widely used in previous works. Thus, we used here the two indices as a way of comparison. AUC was calculated with AccuROC 2.5 (Vida 1993).

Kappa and AUC were calculated for the three model types (supervised, semi-supervised and unsupervised) in three scenarios of evaluation according to an increasing degree of independence between the data used to build the model and the data used to evaluate it: (i) *building scenario*: with the same data used to build the model, (ii) *crossvalidation scenario*: with a ten-fold crossvalidation data repeated 20 times and (iii) *extrapolation scenario*: with data of the same species but from the other study area. The first is a evaluation (Oreskes, Shrader-Frechette & Belitz 1994) that tends to render overoptimistic estimations of discrimination ability, but it may be used both as a maximum reference of explanatory ability of the model and to informally assess the amount of overoptimism in the estimates by comparison with the predictive ability in the *crossvalidation scenario* (moreover it is the only one presented in many research papers). This type of evaluation informs about the *explanatory* ability of the model. The second evaluation is an internal validation that follows one of the variety of resampling approaches most frequently used (this one according to Harrell 2001): data is split in 10 groups of equal size, a model is built using the data of the first nine groups (90% of observations) and evaluated using the data of the tenth group (10% of observations, those not used to build the model); the procedure is repeated ten

Variable	Df	SS	MS	F-value	P-value
Model type	2	0.089	0.045	6.396	0.002
Evaluation scenario	2	1.078	0.539	77.357	0.000
Study zone	1	0.030	0.030	4.275	0.040
Model type*evaluation scenario	4	0.112	0.028	4.010	0.004
Model type*study area	2	0.017	0.008	1.208	0.302
Evaluation type*area	2	0.007	0.004	0.512	0.601
Model type*evaluation scenario*study area	4	0.020	0.005	0.725	0.576
Residuals	162	1.129	0.007		

Table 2. Results of ANOVA of the effect of model type (unsupervised, semi-supervised and supervised), evaluation scenario (building, crossvalidation and extrapolation) and study area (Aracena and Grazalema) on model discrimination ability estimated by AUC.
Interactions marked by asterisks.

Variable	Df	SS	MS	F-value	P-value
Model type	2	0.441	0.221	7.989	0.001
Evaluation scenario	2	3.680	1.840	66.593	0.000
Study area	1	0.152	0.152	5.484	0.020
Model type*evaluation scenario	4	0.499	0.125	4.511	0.002
Model type*study area	2	0.061	0.031	1.108	0.333
Evaluation type*study area	2	0.018	0.009	0.325	0.723
Model type*evaluation scenario*study area	4	0.058	0.014	0.523	0.719
Residuals	162	4.476	0.028		

Table 3. Results of ANOVA of the effect of model type, evaluation scenario and study area on model discrimination ability estimated by Kappa. Interactions marked by asterisks.

times using each group as evaluation set and the remaining nine as building set. This ten-fold crossvalidation was repeated 20 times resuffling the data in each group. The predictors included in the models were the ones resulting from the previously described fitting procedures (*model types*) and only new coefficients were adjusted with the building set. The result is an unbiased estimate of the predictive ability of the model within its universe of application. Finally, the third is an external validation (Harrell 2001) used to assess a model outside the universe where it is statistically valid: the model is applied to a new scenario different from the one where it was built; it evaluates the transferability of the model (Altman & Royston 2000; Bonn & Schröder 2001). From an statistical point of view there is no particular interest in estimating the predictive ability of a model in a universe different from which it was built, but, in real practice, predictive habitat models are frequently built expecting that they will have certain predictive ability when transfered in time (in the future) or in space (to remote areas).

Differences in predictive (discrimination) ability among models due to differences in *model type*, *evaluation scenario*, and *study area* were analyzed with a factorial ANOVA of AUC and Kappa values of models. Pairwise differences of means between factor levels were assessed with 95% simultaneous confidence intervals and the Tukey test. We do not discuss other measures of predictive performance of models such as calibration and refinement (Pearce & Ferrier 2000).

RESULTS

Models better than a null model were built for every species and for each combination of model type, evaluation scenario and study area. Unsupervised models included a significant ($F_{2,57}$=48.38, P<0.0001) higher number of predictors (mean=9, sd=4.5) than both semi-supervised (mean=3, sd=1.1) and supervised (mean=4, sd=1.3).

The estimates of discrimination ability, both AUC and Kappa (Tables 2 and 3), were affected significantly by the model type (AUC: $F_{2,162}$=6.40, P=0.002; Kappa: $F_{2,162}$=7.99, P=0.001), the evaluation scenario (AUC: $F_{2,162}$=77.36, P<0.0001; Kappa: $F_{2,162}$=66.60, P<0.0001), and the interaction model type-evaluation scenario (AUC: $F_{4,162}$=4.01, P=0.0040; Kappa: $F_{4,162}$=4.51, P=0.002). There was also a slightly significant effect of the study area (AUC: $F_{1,162}$=4.28, P=0.040; Kappa: $F_{1,162}$=5.48, P=0.020).

As expected, AUC and Kappa estimates were always higher in the evaluation with building data than in the crossvalidation or in the extrapolation (in this order), ranging from a maximum of AUC=0.95 (SE=0.01) and Kappa=0.78 (0.03) in unsupervised models evaluated with building data, to a minimum of AUC=0.68 (0.02) and Kappa=0.26 (0.04) in unsupervised models evaluated with extrapolation data. This change in discrimination ability of unsupervised models is responsible for the significant interaction detected between model type and evaluation scenario (Fig.2). Unsupervised models had significantly greater discrimination ability, both in terms of AUC and Kappa, when evaluated with building data. In the crossvalidation unsupervised models performed slightly better than supervised ones, but differences were only statistically significant for AUC values between unsupervised and supervised models. In the extrapolation all model types performed poorly (but did not differ significantly), though in this case unsupervised models tended to be the worse. Finally, models built with data from the Aracena zone had greater estimates of both AUC (mean=0.81[SE=0.01]) and Kappa (0.50[0.02]) than models built with data from Grazalema (AUC: 0.78[0.01]; Kappa: 0.44[0.02]).

DISCUSION

Empirical models are typically used in three scenarios. First, they can be used to summarize the information that was used in their building, that is, *to explain* the pattern in data (e.g. Mac Nally 2000). Second and more common, models are used *to predict* a response given a new data set, with values of the predictors that must be in the range observed in the original data (a review in Guisan & Zimmermann 2000). Third, models may be used *to extrapolate* to spatial areas (or temporal contexts) different from the ones in which they were built (Schröder & Richter 1999/2000; Bonn & Schröder 2001). Extrapolating in a diferent spatial or temporal context may be called into question as models may not behave as expected outside the universe of their construction. Therefore extrapolation (or forecasting, Morrison, Marcot & Mannan 1998) is better suited to causal models, while prediction (or hindcasting, Morrison, Marcot & Mannan 1998) is the only result one can expect with a certain degree of reliability from correlational models .

Whatever the scenario, empirical models may potentially benefit from expert opinion incorporated in some of the stages in the process of model building: pre-modeling, in which original variables are synthesized or transformed, model-fitting, when a subset of potentially explanatory

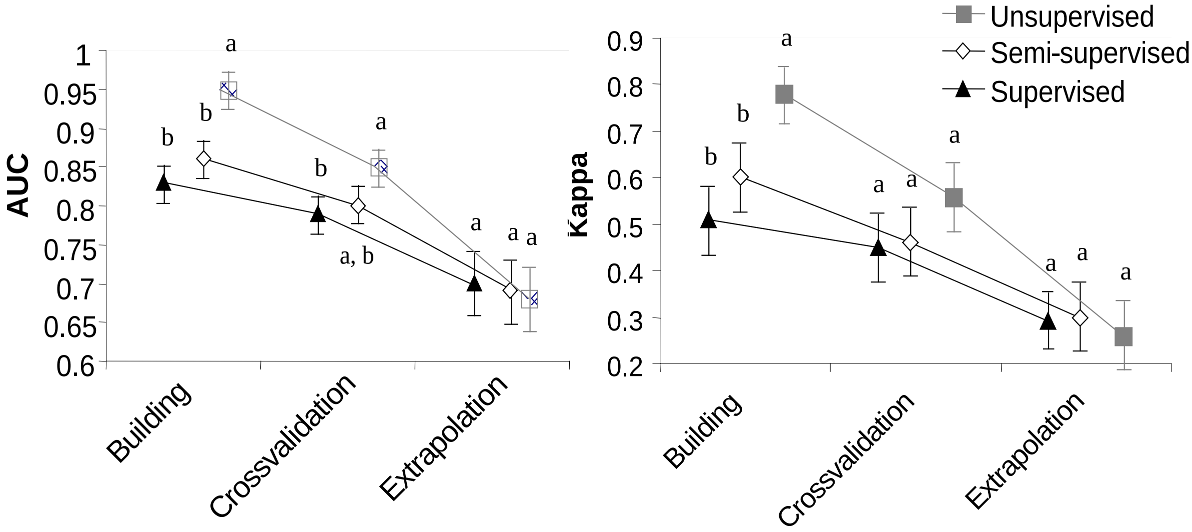

Figure 2. Mean values (and bars for 95% confidence intervals) of estimates of discrimination ability for each combination of evaluation scenario and model type. Superscript letters show comparisons of model type values within each evaluation scenario: same letters for unsignificant differences (95% simultaneous confidence intervals and Tukey test).

variables is selected from the original set, and post-modeling stage, in which purely statistical relationships between response and predictors are modified to satisfy biological criteria (Pearce *et al.* 2001). Completely unsupervised models would not receive expert opinion in any of these stages. Admittedly, our unsupervised models incorporate, in fact, some degree of expert opinion because the explanatory variables derived from the thematic digital cartography were selected and amalgamated in the pre-modeling stage looking for the potential relevance played on predicting bird distribution. However, the distinction that we make here between unsupervised, semi- and supervised models reflects a common situation very relevant to predictive habitat modeling practitioners: in most cases a large pool of potential predictor variables must be reduced or synthesized before modeling, in particular when dealing with vegetation. After that compulsory step (that does not seem to affect final model accuracy, according to Pearce *et al.* 2001), what must be considered is to automate or not the process of selecting predictors and modifying their functional forms according to expert opinion.

On one hand, the unsupervised building of models—by stepwise selection of predictors according to statistical criteria in our study—is relatively fast and may be easily integrated in wider protocols than involve further modeling or manipulation in a GIS (Guisan, Weiss & Weiss 1999). However, this approach is criticized because it tends to incorporate to the model spurious predictors or variables difficult to interpret (Mac Nally 2000; Steyerberg *et al.* 2000; Harrell 2001). On the other hand, supervised procedures may draw relationships more credible, but they are usually highly time-consuming, difficult to standardize and very susceptible to overestimate the statistical significance of the predictors (Chatfield 1995; Harrell 2001). Supervised models are expected to have a greater predictive ability than unsupervised models because of a thoughtful selection of predictors that dismiss relationships particular to a certain set of data or, simply, spurious. They should also be able to extrapolate with a lower loss in accuracy, because it is expected that supervised model will include more frequently causal relationships between birds and their habitats and less spurious correlations.

Indeed, our results suggest that the predictive performance of unsupervised models is acceptable, being as good or better than that of supervised models (at least in what concerns discrimination ability). Unsupervised models have a good explanatory power (as measured by the estimates of discrimination ability on building data), and the same medium predictive power than supervised models (as given by estimates of crossvalidation evaluation). A high explanatory power was partially expected because of the well known effect of predicting on the own building data. We think that this effect may have been exacerbated in our case, since we entered the predictors as complex non-linear smoothed terms that captured the particularities of each study area. Furthermore, the unsupervised models may have a higher explanatory power due to their generally longer list of predictors, which is a consequence of using the somewhat lenient AIC as the criterion to enter or keep predictors (Ludden, Beal & Sheiner 1994; Chatfield 1995; Burnham & Anderson 1998). A few of the variables included in unsupervised models had a difficult interpretation or one opposite to what was expected according to previous knowledge of habitat selection (for example, the probability of presence of Red-legged Partridge increasing with distance to small croplands); these variables could be spurious or just particular to a set of observations, and, if present, were disregarded in the supervised models.

The predictive ability of the three model types (as measured on crossvalidation data) was similar. Although, the results showed a trend towards higher values of discrimination estimates for the unsupervised models; this suggest that some of the variables disregarded in the model-fitting stage had in fact some predictive power, at least at the resolution of our study. Models would correctly classify about 8 in 10 pairs of presence/absence observations (Hanley & McNeil 1982), which is a medium result according to the standards posed by several authors (Monserud & Leemans 1992; Fielding & Bell 1997; Pearce & Ferrier 2000) that suggest to consider the model discrimination ability to be poor when Kappa is below 0.4 (or AUC below 0.7), fair when it is between within 0.4 and 0.7, and good for values greater than 0.7 (AUC above 0.9). However, the values reported in this study are similar to what is commonly found in the wildlife-modeling literature (Manel, Dias & Ormerod 1999; Tobalske & Tobalske 1999; Cumming 2000; Bonn & Schröder 2001), what may reflect a limit in the accuracy of empirical models based on indirect variables (Guisan & Zimmermann 2000) to predict a response at a high spatial resolution (Fielding & Haworth 1995; Manel, Dias & Ormerod 1999; Rico Alcázar *et al.* 2001).

Finally, the discrimination ability of the models evaluated with external data was rather low (though it was significantly better than that of a null model in all cases), what imply that the transferability to neighbouring areas of our models, of either type, is deficient. Our study zones are geographically close and similar in topography, climatology and landscape, at least at the coarse level of variation measured by the variables taken and amalgamated from the tematic cartography used in this work, so we had expected a higher success in the extrapolation of models. This failure may be due to unmodeled historical factors or local processes, such as intra- and interespecific interactions, that adjust finely the habitat distribution of organisms. Currently this factors constitutes an unsolved problem in wildlife-habitat relationship modeling.

To conclude, incorporating expert opinion in the model building in the way we have done is very time-consuming and does not render better models if we consider their predictive ability. Even when extrapolated to neighbouring areas models benefitting from expert opinion do not outperform pure unsupervised models. Considering all this, unsupervised fitting procedures for building predictive habitat models seems an adequate cost-effective way to proceed if the aim is generating habitat suitability maps in a regional context.

ACKNOWLEDGEMENTS

This work is a contribution to the Project “Predictive cartography of land birds: A pilot study in Western Andalusia”, funded by the Dirección General de Enseñanza Superior e Investigación Científica (Ministry of Science and Technology) and FEDER funds from the EU, project # 1DF-97-0648. During the work, J.S. had a predoctoral fellowship from the Ministry of Education and Culture. The extensive field work presented in this paper could not have been done without the help and sense of humour of Daniel López Huertas, Luis M. Carrascal, and

Mario Díaz who also brought intellectual insight to the project.

NOTES

A version of this manuscript, coauthored with J.Bustamante and R.Díaz-Delgado has been submitted to *Conservation Biology*.

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CAPÍTULO IV: ¿Son adecuados los mapas de vegetación existentes para predecir la distribución de las aves?

RESUMEN

Las especies de aves seleccionan los tipos de vegetación en los que se hallan; sin embargo, los modelos predictivos de la distribución de aves que se basan en variables derivadas de mapas de usos y cubiertas del suelo tienen un éxito limitado. Se ha sugerido que la precisión de los mapas disponibles que se usan para derivar predicciones es responsable en parte de ese éxito limitado de los modelos de distribución. En este trabajo se compara la capacidad predictiva de modelos de distribución de aves derivados de dos mapas de usos y cubiertas del suelo, cuyo diseño se hizo con un propósito general y que difieren en su resolución y precisión: un mapa de vegetación de Europa poco detallado (mapa de cubiertas del suelo del CORINE) y un mapa regional minucioso (mapa de 1995 de cubiertas y usos del suelo del SINAMBA, Consejería de Medio Ambiente, Junta de Andalucía). El área de estudio son dos cuadrados de 4900 km^2 en Andalucía occidental (España). Se comparan los modelos de distribución de aves que se derivan de estos mapas de propósito general con otros derivados de dos o más atributos estructurales de la vegetación, que se construyeron prestando especial atención a las variables que influyen la selección del hábitat en aves. Uno se construyó con imágenes de satélite para este estudio, mientras que el otro se obtuvo mejorando la resolución y precisión del mapa del SINAMBA con datos de satélite. Se muestreó la presencia/ausencia de especies de aves en 857 puntos usando estaciones de escucha de 15 min. Se construyeron modelos predictivos para 54 especies de aves como modelos aditivos generalizados (GAM), usando como predictores potenciales un conjunto de variables paisajísticas y de estructura de la vegetación medidas en cada mapa. Para cada especie se comparó la capacidad predictiva del mejor modelo que se derivó de cada mapa. Las medidas estructurales de la vegetación medidas en los puntos de muestreo se usaron como “verdad-terreno” (es decir, como referencia) para comparar la precisión de los mapas de vegetación. Los resultados muestran que sólo el mapa de cubiertas del suelo de CORINE (el más grosero) produjo modelos significativamente peores, aunque todos los mapas difirieron en su resolución y precisión. Los modelos derivados de los mapas detallados de la estructura de la vegetación que se obtuvieron de los datos de satélite no fueron mejores que aquellos

que se derivaron directamente del mapa del SINAMBA. Nuestros resultados sugieren que algunos mapas de usos y cubiertas del suelo, diseñados para satisfacer un propósito general, son suficientemente precisos para derivar buenos modelos de la distribución de aves, y que existe un cierto límite a la posibilidad de mejorar un mapa por encima del cual no hay efecto sobre el poder que tienen las variables de la vegetación para predecir la distribución de las aves.

CHAPTER IV: Are existing vegetation maps adequate to predict bird distributions?

ABSTRACT

Bird species are selective on the vegetation types in which they are found but predictive models of bird distribution based on variables derived from land-use/land cover maps tend to have limited success. It has been suggested that accuracy of existing maps used to derive predictors is in part responsible for the limited success of bird distribution models. In two areas of 4900 km^2 of Western Andalusia, Spain, we compared the predictive ability of bird distribution models derived from two existing general-purpose land-use/land-cover maps, that differ in their resolution and accuracy. A coarse scale vegetation map of Europe, the CORINE land-cover map, and a detailed regional map, the 1995 land-use/land-cover map of Andalusia from the SINAMBA (Consejería de Medio Ambiente, Junta de Andalucía). We compared the bird distribution models derived from these general-purpose vegetation maps with models derived from two more accurate structural vegetation maps built considering directly variables that influence bird habitat selection. One built from satellite images for this study and another obtained by improving the resolution and accuracy of the SINAMBA map with satellite data. We sampled the presence/absence of bird species at 857 points using 15-min point surveys. Predictive models for 54 bird species were built with Generalised Additive Models, using as potential predictors a set of landscape and vegetation structure variables that was measured on each map. We compared for each bird species the predictive accuracy of the best model derived from each map. Vegetation structure measured at bird sample points was used as ground-truth for comparing the accuracy of vegetation maps. The results show that, although maps differed in their resolution and accuracy only the less accurate map, the CORINE land-cover map, produced significantly worse bird distribution models. The models derived from the more accurate vegetation structure maps obtained from satellite data were not more accurate than those derived directly from the SINAMBA map. Our results suggest that some general-purpose land-use/land-cover maps are accurate enough to derive good bird distribution models, and that there is a certain limit to map improvement above which there is no effect in the power of vegetation variables to predict of bird distribution.

1. INTRODUCTION

Bird species are selective on the vegetation types in which they inhabit (Cody 1985). It is considered that the vegetation holds a great predictive potential for the distribution of birds, and several ongoing projects are using vegetation types to map potential distribution of bird species, for example the GAP project in USA (Scott *et al.* 1993), or are using vegetation variables to build predictive models of bird distribution (Pearce & Ferrier 2000). Statistical models of bird distribution using as predictors variables derived from vegetation are rarely able to explain perfectly observed distributions. There are several possible reasons for this fact (Fielding & Bell 1997; Beutel, Beeton & Baxter 1999): (a) Statistical reasons (e.g. when using logistic regression to model presence/absence data the predicted values are in a continuous scale from 0 to 1 while observed data are discrete presences and absences). (b) Historical reasons (e.g. an species has not occupied all potential adequate habitat because of geographical barriers, or because it has been extirpated by man from otherwise suitable habitat). (c) Unsaturated habitats (small populations are not able to occupy all suitable habitats, but also demographic stochasticity and localized dispersal generate an imperfect correlation between habitat suitability and species distribution Tyre, Possingham & Lindenmayer 2001). (d) Poor quality of the response variable (e.g. an inadequate census method for a species difficult to detect may render a distribution pattern of observed presences that does not reflect the real pattern of distribution or abundance). (e) Poor quality of the predictive variables (e.g. when the predictors we are measuring are not adequate to explain the distribution of the species or they are measured with too much error Guisan & Zimmermann 2000).

Land-use/land-cover or vegetation maps can be used as the source of predictive variables in statistical models of the distribution of bird species (Tobalske & Tobalske 1999; Guisan & Zimmermann 2000; Pearce & Ferrier 2000). Maps are themselves models of reality and as such they are always a simplification. Available vegetation maps may not represent adequately the vegetation variables relevant for the species of bird whose distribution we want to predict, or may have not the adequate spatial resolution (Pearce *et al.* 2001). We may be able to measure directly at bird sampling points those vegetation variables that an expert on the species would consider more relevant, but the final model obtained will not be useful to map the potential habitat for the species if the maps of these vegetation variables are not available. Vegetation, land use and land cover maps are currently built by governmental agencies at different resolutions and for different purposes. Existing environmental maps are cheap predictors for mapping potential habitat for birds while the best potential predictors we might think about may never be mapped. On the other hand, remote sensing is a potential tool for mapping the vegetation variables that we might consider more relevant for the distribution of a species of bird (Palmeirin 1988; Avery & Haines-Young 1990; Franklin & Steadman 1991; Andries, Gulinck & Herremans 1994; Paruelo & Golluscio 1994; Wu & Strahler 1994; Roy, Sharma & Jain 1996; Trodd 1996; Ormerod & Watkinson 2000). Remote sensing imagery *sensu lato* (airborne sensors, aerial photography and satellite images) is the tool most widely used nowadays to create new land cover maps (CORINE project in Europe, MIOMBO project in Southern Africa, etc.), to improve thematic maps accuracy (Stehman 1996), or final map spatial resolution (Defries & Belward 2000).

In this paper we compare the capacity to predict the distribution of 54 species of birds of variables derived from two existing vegetation maps (a coarse scale vegetation map of Europe and a more detailed regional land use/land cover map), a vegetation map derived from satellite data, and a vegetation map obtained by improving the accuracy of the existing regional map with satellite data. It has been suggested that higher accuracy and resolution of input maps is necessary to improve predictions of plants and animal distributions models (Guisan & Zimmermann 2000). As we were more interested in the effect of map accuracy in predictive capacity than in the potential of different maps to measure different predictors we measured the same set of predictors in all vegetation maps.

2. STUDY AREA AND METHODS

We performed 1144 unlimited-distance bird point surveys in two 70x70 km squares in Western Andalusia, Southern Spain (centres: 6° 21’ W 37° 39’ N, and 5° 28’ W 36° 44’ N), during the springs of 1999 and 2000 (Fig. 1). Both areas have a similar proportion of different land-cover types and have approximately 20% of cropland (mainly wheat, sunflower and olive groves), 70% of scrubland and forests (mainly Mediterranean scrubland, evergreen oak *Quercus rotundifolia* and cork oak *Q. suber* forests and “dehesas” open oak forest with pastures). At each survey point the presence/absence of breeding bird species was recorded during 15 minutes. For subsequent modelling, we selected 857 points in natural and seminatural areas (that means, excluding those in agricultural and urban areas), and we selected 54 bird species that appeared in more than 5% of these sampling points.

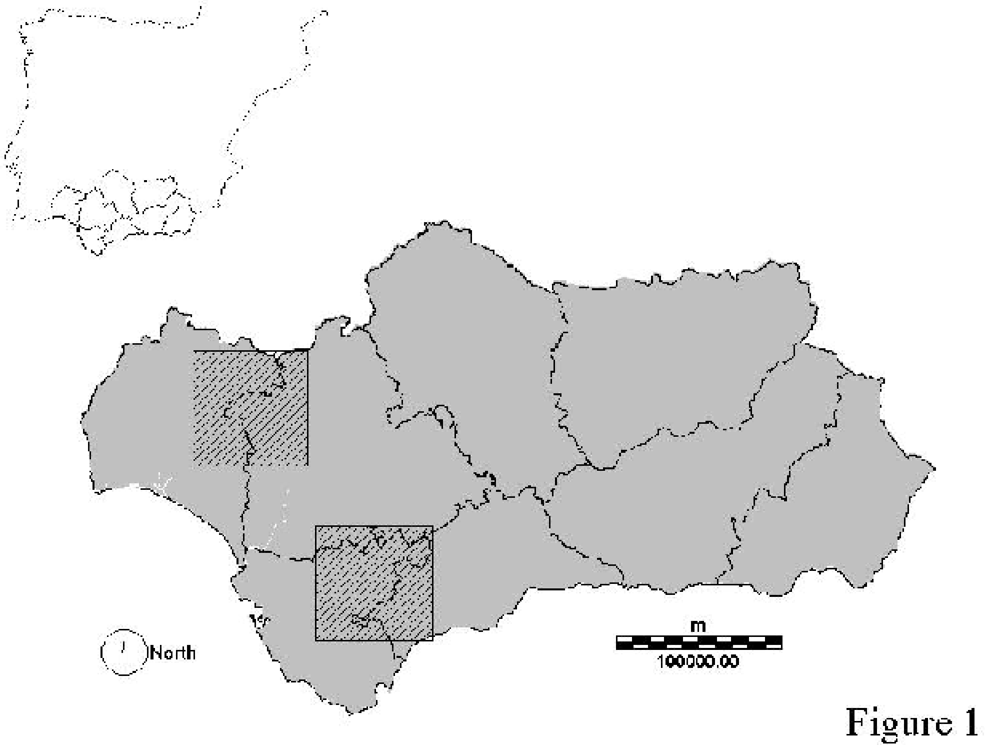

Figure 1.- Location of study areas.

2.1. *Vegetation maps*

We used seven different vegetation maps of each study area to derive the predictive variables to model bird distribution: Three of them were independent vegetation maps: 1) CORINE land cover map of Europe from the European Environmental Agency (CORINE_250). Original data in raster format at 250 m resolution (v.12/1989) were obtained from the European Topic Center on Land Cover, Kiruna, Sweden. The CORINE map legend has 44 land cover classes for the whole Europe. Source data correspond nominally to the period 1989-91. 2) The SinambA land use/land cover digital map of Andalusia (SINAMBA_50) from the Environmental Department of the Junta de Andalucía. Original data in vector format were rasterised to 50 m resolution. The map legend has 112 classes. Source data correspond nominally to 1995. 3) A vegetation structure map derived from satellite images from 1999 and 2000 (SATELLITE_30, see below for details). Original data were in raster format at 30 m resolution and consisted of two maps in a continuous scale: degree of tree cover and degree of shrub cover. We generated another vegetation map 4) by combining information of SINAMBA map and satellite images (MIXED_30). This map at 30 m resolution consisted also in a tree cover and a shrub cover map and had a significantly greater accuracy than SATELLITE_30.

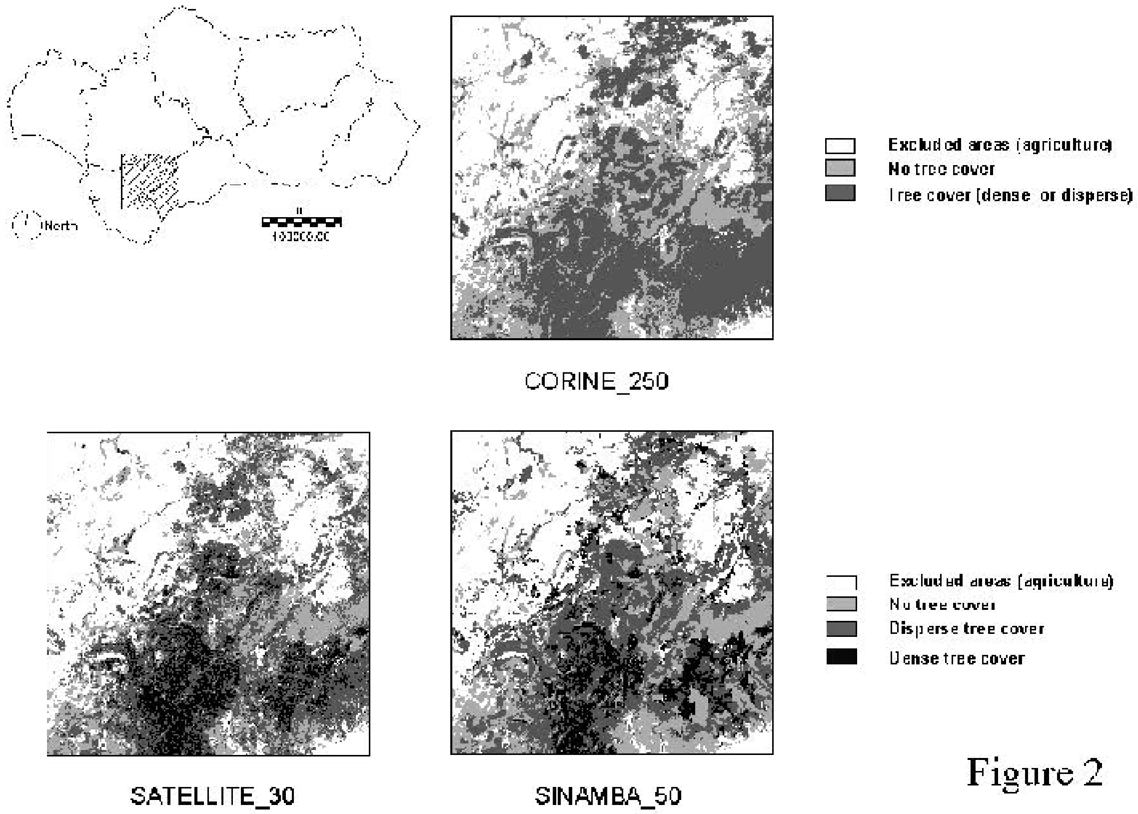

Figure 2.- Tree cover coverages from the CORINE_250, SINAMBA_50 and SATELLITE_30 maps for one of the study areas.

To test whether differences in predictive accuracy were due to differences in data quality, predictors used, or map resolution we generated another three maps: 5) SINAMBA_250 was obtained resampling the SINAMBA_50 map at 250 m resolution. 6) SINAMBA_250R was also obtained by resampling the SINAMBA_50 map at 250 m resolution but then using only the reduced set of predictors that could be measured in CORINE_250. 7) SATELLITE_50 was generated by resampling the SATELLITE_30 map at 50 m, the same resolution as SINAMBA_50.

In each vegetation map the original legend categories (or the values in a continuous scale) were reclassed into three categories of shrub cover and three categories of tree cover: 1) no cover, 2) disperse cover, and 3) dense cover (Fig. 2). With the help of a GIS we derived from each vegetation map at each bird survey point the set of vegetation structure and landscape predictors indicated in Table 1. These predictors included variables descriptive of vegetation structure in a circle of 350 m diameter centred in the bird survey point and variables indicating distances to landscape features of different sizes. The same predictors were measured in each map with a few exceptions. The CORINE_250 map legend did not distinguish clearly between disperse and dense tree cover and between disperse and

Table 1. List of variables measured in each map and used in the initial sets of potential predictors of bird distribution models.

Variable description
Shrub cover fraction [+]
Forest cover fraction (including dense and disperse forest categories like “dehesas”)
Dense forest fraction *
Length of boundaries between forested landcover categories and the rest of vegetation categories *
Length of boundaries between forest and shrubland
Compactness ratio of dense forest areas (an indirect estimate of surface-perimeter ratio) *
Presence/absence of disperse tree cover (for example, included in a heterogeneous shrubland area) *
Presence/absence of dense tree cover (for example, included in a heterogeneous shrubland area) *
Presence/absence of disperse shrubland (for example in areas dominated by forest) *
Presence/absence of dense shrubland (for example in areas dominated by forest) *
Distance to the nearest patch of shrubland (dense or disperse) [++]
Distance to the nearest patch of forest (dense or disperse) [++]
Distance to the nearest patch of dense forest [* ++]

[+] Variable values are estimated in a circle of 350 m radius centered in bird point surveys.For example, shrub cover fraction is the fraction of 30 or 50 m pixels in the circle that have dense or disperse shrub cover (In maps of 250 m pixel resolution the value can only be 0 or 1).

[*] Variables that could not be measured in the CORINE_250 map and consecuently were also excluded as potential predictors in the SINAMBA_250R models.

[++] Each distance was 4 variables: (1) distance to the nearest patch of any size, (2) distance to the nearest patch 2-10 ha. in size, (3) distance to the nearest patch 10-100 ha. in size, (4) distance to the nearest patch > 100 ha.

dense shrub cover in its legend, and some predictors involving these variables could not be measured (see Table 1). For this reason we generated the SINAMBA_250R map that had the same predictors as CORINE_250. Also, a few predictors changed their range of possible values when measured at 250 m resolution.

Extraction of variables from the GIS was done using IDRISI 32 (Eastman 1999), IDRISI for Windows (Eastman 1997) and MIRAMON (Pons 2000).

2.2. *Vegetation maps derived from satellite data*

At each bird survey point the observer recorded structural attributes of vegetation that we had considered *a priori* important for bird distribution (Table 2). We performed a Principal Components Analysis (PCA) on these structural variables (excluding the survey points in agricultural or urban areas). The two first components explained 32.9 and 23.2 % respectively of the original variance (a total of 56.2%). The first component defined a gradient of tree cover (high loads for variables: Mean tree DBH, and cover of trees > 6m high). The second component defined a gradient of shrub cover (high positive loads for variables like cover of shrubs < 0.50 m tall, and cover of shrubs 0.5 to 2m tall, and high negative load for cover of herbaceous vegetation). Then we used the first two components of the PCA as the response variable in a generalised additive model (GAM, Hastie & Tibshirani 1990) with normal errors and identity link. We used as predictors reflectance values of bands 1 to 7, and NDVI of three Landsat scenes (TM and ETM+) for each study area corresponding to early spring, mid spring and summer of the years 1999 and 2000. Images were geometrically corrected with the aid of a Digital Elevation Model (Palà & Pons 1995) and radiometrically calibrated according to Pons and Solé-Sugrañes model (1994). GAM models (J. Bustamante and R.Díaz-Delgado, unpub. data) explained 37-40 % variance of the tree cover gradient (each study area respectively) and 21-30 % variance of the shrub cover gradient. GAM models predicted tree cover and shrub cover values in a continuous scale (0-255) for each 30 m pixel in the study area. We selected cut-points in this gradient to recode tree and shrub cover in three classes (no cover, disperse cover, and dense cover), so that surface covered by each tree cover and shrub cover class was as close as possible to that of the SINAMBA_50 map. The resulting coverages defined the SATELLITE_30 vegetation map. The tree cover models and shrub cover models improved significantly if the land-use/land-cover class of the SINAMBA map at the location of each sampling point was included as a factor. We refitted the GAM models for the tree cover and shrub cover gradients of each study area using the SINAMBA class as a factor , satellite reflectance values and NDVI values. These new GAM models explained 55-56 % of the variance in tree cover and 26-49% of the variance in shrub cover. The gradients were reclassified to three discrete classes and generated the MIXED_30 map.

2.3. *Predictive models for birds*

We built a generalised additive model (GAM, Hastie & Tibshirani 1990) for the presence/absence of each species in each study area with binomial errors and logit link using as predictors the variables in Table 1. Seven models were generated for each bird species with the predictors derived from each one of the seven vegetation maps. We selected the variables to include in the models with a forward-backward stepwise selection from the complete set of predictive variables measured from each map (with the step.gam procedure of S-PLUS 2000, MathSoft 1999). We started from a null model and tested each predictor sequentially as a smoothing spline with 3 degrees of freedom. The predictor that reduced the most the residual deviance was included in the model and the procedure was repeated until no more predictors improved the model. Then, we tried to simplify the resulting model by decreasing the complexity of each of the predictors included (by means of a smoothing spline with 2 degrees of freedom and a linear term). The criteria to enter, remove or simplify a term was the Akaike's Information Criterion (AIC Sakamoto, Ishiguro & Kitagawa 1986), that takes into account the reduction both in residual deviance and in residual degrees of freedom due to a certain predictor. Automatic procedures for selection of predictors have been criticised because they can yield ecologically implausible models (Greenland 1989; James & McCulloch 1990); but it is a method that allows for rapid development of models (Pearce & Ferrier 2000), and it has been shown empirically that frequently perform better than tedious manual selection techniques incorporating opinion of experts (Pearce *et al.* 2001). In our study, the random inclusion of spurious correlations in the predictive models could affect equally the models derived from each map and would not bias the comparition between models.

2.4. *Comparition of predictive accuracy of maps*

The predictive ability of each model was assessed by the Area Under the Curve (AUC) of Receiver Operating Characteristics (ROC) plots (Murtaugh 1996; Pearce & Ferrier 2000). AUC was calculated with AccuROC 2.5 (Vida 1993). The interest of the analysis is in the potential differences in predictive performance of the models generated with different data sources, and not in the absolute values of AUC, therefore we did not evaluate the data with an independent data set. Differences among model types were tested with a repeated measures factorial ANOVA (with an error term due to species to control for the between-species variation, of no interest in this study). Preplanned comparisons (Montgomery 2001) were performed to test differences between particular models.

First we compared the different vegetation maps to see if they differed in their accuracy regarding the structural vegetation classes defined, using as ground-truth the vegetation data measured at the 857 bird survey points. Then we tested if there were differences in predictive accuracy of bird distribution related to the original map source of predictors: CORINE_250, SINAMBA_50 or SATELLITE_30. Then we tested if differences in predictive ability between CORINE and SINAMBA maps were due to differences in: map quality (comparing CORINE_250 vs. SINAMBA_250R), predictors used (SINAMBA_250R vs. SINAMBA_250), or map spatial resolution (SINAMBA_250 vs. SINAMBA_50). Then we tested if there were any differences in predictive accuracy related to a difference in spatial resolution of 50 to 30 m (SATELLITE_30 vs. SATELLITE_50) or if a more accurate vegetation map derived from two sources (MIXED_30) differed in predictive accuracy from the original maps (SINAMBA_50 and SATELLITE_30) .

3. RESULTS

3.1. *Accuracy of vegetation maps*

Each sampling point was classified into one of nine exclusive categories (Table 3) using the coordinates in the tree cover and shrub cover gradients of the PCA and the cut-points selected for the satellite vegetation maps. These points were used as ground-truth for all vegetation maps. A confusion matrix was generated comparing ground-truth classification with classification from each map. Percentage of agreement and Kappa values (classification rate corrected for chanceTitus, Mosher & Williams 1984) indicated that greatest map quality (or accuracy) corresponded to the MIXED_30 map. Map quality declined in this order MIXED_30 > SATELLITE_30 > SATELLITE_50 > SINAMBA_50 > SINAMBA_250 > CORINE_250 (Table 4)

3.2. *Bird distribution models*

It was possible to build predictive models significantly better than a null model for 48 out of 54 species of birds using maps at a spatial resolution of 250 m. All bird species gave models better than the null model when predictors were derived from maps at spatial resolution of 50 or 30 meters. Mean AUC for each map ranged from 0.59(SE=0.05) for CORINE_250 to 0.80(SE=0.06) for SINAMBA_50 (Table 5).

There were significant differences in bird predictive ability (AUC values) when comparing the models derived from different data sources (CORINE_250 vs. SINAMBA_50 vs. SATELLITE_30) (Table 6). CORINE_250 gave bird distribution models of significantly lower predictive accuracy than SINAMBA_50, while SINAMBA_50 and SATELLITE_30 did not differ. CORINE_250 differed from SINAMBA_50 in map quality, the number of predictors derived, and the spatial resolution of the source map. To study the effect of each of these factors independently we compared the models derived from CORINE_250, SINAMBA_250R, SINAMBA_250 and SINAMBA_50 (Table 7). There were significant differences in predictive ability of models derived from each map. Planned comparitions indicated that differences

Table 2. Vegetation variables measured at bird survey points in a circle of 50 m radius.

Variables	possible values
Cover of herbaceous vegetation	<10%, 10-50%, >50%
Cover of shrubs < 0.5 m tall	absence, < 25%, > 25%
Cover of shrubs 0.5-2 m tall	absence, < 25%, > 25%
Cover of trees 2-6 m tall	absence, < 25%, > 25%
Cover of trees > 6 m tall	absence, < 25%, > 25%
Mean diameter at breast height (DBH) of the 5 biggest trees	m (continuous)
Number of trees with DBH > 0.2 m in a circle 25 m radius	integer

Table 3. Categories used in vegetation maps (structural categories) to compare map quality (accuracy).

Categories
no tree cover no shrub cover
no tree cover disperse shrub cover
no tree cover dense shrub cover
disperse tree cover no shrub cover
disperse tree cover disperse shrub cover
disperse tree cover dense shrub cover
dense tree cover no shrub cover
dense tree cover disperse shrub cover
dense tree cover dense shrub cover

could be attributed in this order: first to map source quality (CORINE_250 vs. SINAMBA_250R, F = 937.59, P < 0.001), second to the reduced set of predictors that could be derived from the CORINE map (SINAMBA_250 vs. SINAMBA_250R, F = 39.37, P <0.001) and third to map resolution (SINAMBA_50 vs. SINAMBA_250, F = 32.80, P < 0.001). Improving the quality of the SINAMBA map by generating a MIXED map, or degrading the spatial resolution of the SATELLITE map from 30 to 50 m had no significant effect on the predictive ability of bird models derived from each map (Table 8). Planned comparitions indicated that there was a statistically significant (but very small) difference attributed to the source (SINAMBA_50 vs. SATELLITE_50, F = 4.75, P = 0.031) but this was not related to map quality. SATELLITE_50 was a slightly better map (Table 4) but rendered predictive models of bird distribution with slightly lower AUC. There was no significant effects of either map resolution (SATELLITE_30 vs. SATELLITE_50, F = 3.80, P = 0.05), or map quality improvement (SINAMBA_50 vs. MIXED_30, F = 0.17, P = 0.7, SATELLITE_30 vs. MIXED_30, F = 0.68, P = 0.4).

Table 4. Percentage of agreement between map categories and ground-truth data (n= 857) for each map, and Kappa values that indicate percentage improvement over a random classification.

Map	Percentage of agreement *	Kappa	Sk (C.I. 95%)	z value (p)
CORINE_250	36.6	0.01	0.06	0.22 (=0.41)
SINAMBA_250R	44.4	0.12	0.05	4.39 (<0.001)
SINAMBA_50	20.3	0.12	0.03	10.12 (<0.001)
SATELLITE_50	23.7	0.14	0.03	11.37 (<0.001)
SATELLITE_30	26.5	0.17	0.03	13.56 (<0.001)
MIXED_30	29.7	0.22	0.03	19.16 (<0.001)

* Percentage agreement value of CORINE_250 can only be compared with SINAMBA_250R that has a reduced set of 4 classes also: no tree cover no shrub cover, no tree cover disperse or dense shrub cover, disperse or dense tree cover no shrub cover , and disperse or dense tree cover disperse or dense shrub cover.

Table 5. Bird prediction accuracy, mean AUC (and SE) values, for the models generated with the different maps

Model (map source)	AUC (SE)
CORINE_250	0.595 (0.051)
SINAMBA_250R	0.742 (0.069)
SINAMBA_250	0.788 (0.070)
SINAMBA_50	0.801 (0.059)
SATELLITE_50	0.798 (0.065)
SATELLITE_30	0.789 (0.071)
MIXED_30	0.799 (0.070)

Table 6. Results of repeated measures ANOVA testing the effect in bird prediction accuracy (model AUC) of original independent map sources (CORINE_250, SINAMBA_50 and SATELLITE_30), and planned comparisons between them.

Variable	Df	SS	MS	F	P
Error: species					
Residuals	53	0.409	0.008	-	-
Error: within					
Map source	2	1.446	0.723	432.17	<0.0001
CORINE_250 vs. SINAMBA_50	1	1.442	1.442	861.86	<0.0001
SATELLITE_30 vs. SINAMBA_50	1	0.004	0.004	2.47	0.118
Residuals	106	0.177	0.0017		

4. DISCUSSION

Our original vegetation maps show a gradient in quality (accuracy) for several reason. The CORINE map has a coarser resolution (250 m), has a reduced set of land cover classes (44 for the whole Europe) it does not reflect well differences in vegetation structure (for example, most classes do not distinguish between dense and disperse tree and shrub cover) and is ten year older than our ground-truth data. The SINAMBA map has a finer spatial resolution (50 m), has more land cover classes (that are easier to reclassify as disperse or dense tree and shrub cover), but is five year older that ground-truth data. The SATELLITE map has the finer spatial resolution (30 m), is contemporaneous with ground truth data (1999-2000) and uses models to discriminate directly the structural variables we were interested in (degree of tree cover and degree of shrub cover). The confusion matrix of map classification and ground-truth data for sampling points indicates that map accuracy increases in a gradient CORINE < SINAMBA < SATELLITE .Interestingly, measuring the same predictors on each map --that reflect characteristics of vegetation structure in a 350 m radius around the bird survey points, and distances to landscape features-- we find that CORINE is a significantly poorer predictor of bird distribution but that SINAMBA and SATELLITE maps do not differ in their predictive ability. The differences in predictive ability between CORINE and SINAMBA can be attributed mainly to the difference in quality (accuracy), and to a lesser extent to both the difference in the number of predictors that can be measured on each map, and the difference in resolution between the two maps. SINAMBA and SATELLITE vegetation maps do not differ in their predictive accuracy of bird distribution, even though the SATELLITE map was temporally closer to our bird survey, had a finer spatial resolution, and actually better agreement with ground-truth data. Even improving the SINAMBA map with satellite data (MIXED_30) does not improve the predictive performance of models. The MIXED_30 map derives from models that are significantly better than those from the SATELLITE map, and also shows a better agreement with ground-truth data (Table 4).

Table 7. Results of repeated measures ANOVA testing the effect in bird prediction accuracy (model AUC) of map source type, and planned comparisons between them to test the effect of map quality, spatial resolution and set of predictors derived.

Variable	Df	SS	MS	F	P
Error: species					
Residuals	53	0.605	0.011	-	-
Error: within					
Map source type	3	1.178	0.393	308.25	<0.0001
quality (CORINE_250 vs. SINAMBA_250R)	1	1.345	1.345	937.59	<0.0001
resolution (SINAMBA_50 vs. SINAMBA_250)	1	0.047	0.047	32.80	<0.0001
predictors (SINAMBA_250 vs. SINAMBA_250R)	1	0.056	0.056	39.37	<0.0001
Residuals	159	0.228	0.0014		

Table 8. Results of repeated measures ANOVA testing the effect in bird prediction accuracy (model AUC) of map source type, and planned comparitions between them to test the effect of map quality, resolution and map improvement (map sources: SINAMBA_50, SATELLITE_50, SATELLITE_30 and MIXED_30).

Variable	Df	SS	MS	F	P
Error: species					
Residuals	53	0.839	0.016	-	-
Error: within					
Map source type	3	0.0049	0.0016	2.91	0.036
source (SINAMBA_50 vs SATELLITE_50)	1	0.0027	0.0027	4.75	0.031
resolution (SATELLITE_30 vs SATELLITE_50)	1	0.0021	0.0021	3.80	0.053
improvement (MIXED_30 vs SINAMBA_50)	1	0.0000	0.0000	0.17	0.678
Residuals	159	0.0889	0.0006		

Our results show that there are differences in information content of available, general purpose, vegetation maps that affect the predictive ability of bird distribution models. Differences in predictive ability of the two maps we compared were due to differences in map quality (accuracy to distinguish vegetation structural classes) but also the number of land cover classes initially distinguished and the difference in spatial resolution influenced the result. Our results also show that there is a certain limit to map improvement. The SINAMBA land use/land cover map is clearly not perfect, but increasing its resolution, or improving its accuracy with ancillary data like satellite images does not improve bird distribution models. Our results are encouraging because existing vegetation maps produced with a general purpose can show a relatively high predictive ability of bird distribution. It has to be considered that demographic stochasticity and dispersal can prevent a perfect adjustment between predictive models and wildlife distribution as Tyre et al. (2001) have shown with computer simulation models. Also, it is interesting to note that when maps of enough accuracy and resolution are not available there is the alternative of deriving vegetation structural characteristics from satellite images

ACKNOWLEDGEMENTS

This work is a contribution to the Project “Predictive cartography of land birds: A pilot study in Western Andalusia", funded by the Dirección General de Enseñanza Superior e Investigación Científica (Ministry of Science and Technology) and FEDER funds from the European Union (EU), project # 1DF-97-0648. During the work, J.S. had a predoctoral fellowship from the Ministry of Education and Culture. The extensive field work presented in this paper could not have been done without the help and sense of humour of Daniel López Huertas, Luis M. Carrascal, and Mario Díaz who also brought intellectual insight to the project. We are grateful to the Environmental Department of the Junta de Andalucía for providing access to the 1995 SinambA land use/land cover map of Andalusia and to the European Environmental Agency (EEA) and the European Topic Center on Land Cover (ETC/LC) for providing access to the CORINE Land Cover databases.

NOTES

A version of this chapter has been submitted to *Ecological Modelling*, with J.Bustamante and R.Díaz-Delgado.

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CAPÍTULO V: La elección de la mejor resolución espacial en los modelos predictivos de la distribución de aves

RESUMEN

¿Cuál es el *grano* apropiado para generar modelos predictivos de la distribución de especies?. Se ha sugerido que el grano, o máxima resolución espacial, debería seleccionarse de acuerdo con el uso que se espera hacer del modelo, o bien con la percepción del ambiente que se asuma que tenga la especie. Sin embargo, no existe todavía una guía cuantitativa en la que basarse para seleccionar el grano de medición de predictores dentro del contínuo entre los extremos de baja y de alta resolución. En este trabajo exploramos el efecto que tiene medir predictores ambientales a diferentes resoluciones espaciales sobre la capacidad discriminativa de distintos modelos de la distribución reproductora de aves. Los modelos más discriminativos fueron en promedio aquellos que se hicieron con predictores medidos en círculos de gran diámetro (es decir, con baja resolución espacial: 2450 m). El área de estos círculos (471 ha) fue generalmente mucho mayor que el tamaño del área de campeo para la mayor parte de las especies (con la excepción de las rapaces), lo que sugiere que la probabilidad de detectar a una especie en particular depende de las características del hábitat en un entorno amplio, y no sólo en los aspectos particulares a un punto de muestreo. Se discute después que este resultado puede deberse a efectos de la dinámica metapoblacional sobre los patrones de distribución.

CHAPTER V: Choosing the best spatial resolution for predictive models of bird distribution

ABSTRACT

What is the appropriate grain for predictive models of species distribution? The grain, or maximum spatial resolution, has been suggested to be selected according to either the expected use of the model, or to the assumed species' perception of the environment. However, there is no widely available quantitative guidelines to select the grain of predictors from a low-high resolution continuum. In this work we explore the effect of measuring environmental predictors at different spatial resolutions on the discriminative ability of breeding bird distribution models. The more discriminative models were on average those made with predictors measured in circles of large diameters (i.e., low grain: 2450 m). The area of these circles (471 ha) were generally much larger than the area of home range for most species, with the exception of raptors, what suggest that the probability of detecting a particular species depend on habitat characteristics measured in an wide neighboring area, and not only on in-site specific features of the sampling point. We discuss that this result may be due to metapopulation dynamics on patterns of occurrence.

INTRODUCTION

Scale is a main theme in ecology (Levin 1992) because of its wide implications in theoretical and practical studies (Peterson & Parker 1998). Scale is also such a central issue in predictive habitat modeling (Guisan & Zimmermann 2000) that it has recently been the focus of a entire symposium on the subject (Scott *et al.* in press). And, among the multiple facets of scale, modelers are mainly concerned with the selection of an appropriate grain to measure environmental variables that will serve as predictors of species distribution (Morrison, Marcot & Mannan 1998, p. 141). The grain, or maximum spatial resolution (O'Neill & King 1998), has been suggested to be selected according to the expected use of the model (Morrison, Marcot & Mannan 1998). Thus, variables measured at low spatial resolution (typically broad macrohabitat summaries) suit models of general distribution, while variables measured with detail at high resolution (generally microhabitat descriptors) are adequate for models of spatial use on particular habitats or areas. However, there is no widely available quantitative guidelines to select the grain of predictors from the low-high resolution continuum. Besides, an alternative to this criterion is to consider the species’s perception of its environment. Animal’s habitat selection, according to the hierachical theory (Johnson 1980; Holling 1992), proceeds first at the broad level of geographical area, then at the home range level, then within specific sites within home ranges, and finally at microsites --or specific features of selected sites (see two examples in Holling 1992, for Egretta alba y). Thus, the appropriate grain for predictors may be chosen depending on our interest in one or other level of habitat selection.

Moreover, a practical consideration must be made to select the appropriate grain for predictors in habitat distribution modelling. There are severe logistic and budget limits to both the spatial extent and the grain used to record habitat features during fieldwork; besides, sample units may be difficult to standardize. For example, in a study of birds of the Baja California Xerophytic scrub (R. Rodríguez-Estrella and J. Bustamante, unpublished), one of us (JB) employed between 30 to 60 minutes to reach each aleatorily-selected sampling point and more than 120 minutes to record habitat variables (vegetation floristic and structure) within an 50x5 m linear transect. Measuring vegetation on a bigger area seemed desiderable but impractical. On the contrary, logistics and budget are not so limiting if environmental predictors are measured within a GIS framework, and researchers may choose among almost limitless possibilities for the grain of predictors (though, grain is conditioned to be a multiple of the original spatial resolution of thematic layers). In the example above, habitat variables could have been measured equally almost effortlessly in circles of diameter of, say, 100, 200 or 500 meters, so which one to use then?

Many studies on predictive models of bird distribution for a single species measure environmental factors and species distribution at the same resolution, approximately that of the species home range (i.e.: González, Bustamante & Hiraldo 1992; Donázar, Hiraldo & Bustamante 1993; Bustamante 1997), others opportunistically measure both species distribution and environmental factors at the resolution provided by preexisting regional atlas (typically with 1x1 or 10x10 km squares). When using point-surveys to record presence/absence or abundance of several bird species simultaneously, two strategies are possible to record bird data. (1) To use a fixed radius detection circle, so that the census area is known and it is the same for all species. This has the

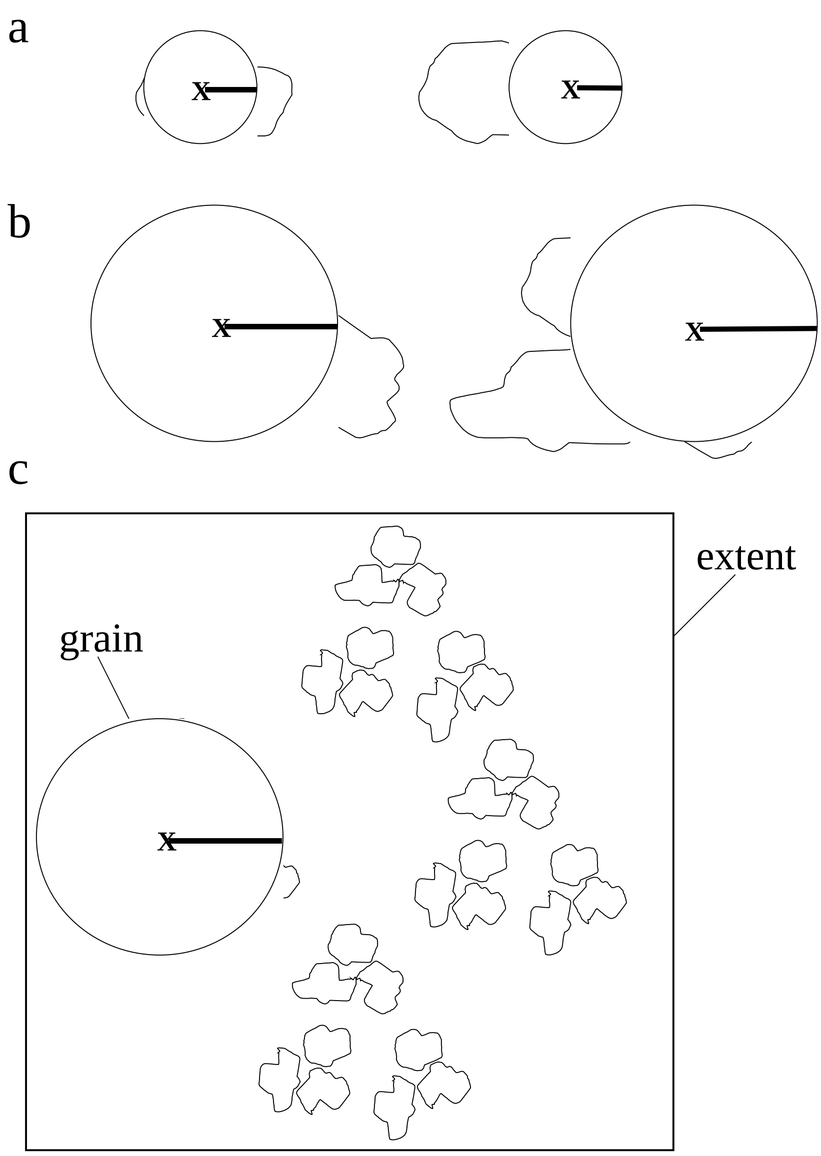

Figure 1. Scale has two dimensions: grain and extent (O'Neill & King 1998). In the context of predictive habitat modelling the extent is the area of study while the grain is the minimum unit in which the area of study is divided to measure environmental predictors. The figure is a idealized representation of three possible choices of grain for environmental variables in predictive habitat modelling. Hatched areas delimit home ranges for a single individual of a species, circles are the grain. Inside circles, it is shown the radius (thick line) and the area in which detections of birds are possible (crosses): a bird is recorded if the cross hit the home range area. **a)** grain approximately equal to home range. **b)** grain approximately equal to several neighboring home ranges. In both **a** and **b** the left figure shows that most of the area sampled for predictors is suitable for the species, while in the right figure the species is detected at the border of home range (or group of neighboring home ranges) and thus a large part of the area sampled for predictors is unsuitable for the species (we expect that, in the average, center of sampling circles coincide with center of home ranges (or group of home ranges). **c)** large grain approximately equal to the extent of a local subpopulation.

disadvantage that contacts with birds outside the circle are wasted. (2) To use an unlimited detection circle. This makes an optimal use of all data recorded, but has the disadvantage that census area is unknown and varies with species body-size, because larger birds are seen or heard from greater distance (Calder III 1990). Census-area size may influence the grain at which environmental variables have greater predictive power of birds-species occurrences. In that case the grain at which environmental predictors give optimal predictive power should be smaller when using fixed-radius *vs.* unlimited-radius designs. If species body size, by its effect on species home-range size, affects the grain at which environmental predictors give optimal predictive power this effect should be greater with unlimited-radius designs in which the effect of home-range size and size of censused area add to each other.

Even though, it is not necessarily clear if the grain at which bird species is habitually thought to perceive the environment –the size of the home range—is of the same magnitude as the grain at which environmental variables have optimal predictive power of their distributions (fig. 1). An individual of a bird species might be present at a sampling point depending exclusively on the environmental characteristics of the habitat in a radius that encompases its home range (that is, in-site specific habitat features could affect the most the probability of occurrence or the abundance of the species). If we consider the effect of conspecific attraction and dispersal it may be more important for the presence of the individual at the sampling point (Goodwing & Fahrig 1998) the habitat in a larger circle that encompases the territories of several conspecifics or perhaps a whole subpopulation. In such a case, species characteristics that influence abundance and dispersal might be more important to determine the grain at which environmental predictors give optimal predictive power than home-range size or the effect of body-size in detection distance.

In this work we explore the effect of measuring environmental predictors at different spatial resolutions (or with a different grain) on the discriminative ability of breeding bird distribution models. We assume that the grain at which models are more discriminative shows the level at which the environment is affecting more the observed pattern of species distribution. Our aims with this study are to explore: (1) if the grain at which environmental variables are measured has an effect on the predictive power of bird occurrence models, (2) if sampling-area size has an effect on the grain at which environmental predictors have greater predictive power (fixed *vs* unlimited-radius designs), (3) if optimal grain is equivalent or proportional to species home-range size, or is affected by factors operating at larger spatial scales, (4) if species body-size or other ecological factors influence the grain at which environmental variables have optimal predictive power. Our comparison across spatial resolutions serve also as a guide of how much predictive ability one is losing when selecting a certain grain to measure predictors.

METHODS

Study area

The study area are two 70 x 70 km squares in Western Andalusia, Southern Spain. Both of them include low, flat areas, mainly devoted to agriculture, surrounded by mountainous areas with more natural vegetation (altitude ranges from 0 to 1600 m a.s.l.). In both areas land-cover is mainly dominated (approximately 70%) by Mediterranean vegetation (shrubland and evergreen oak *Quercus ilex* subsp. *ballota* L. and cork oak *Quercus suber* L. forests and *dehesas*), and pine and eucalyptus plantations, and 30% is mainly agricultural land, mainly non-irrigated wheat and sunflower crops and olive groves. Villages and urbanized areas are widely interspersed.

We analyzed occurrence of 79 species detected in 1144 point surveys of 15 min duration made between April and June in 1999 and 2000. We differentiated among birds detected within a circle of 100 m diameter centered in the sampling point, and birds detected outside the circle (we pooled the data for some analyses). Bird species were mostly passerines (80%), and their sizes ranged between Firecrest *Regulus ignicapillus* Temminck (~5,3 gr) to Short-toed eagle *Circaetus gallicus* Gmelin (~1700 gr). Weights (a surrogate for body size) and home ranges for each species were taken from Perrins (1998). We selected weights and home range sizes for the same subespecies and the location closest to, and climatically more similar to, our study area, and averaged values across sexes (or areas) if appropriate (Appendix 1). Home range estimates were of varying quality, and a number of species lacked reliable measures; in some cases we had to estimate home range size as the inverse of population density. Moreover, the distinction between territory size (the area surrounding the nest that is actively defended) and home range (the total area used by a breeding pair to forage) was not clear for all species. For these reasons we focused the analysis on weights rather than on home ranges, assuming that they are well correlated (Peters 1983).

Environmental predictors used as explanatory variables in the models (table 1 and see below) were a set of land-cover variables extracted and amalgamated from the 1995 land-use/land-cover digital map of Andalusia (SinambA), provided by the Environmental Department of the Junta de Andalucía (Moreira & Fernández-Palacios 1995). Original data in vector format were rasterized to 50 m spatial resolution. To simulate different available spatial resolutions of explanatory variables, predictors were averaged in circles of increasing diameter (150, 350, 650, 1250, 2450 and 4850 m, fig. 2) centered in sampling points, and models were built separately for each diameter. For some analyses we considered diameter as an ordered factor with 6 levels.

Statistical analyses

We performed Generalized Additive Models (Hastie & Tibshirani 1990) of presence/absence of each bird species for each diameter, using binomial errors and logit link. Explanatory variables for each model were selected from each set of potential predictors (table 1) by a forward-backward stepwise procedure (with the step.gam function of S-PLUS 2000 software, MathSoft 1999) that used an approximation of AIC (Akaike´s Information Criterion, Burnham & Anderson 1998) as the criterion to enter or to remove variables. Predictors were allowed to enter the models as linear terms or as smoothing splines with 2 or 3 degrees of freedom (to achieve, respectively, a lower or higher degree of smoothing). The procedure we implemented tested first each predictor as a smoothing spline with 3 degrees of freedom, and then tried to simplify the model by testing the variables entered previously as smoothing splines with 2 degrees of freedom and, finally, as linear terms.

The discriminative ability of the bird distribution models were assessed by the area under the curve (AUC) of a Receiver Operator Characteristic (ROC) plot (Swets 1988; Murtaugh 1996). The AUC summarizes ROC plots with a measure of discrimination independent of a threshold (Fielding & Bell 1997). AUC ranges between 0.5 (chance performance) to 1 (perfect discrimination), and can be interpreted as the probability of a model to render a higher predicted value of presence for a species in a site where the species exists than for a site where the species is not present (Zweig & Campbell 1993; Cumming 2000)

We used two methods to analyze the relationship between grain of predictors and discriminative ability of models. Firstly, we select the more

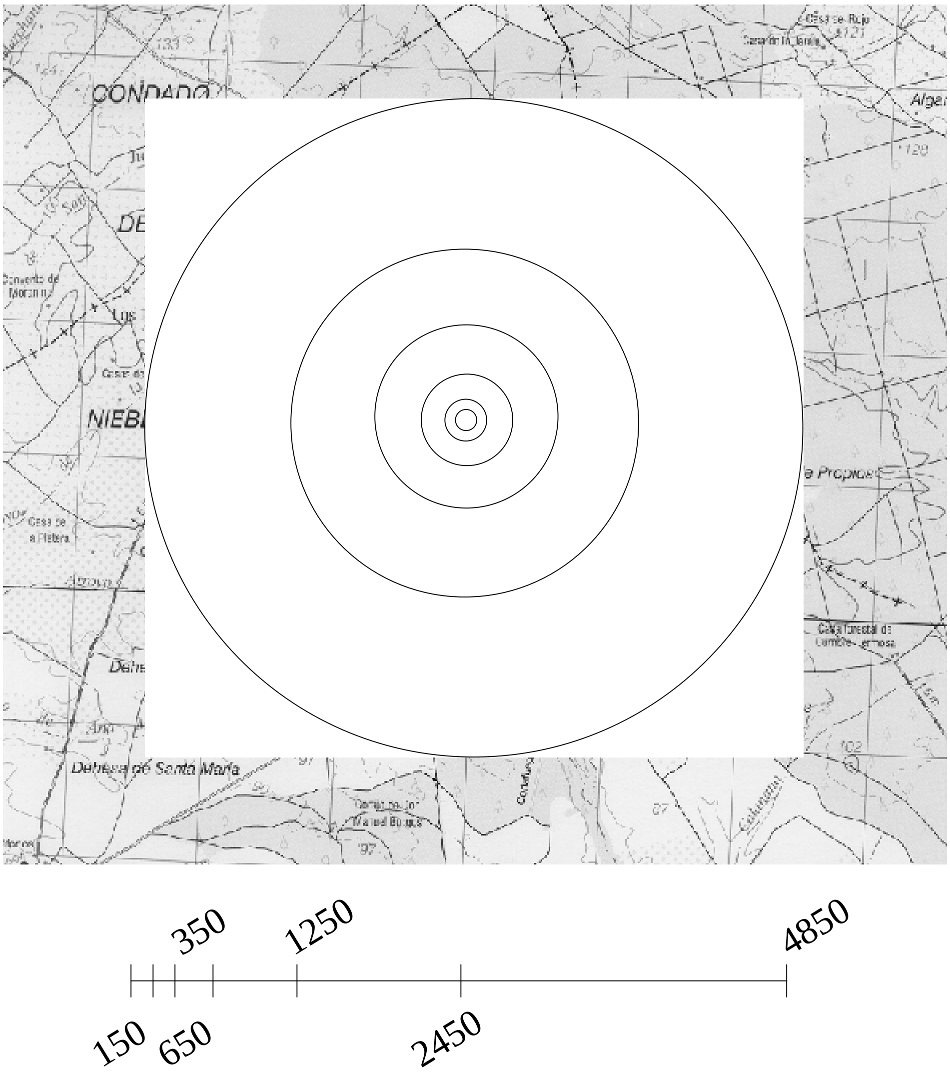

Figure 2. Comparison of the different grains tested. Circles to measure predictors increase from diameter 150 m (17.6 ha, but only 12.5 ha with our raster approximation) to diameter 4850 m (185 ha that we approximated to 183 ha).

discriminative diameter level for each species (i.e., the one used to build the model with highest AUC among the 6 models for each particular species). The spatial resolution of predictors that achieve maximum discrimination may be influenced by body size (as a surrogate of home range and detectability: the bigger the bird, the bigger the diameter to measure environmental predictors), by frequency of occurrence in the sample (because rarer birds may be responding to very local features of landscape and perceiving the environment with a finer grain), and by particular characteristics of the species (that we resumed in a factor grouping species similar in its habitat requirements and trophic habits, see \Boone, 1999 #25, and appendix 1). Then we performed an ordinal logistic regression (Guisan & Harrell 2000) of diameter level on species' weight (log transformed), prevalence and ecological group (Harestad & Bunnel 1979). Preliminar analysis of ordinality of diameter category showed the data satisfied the assumptions of a continuation ratio model, that we finally implemented in its extended version (Harrell 2001, pages 339-340). The continuation ratio model fits an ordinal logistic regression for each diameter level, and its extended version allows for different slopes among levels (Harrell, 2001 #12, pages 331-373, and see Harrell *et al.* 1998, for background; Guisan & Harrell 2000). We acknowledge that the spatial resolution of predictors that yield the more discriminatory models can be best considered as a continuous measure, rather than having to select one of a diameter levels that were sometimes very similar in its resulting AUC's. Therefore, we secondly estimate the optimum diameter (OD) as the averaged diameter weighted by AUC, OD= $\Sigma r_i AUC_i / \Sigma AUC_i$, where r_i is the diameter (in meters) for category i, and AUC_i is the estimated AUC for the model performed with predictors measured in a circle of diameter i. OD was linearly regressed on body weight (log transformed), frequency of occurrence in the sample (named prevalence) and ecological group. In the two analyses we only considered the species with at least one fairly discriminative model (AUC>0.75, Elith 2000).

All analyses were made using S-plus 2000 (MathSoft 1999). The extended continuation ratio was made with the Design library (described in Harrell 2001). AUC's were estimated with AccuROC 2.5 (Vida 1993).

RESULTS

For unlimited-radius census (recall that in these surveys birds recordings were taken into account only if they were made within a circle of diameter 100 m), the ordinal regression does not show a significant effect of neither one of the predictors tested: weight (log transformed), prevalence or ecological group, on the spatial resolution at which models are more discriminative (table 2). However, the effect of cohort is highly significant (p<0.0001), what can be interpreted as different base rates of discrimination among levels of diameter. The observed number of models with maximum discriminative values (AUC) at each category of spatial resolution for predictors differs significantly from what expected at random: level 5 (diameter 2450 m) has twice the expected value for a regular distribution, while level 1 (150 m) and 2 (350 m) have about half the expected value (χ^2=14.05, df=5, p=0.015, fig. 3). That is, the "best" diameter is frequently 2450 m. On the contrary, for fixed-radius census the effect of cohort was significant (p=0.01), but there were not differences in discriminative values

Table 1. Variables tested as environmental predictors in the six models of breeding bird species occurrence in two areas of Western Andalusia. Values were averaged for circles of increasing diameters (150, 350, 650, 1250, 2450 and 4850 m) centered in sampling points, and a model was built for each species and diameter of circle. Sources: **a** 1995 land-use/land-cover cover digital map of Andalusia from the SinambA (Consejería de Medio Ambiente, Junta de Andalucía), **b** IRS satellite image, sensor LISS III (dates: 19/07/99 and 16/07/99 for the two study areas). Fractal dimension estimated with IDRISI 32 on a NDVI (Normalized Difference Vegetation Index) image, **c** Digital Elevation Model of Andalusia at 50 m resolution.

Predictive variable type and name	Description
1.-Vegetation variables	
1.1.- Land-cover	
Forest [a]	Proportion of pixels belonging to any forest type category (including sparse forested areas such as dehesas but not olive groves)
Dense Forest [a]	Proportion of pixels belonging to dense forest category (excluding dehesas)
Coniferous forest [a]	Proportion of pixels belonging to coniferous forest type category (mainly reafforestations of coniferous but we included those of eucalyptus)
Broad-leave forest [a]	Proportion of pixels belonging to any broad-leave forest type category
Riparian vegetation [b, c]	Proportion of pixels belonging to any riparian type category (from shrubs to riparian)
Shrub [a]	Proportion of pixels belonging to any shrub type category
Agriculture [a]	Proportion of pixels belonging to agricultural land use categories (irrigated and non-irrigated crops and olive groves)
Herbaceous [a]	Proportion of pixels belonging to any herbaceous type category (whether natural or cultivated)
Tree cultures [a]	Proportion of pixels belonging to tree cultures (mainly olive groves)
Urbanized [a]	Proportion of pixels in urbanized or industrial areas
1.2.- Landscape	
Borders (all) [a]	Length of boundaries between forested landcover categories and the rest of vegetation categories
Borders (forest-shrub) [a]	Length of boundaries between forest and shrubland
Cropland heterogeneity [b]	Fractal dimension of Normalized Differenced Vegetation Index values of a satellite image as an index of heterogeneity in croplands
2.- Topographic variables	
Altitude [c]	Mean altitude (in m)
Slope [c]	Mean slope (in degrees)

among levels of spatial resolution (χ^2=5.92, df=5, p=0.314, fig.3). Using either the home range extracted from the bibliography (appendix 1), or the allometric predictions from weight estimated with our data ($HR=W^{1.06}$), instead of body weight made no differences in the results of ordinal regressions.

Estimates of OD for unlimited-distance surveys did not differ from estimates for fixed-distance point surveys (wilcoxon test, Z=0.91, p=0.36, n=54). Equally, the "best" diameter for unlimited-distance point surveys did not differ from that for fixed-distance point surveys (wilcoxon test, Z=1.17, p=0.24, n=54). For the 65 especies with data for both the unlimited-distance and the fixed-radius surveys, there were not differences between survey type, nor among the six levels of spatial resolution (ANOVA: spatial resolution, F=0.90, p=0.48; survey type, F=1.41, p=0.24; interaction, F=0.03, p=0.99).

There is a small positive and significant effect of weight on the optimum (averaged) diameter for unlimited-distance surveys (OD, table 4). However, the range of predicted OD is low (1598-1678 m), and the corresponding areas of circles with those diameters vary only between 200 and 221 ha. Using recorded home range or estimated home range did not change the results. The inclusion of the complete set of species (rather than selecting those with at least one fairly discriminative models) renders similar results (both for the single more discriminative diameter and the OD) and is not discussed further. No effect of weight (or home range), prevalence or ecological group could be found for fixed-radius surveys

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Table 2. Ordinal logistic regression (extended continuation ratio model) for the length of diameter that renders the more discriminative models (unlimited-distance census). Predictive factors were log(weight), prevalence (frequency of occurrence in the point surveys taken as a whole) and ecological group. Cohort is a factor that was included for testing if the effect of weight or prevalence on predictive ability varied among the different diameter lengths.

Wald statistic (response: diameter level) Factor	Chi-square	d.f.	P
Cohort (Factor + Higher order factors)	45.31	12	<0.0001
All interactions	10.05	8	0.2617
Log(weight) (Factor + Higher order factors)	9.30	5	0.0977
All interactions	7.83	4	0.0981
Prevalence (Factor + Higher order factors)	2.62	5	0.7585
All interactions	2.62	4	0.6236
Ecological group	9.67	6	0.1394
Cohort X log(weight) (Factor + Higher order factors)	7.83	4	0.0981
Cohort X prevalence (Factor + Higher order factors)	2.62	4	0.6236
Total interaction	10.05	8	0.2617
Total	48.09	20	0.0004

The sampling circles corresponding for both the single "best" and the optimal diameters had surfaces larger than home ranges (appendix 1). For example, *Certhia brachydactyla*, a small passerine with home range of 4 ha, had an optimal diameter of 1547 m, which corresponds to a circle of 188 ha for sampling predictors. Thus, larger birds could have single "best" and optimal diameters actually larger than the ones we analyzed (4850 m) and, consequently, an artifact may arise due to the limited range of diameters we considered. However, excluding the 8 bigger species, heavier than 300 g (for which the point surveys may not be such an adequate sampling method) did not change noticeably the results.

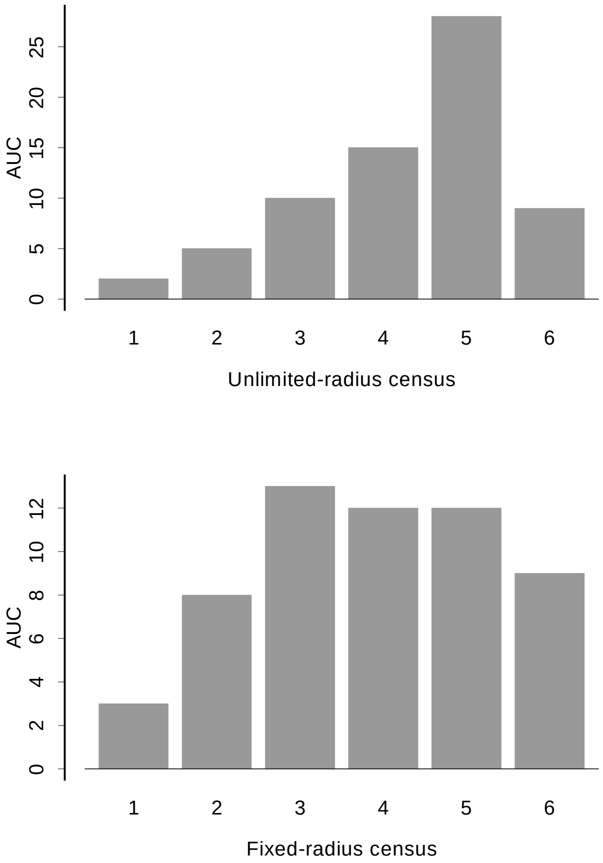

Figure 3. Histograms of predictive ability (AUC) among the six levels of spatial resolution for the two survey types.

DISCUSSION

A surprising result of our analyses is that the more discriminative models were on average those made with predictors measured in circles of large diameters (i.e., low grain: 2450 m). Indeed, the area of these circles (471 ha) were generally much larger than the area of home range for most species, with the exception of raptors. We had expected a closer match between sizes of home ranges and "best" grain, because both the quality and original spatial resolution of our environmental predictors (they are broad descriptors of vegetation measured at spatial resolution 50 m) were more suited to detect habitat selection at the home range level (for example, we would have needed more detailed vegetation variables had we been interested in habitat selection of within-home range or nesting site features). What are the reasons for this disagreement? Our results mean that the probability of detecting a particular species depend on habitat characteristics measured in an wide neighboring area, and not only on in-site specific features of the sampling point. That is, a certain species will be present in a survey point in part because of what habitat characteristics it may find in this point, but also because of what habitat characteristics exists in the surroundings (Goodwing & Fahrig 1998; Saab 1999). It is known that suboptimal areas close to source nucleus can be occupied more frequently than expected according to quality of habitat, because of social interactions (less experienced or competitive individuals may be forced to settle in the perimeter of a preferred area Van Horne 1983; Hobbs & Hanley 1990). Also, patches of habitat are subject to the effects of demographic stochasticity and limited dispersal of individuals, by which isolated or peripheral fragments are expected to be frequently unoccupied even if they are suitable for the species (Tyre, Possingham & Lindenmayer 2001). This view of the relevance of the neighborhood on the probability of occurrence of a species in a point is supported by neither optimum nor best diameter differing for unlimited-distance or fixed-distance point surveys (since unlimited-distance implies a larger sampling area, we expected OD to be greater for these surveys than for fixed-distance points).

For unlimited-distance surveys, we also found a positive relation between body size and the spatial extent to measure predictors that yields the more discriminative models. This result is in agreement with what may have been expected: models for larger birds are more predictive when built with predictors measured in larger circles. However, this relationship is not strong and clear predictions of optimal diameter to measure environmental variables can not be made. Indeed, the effect of weight is so small that optimum diameter can be seen as a constant (around 1430 m or 160 ha) for our set of species. Body size and home range —a variable difficult to measure reliably in the field— are correlated. The extension of home range (HR) in birds grows with body size (estimated by weight: W) according to the allometric expression: $HR=W^{1.14}$ (Schoener, 1968 #9, and see also Peters 1983), that is, the regression of (log)home range on (log)body weight has a slope of 1.14 using our data (appendix 1). For our data $HR=W^{1.37}$ (or $HR=W^{1.06}$ if we exclude the 8 bigger species). Recalling that optimum diameter is nearly a constant, the allometric expressions imply that predictors for small birds should be sampled in circles much larger than their home ranges, while the difference

Table 3. Ordinal logistic regression (extended continuation ratio model) for the length of diameter that renders the more discriminative models (fixed-distance census). Predictive factors were log(weight), prevalence (frequency of occurrence in the point surveys taken as a whole) and ecological group. Cohort is a factor that was included for testing if the effect of weight or prevalence on predictive ability varied among the different diameter lengths.

Wald statistic (response: diameter level) Factor	Chi-square	d.f.	P
Cohort (Factor + Higher order factors)	28.38	12	0.0049
All interactions	10.32	8	0.2432
Log(weight) (Factor + Higher order factors)	8.00	5	0.1564
All interactions	7.93	4	0.0942
Prevalence (Factor + Higher order factors)	2.39	5	0.7934
All interactions	2.29	4	0.6828
Ecological group	4.38	5	0.4963
Cohort X log(weight) (Factor + Higher order factors)	7.93	4	0.0942
Cohort X prevalence (Factor + Higher order factors)	2.29	4	0.6828
Total interaction	10.32	8	0.2432
Total	29.80	19	0.0544

Table 4. Linear regression of optimum diameter on logarithm of weight for unlimited-distance census (neither prevalence nor ecological group were significant).

Terms	Coefficient	Change in deviance	F value	P value
Intercept	1610			
Log(weight)	4.6	2662 (6%)	4.19	0.045

is not that large for big species. For example, a 20-g bird is predicted to have the most discriminative model when environmental predictors are measured in an area of 207 ha (diameter of 1624 m), and this area equals 8.6 predicted home ranges (24 ha each), according to the relationship $HR=W^{1.06}$. In contrast, a 150-g bird is predicted to have the most discriminative model for predictors measured in an area of 211 ha (diameter of 1637 m), what equals only 1 predicted home ranges (203 ha each). Such a difference between small and big birds may be explained following the same reasoning about metapopulation dynamics outlined above. Small species can be expected to have a relatively limited dispersal ability (compared with large species) from established breeding nucleus to new, unoccupied, and favorable areas. Also, small species live usually shorter than large species, and may exhibit a higher demographic variation. Therefore, the effects of local extinctions (lose of occupied home ranges) and limited dispersal (fail to reoccupy lost or new home ranges) would probably result in more suitable areas being unoccupied for small species than for big species.

The areas that our analyses suggest as optima to sample environmental predictors may seem very large but, in fact, they are of a magnitude similar to the spatial resolution utilized in the firsts Gap projects (100 ha, what is the area covered by a circle of diameter 1128 m, Scott *et al.* 1993, and see the Gap analysis program WWW page: http://www.gap.uidaho.edu/). On the other hand, that magnitude is larger than spatial resolutions used in other successful regional modelling (4 ha, or diameter 226 m, in Australian forests Pearce, Ferrier & Scotts 2001), though in this case some of the predictive variables considered in the models were measured within 2 km. Therefore, our findings, though initially surprising, are in accord with common practice in regional modelling.

To summarize, our empirical results suggest that the grain to measure environmental predictors in habitat modelling for birds should be relatively large (a general recommendation of about 200 ha that correspond to circles of diameter ~1.5 km), probably because of the effect of metapopulation dynamics on patterns of occurrence. It remains, however, to articulate this qualitative assertion with a more appropriate quantitative model. A final caveat should be made. Habitats in our study area are quite fragmented, and this may exacerbate the metapopulation dynamics discussed above, thus making more relevant to consider ample areas to measure environmental variables in predictive habitat modelling. It may well be that that our results are not fully extrapolable to more homogeneous areas.

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Appendix 1. Species considered initially in the analyses, with their estimated body weight, home-range size, prevalence in the sampled points, and ecological group at which they belong (see text for details). It is also shown the "best" level of factor diameter (the spatial resolution of predictors that yield maximum discriminative ability), its corresponding AUC, and the optimum diameter (the averaged diameter weighted by AUC). FOREST, forest-dwelling species, OPEN, species of open areas, GROUND, species linked to mixed habitats that usually feed on the ground, SHRUB, species occupying a variety of shrub habitats, RIPARIAN, species linked to a variety of riparian habitats, RAPTOR, big species (mainly raptors) that forage in large extensions of terrain. A perfect circle cannot be made in a raster GIS, so predictors were measured within figures that approximated circles with surfaces of 1.3 ha (for circles of 150 m diameter), 9.3 ha (350 m), 31.3 ha (650 m), 120.3 ha (1250 m), 465.3 ha (2450 m), 1832.3 ha (4850 m).

Species	Weight (g)	Ecological group	Home-range size (ha)	Prevalence	"Best" diameter (m)	AUC	Optimum Diameter (m)
Aegithalos caudatus	8	FOREST	16.7	0.05	4850	0.81	1649
Alectoris rufa	508	OPEN	20	0.19	2450	0.79	1633
Athene noctua	168	GROUND	20	0.04	2450	0.84	1591
Burhinus oedicnemus	462	OPEN	100	0.01	2450	0.97	1628
Calandrella brachydactyla	22.3	OPEN	2.5	0.01	350	0.95	1619
Carduelis cannabina	14.5	SHRUB	16.7	0.28	650	0.74	1629
Carduelis chloris	25.9	GROUND	6.7	0.43	2450	0.73	1683
Carduelis carduelis	13.2	GROUND	3.2	0.56	4850	0.74	1639
Cercotrichas galactotes	23.4	SHRUB	5	0.01	4850	0.46	1732
Certhia brachydactyla	8.2	OPEN	4	0.27	2450	0.29	1547
Cettia cetti	13.8	RIPARIAN	10.6	0.06	650	0.88	1597
Circaetus gallicus	1700	RAPTOR	7875	0.02	2450	0.84	1627
Circus pygargus	316	RAPTOR	20106	0.02	2450	0.96	1618
Cisticola juncidis	8.7	OPEN	1.44	0.15	350	0.92	1609
Coccothraustes coccothraustes	54.7	FOREST	66	0.02	650	0.88	1538
Columba palumbus	489	GROUND	no data	0.13	2450	0.78	1671
Corvus corax	1131	RAPTOR	3475	0.03	2450	0.82	1636
Corvus monedula	234	GROUND	20	0.03	1250	0.94	1651
Coturnix coturnix	98.8	OPEN	1.5	0.06	2450	0.83	1619
Cuculus canorus	103	FOREST	30	0.16	4850	0.71	1686
Cyanopica cyana	74.6	FOREST	26.3	0.09	4850	0.90	1642
Delichon urbica	19.5	AEREAN	3.33	0.09	2450	0.79	1653
Dendrocopos major	74.4	FOREST	32	0.05	2450	0.88	1639
Emberiza cia	23.3	SHRUB	10.2	0.08	2450	0.81	1652
Emberiza cirlus	25.6	FOREST	0.94	0.04	650	0.83	1623
Erithacus rubecula	16.5	RIPARIAN	7.3	0.14	2450	0.92	1627

Species	Weight (g)	Ecological group	Home-range size (ha)	Prevalence	“Best” diameter (m)	AUC	Optimum Diameter (m)
Falco tinnunculus	233	RAPTOR	no data	0.03	2450	0.86	1716
Fringilla coelebs	23.1	GROUND	2.6	0.45	2450	0.89	1631
Galerida cristata	41.4	OPEN	4	0.22	2450	0.90	1632
Galerida theklae	36.8	SHRUB	1	0.12	1250	0.80	1613
Garrulus glandarius	171	FOREST	10	0.07	2450	0.84	1634
Hieraaetus pennatus	842	RAPTOR	314	0.03	1250	0.89	1632
Hippolais pallida	11.9	RIPARIAN	no data	0.01	2450	0.97	1633
Hippolais polyglotta	10.5	RIPARIAN	2	0.10	4850	0.73	1643
Hirundo daurica	19.1	AEREAN	no data	0.08	4850	0.76	1642
Hirundo rustica	22.2	AEREAN	10	0.24	1250	0.75	1624
Jynx torquilla	38.4	FOREST	78.5	0.07	4850	0.85	1652
Lanius excubitor	63.4	GROUND	55	0.03	650	0.52	1604
Lanius senator	29	GROUND	8	0.16	1250	0.78	1631
Lullula arborea	26.1	GROUND	16.8	0.18	1250	0.85	1621
Luscinia megarhynchos	20.5	RIPARIAN	0.67	0.34	2450	0.81	1622
Melanocorypha calandra	65	OPEN	3.25	0.07	1250	0.98	1620
Merops apiaster	55.2	AEREAN	314	0.33	4850	0.75	1658
Miliaria calandra	47.6	OPEN	2	0.50	2450	0.82	1629
Monticola solitarius	58	SHRUB	2.5	0.05	150	0.95	1592
Motacilla cinerea	17.4	RIPARIAN	150	0.01	650	0.98	1610
Motacilla flava	16.2	OPEN	0.9	0.02	650	0.96	1612
Muscicapa striata	14.2	GROUND	0.64	0.02	350	0.94	1611
Oenanthe hispanica	16.4	OPEN	1.7	0.09	2450	0.83	1653
Oenanthe leucura	38	SHRUB	32	0.01	2450	0.93	1604
Oriolus oriolus	68.5	FOREST	186	0.07	2450	0.76	1663
Parus caeruleus	10.8	FOREST	0.53	0.29	2450	0.82	1626
Parus cristatus	10.4	FOREST	7.7	0.07	650	0.91	1641
Parus major	18	FOREST	1.54	0.35	650	0.76	1586
Passer domesticus	28.5	GROUND	0.5	0.23	1250	0.77	1632
Petronia petronia	32	FOREST	0.1	0.08	2450	0.88	1658
Phoenicurus ochruros	16.5	SHRUB	0.66	0.03	650	0.95	1611
Phoenicurus phoenicurus	15.7	FOREST	1	0.04	4850	0.91	1678
Phylloscopus bonelli	7	FOREST	1	0.08	2450	0.87	1627
Phylloscopus collybita	7.7	FOREST	9.9	0.05	1250	0.90	1620

Species	Weight (g)	Ecological group	Home-range size (ha)	Prevalence	"Best" diameter (m)	AUC	Optimum Diameter (m)
Picus viridis	175	FOREST	467	0.07	4850	0.79	1647
Ptyonoprogne rupestris	23	AEREAN	12	0.03	350	0.85	1602
Pyrrhocorax pyrrhocorax	322	RAPTOR	941	0.05	4850	0.98	1646
Regulus ignicapillus	5.3	FOREST	0.1	0.07	1250	0.89	1622
Saxicola torquata	14.5	GROUND	3	0.12	150	0.82	1558
Serinus serinus	11.9	GROUND	1	0.45	1250	0.72	1611
Sitta europaea	21.5	FOREST	1.5	0.15	1250	0.87	1624
Streptopelia turtur	125	FOREST	200	0.13	4850	0.76	1655
Sturnus unicolor	86.5	GROUND	201	0.13	1250	0.79	1630
Sylvia atricapilla	17.6	RIPARIAN	7.4	0.15	650	0.90	1608
Sylvia cantillans	10.9	SHRUB	5	0.03	1250	0.85	1619
Sylvia conspicillata	8.8	OPEN	15	0.02	2450	0.93	1659
Sylvia hortensis	21.1	FOREST	2.4	0.06	350	0.76	1620
Sylvia melanocephala	10.9	SHRUB	0.21	0.44	650	0.78	1607
Sylvia undata	9.5	SHRUB	1.6	0.08	2450	0.77	1620
Troglodytes troglodytes	9	FOREST	0.71	0.15	1250	0.82	1596
Turdus merula	95.9	SHRUB	1	0.55	1250	0.84	1635
Turdus viscivorus	117	GROUND	16	0.04	2450	0.85	1633
Upupa epops	66.2	FOREST	257	0.18	4850	0.80	1640

CHAPTER VI: A comparison of different explanatory variables for predictive models of breeding bird distribution: competing roles for landscape, land-cover, topography and climate

ABSTRACT

Predictive habitat models rely on the relationship between a response variable (either occurrence or abundance of species) and a set of explanatory variables. Vegetation is habitually preferred as a source of potential predictors because of having a more direct link with reproductive necessities of species than topography and climate. However vegetation cartography is costly to produce and update, and most land-cover maps are usually made with a general purpose, focused on land management. On the contrary, basic topographic and climatic data are easier to obtain. In this study we compare the predictive ability (as estimated by the Area Under the Curve, AUC, of Receiver Operating Characteristic plots) of different predictive bird distribution models generated for 79 species in Southwestern Spain. The presence of each species were modelled with Generalized Additive Models with binomial errors and logit link. Within each species, several models were created that differ in the set of candidate variables (either vegetation or topography and climate), or in the order in which those were tested. A similar strategy were used to ascertain the relative relevance of landscape and land-cover variables within vegetation variables. Vegetation models were significantly more accurate than topo-climatic models, but the difference was due to the higher number of potential predictors in the set of vegetation variables. Landscape models were significantly more accurate than land-cover models, even when controlling the number of candidate predictors. Mixed models improved slightly the predictive ability. Our results suggests that the selection of a set of candidate variables (if any) should be done on the grounds of data availability, though a mixed set is best, and that landscape reflects an important information not revealed by land-cover measures. Thus regional modelling programmes would gain predictive ability by including landscape measures.

CAPÍTULO VI: Una comparación de diferentes variables predictoras para los modelos de la distribución de aves:

el paisaje, la cubierta vegetal, la topografía y el clima

RESUMEN

Los modelos predictivos de la distribución de especies se basan en la relación entre una variables respuesta (bien la frecuencia de aparición, o bien la abundancia) y un conjunto de variables explicativas. La vegetación se suele preferir a la topografía y el clima como fuente de predictores potenciales, ya que está ligada más directamente con los requerimientos reproductivos de las especies. Sin embargo, la cartografía de la vegetación es costosa de producir y actualizar, y la mayoría de los mapas de coberturas se crean con un propósito general, centrado en la gestión del territorio. Por el contrario, ciertos datos básicos de topografía y clima son fáciles de obtener. En este estudio comparamos la capacidad predictiva (estimada por el área bajo la curva, AUC, de gráficos característicos de operador-receptor) de diferentes modelos predictivos de la distribución de aves, que se generaron para 79 especies en el suroeste de España. La presencia de cada especie se modeló mediante modelos aditivos generalizados (GAM) con errores binomiales y vínculo logístico. Dentro de cada especie se generaron varios modelos que diferían en el conjunto de potenciales variables explicativas (de vegetación o bien topográfico-climáticas), o en el orden en que se comprobaba su inclusión en los modelos. Una estrategia similar se usó para investigar la importancia relativa de las variables de paisaje y de cobertura dentro del conjunto de variables de vegetación.

Los modelos de vegetación alcanzaron una capacidad predictiva significativamente mayor que los topográfico-climáticos, pero la diferencia se debió al mayor número de predictores potenciales en el conjunto de variables de vegetación. Los modelos paisajísticos tuvieron una capacidad predictiva significativamente mayor que los modelos de cobertura incluso cuando se controló la cantidad de variables potenciales. Los modelos mixtos mejoraron ligeramente la capacidad predictiva. Nuestros resultados sugieren que la selección de un conjunto de variables explicativas potenciales debe hacerse en función de su disponibilidad (aunque un conjunto mixto es la mejor opción), y que el paisaje tiene una información que no revelan las medidas de cobertura. Por

tanto, los programas regionales de modelado ganarían en capacidad predictiva si incluyeran medidas de paisaje.

INTRODUCTION

The study of the relationships between species and their habitats has been traditionally a central issue in ecology and is nowadays of prime importance in conservation and planning (see a review in Morrison, Marcot & Mannan 1998). Accurate distribution maps are welcome in, for example, the selection and design of natural parks (Scott *et al.* 1993), the assessment of human impacts on biodiversity (Lavers & Haines-Young 1996), or the testing of biogeographical hypotheses (Mourell & Ezcurra 1996; Leathwick 1998). However, even a perfect knowledge of the biology of a species cannot guarantee that a static map will reflect dynamic properties of species distribution (Tyre, Possingham & Lindenmayer 2001). Moreover, human and logistic limitations make impractical to survey extense areas and, inevitably, our knowledge of the spatial distribution of most species will have many gaps. Then, a common solution is to resort to predictive habitat modelling (reviewed in Guisan & Zimmermann 2000; and see a fine recent example in Osborne, Alonso & Bryant 2001) and regard the results as potential habitat, able to be reached and colonized by a species (Tyre, Possingham & Lindenmayer 2001).

The predictive habitat models relate typically the occurrence pattern of a species (either presence/absence or abundance) with some predictors selected from a set of biologically plausible candidate variables. A large number of potentially explanatory variables are currently easy to obtain thanks to the increasing development of GIS techniques and digital cartography (thematic maps and satellite imagery). Thus, potential predictors such as topographic and climatic data on the one hand, and vegetation digital mapas on the other, are widely spread as potential sources of information for modelling (Goodchild, Parks & Steyaert 1996). Now, the raw data must be preprocessed before the analysis and this can be very time-consuming (Lillesand & Kiefer 1994; Goodchild, Parks & Steyaert 1996), so given time and budget constraints, what kind of data should a modeller prioritize?

It may be argued that vegetation affects the distribution of animals proximally, by providing shelter, food and potential nest-sites, while topography and climate affect indirectly, by modifying the relationships of bird species with vegetation (e.g., different habitat selection may be selected under different climatic conditions, Tellería, Pérez-Tris & Carbonell 2001; Tellería *et al.* 2001) or, simply, by modifying the vegetation itself. Therefore, vegetation is expected to generally be a better predictor of animal distribution than topography and climate at local scales. However, high-resolution digital vegetation maps are costly to produce and update. Moreover, land-cover cartography is habitually built by govermental agencies with a general purpose (often focused on land-use) and the categories of natural land are not described in enough detail for the modeler of species distribution (see an example for Southern Spain in Moreira & Fernández-Palacios 1995). On the contrary topographic digital bases (Digital Elevation Models) and, to a lesser extent, meteorological data, are more easily available and will be spatially correlated with vegetation in most instances (so conveying information redundant to some degree). It is desirable to know whether one source may render predictors that lead to more accurate models (such a case would be if both sets of variables had a completely redundant information) or both are necessary to achieve high predictive ability.

We assume that, within vegetation variables, the relative effect of site-specific local descriptors or landscape configuration on the distribution of animals is of great interest for conservation management. If landscape has any relevance in the patterns of occurrence for a particular species, then the design of reserves or corridors for this species should take landscape into account. This is so because apparently suitable areas may be in fact unsuitable, for example, if the areas are too small or close to a border. A major effect of landscape would render useless all efforts of habitat description in the field. However the effects of landscape and its relative importance compared to site-specific features are not yet well understood. Landscape has been found to seriously affect patterns of abundance and distribution in some studies (Bolger, Scott & Rotenberry 1997; Vander Haegen, Dobler & Pierce 2000), but the ubiquity and relevance of this effect is controversial (Mac Garigal & Mac Comb 1995), and it is not explicitly considered in some successful regional modelling programmes like the GAP program in USA (Scott *et al.* 1993). Once one has a GIS database, obtaining landscape and site-specific vegetation variables requires approximately the same effort, so selecting either one or the other (or both) type of variables should be done on the grounds of accuracy of predictions.

In this work we build predictive models for several breeding birds in Southwestern Spain and address the following questions: (i) what set of variables has a greater predictive ability, the vegetation variables or the topographic and climatic variables?; (ii) both sets of variables are expected to be correlated, but do they have some degree of independent information?; (iii) is a single set of variables enough to generate reasonably accurate models, or do we need mixed sets?; (iv) within vegetation variables, does landscape contribute to obtain a greater predictive accuracy?; and (v) as a last, methodological, issue, are the results influenced by the particular characteristics of the analysis (namely: the number of predictors in each set and the order in which variables are incorporated to the models)?

STUDY AREA AND METHODS

The study area are two 70 x 70 km squares in Western Andalusia, Southern Spain. Both of them include low, flat areas, mainly devoted to agriculture, surrounded by mountainous areas with more natural vegetation (altitude ranges from 0 to 1600 m a.s.l.). In both areas land-cover is mainly dominated (approximately 70%) by Mediterranean vegetation (shrubland and evergreen oak *Quercus ilex* subsp. *ballota* L. and cork oak *Quercus suber* L. forests and *dehesas*), and pine and *Eucalyptus* spp. plantation, and 30% is mainly cultivated land, mainly non-irrigated wheat and sunflower crops and olive groves. Villages and urbanized areas are widely interspersed.

We analyzed occurrence of 79 species detected in 1144 unlimited-distance point counts of 15 min duration made between April and June in 1999 and 2000. Bird species were mostly passerines (80%), and their sizes ranged between Firecrest *Regulus ignicapillus* Temminck (~5,3 gr) to Short-toed eagle *Circaetus gallicus* Gmelin (~1600 gr).

Table 1. Predictive variables tested to model breeding bird species occurrences in two areas of Western Andalusia.

Predictive variable type and name	Description
1.-Vegetation variables	
1.1.- Land-cover	
Agriculture	Proportion of pixels belonging to agricultural land use categories (non-irrigated cereal crops and olive groves) in a circle of radius of 150 mts centered in sampling point
Herbaceous	Proportion of pixels belonging to any herbaceous type category (whether natural or cultivated) in a circle of radius of 150 mts centered in sampling point
Forest	Proportion of pixels belonging to any forest type category (including sparse forested areas such as dehesas but not olive groves) in a circle of radius of 150 mts centered in sampling point
Shrub	Proportion of pixels belonging to any shrub type category in a circle of radius of 150 mts centered in sampling point
Riparian vegetation	Proportion of pixels belonging to any riparian type category (from scrub to forested masses) in a circle of radius of 150 mts centered in sampling point
1.2. –Landscape	
Distance to agricultural patches	(3 variables) Distance (in m.) to the nearest patch with an agricultural land use (1) larger than 2 ha. (2) larger than 10 ha. (3) larger than 100 ha.
Distance to herbaceous vegetation patches	(3 variables) Distance (in m.) to the nearest patch with herbaceosu vegetation (1) larger than 2 ha. (2) larger than 10 ha. (3) larger than 100 ha.
Distance to forest patches	(3 variables) Distance (in m.) to the nearest forest patch (1) larger than 2 ha. (2) larger than 10 ha. (3) larger than 100 ha.
Distance to shrub patches	(3 variables) Distance (in m.) to the nearest shrub patch (1) larger than 2 ha. (2) larger than 10 ha. (3) larger than 100 ha
Distance to riparian vegetation patches	(3 variables) Distance (in m.) to the nearest riparian vegetation patch (1) larger than 2 ha. (2) larger than 10 ha. (3) larger than 100 ha
Perimeter/area	Perimeter/area ratio of the patch were the sampling point was performed considering any of the above land-cover variables (except riparian vegetation)
2.- Topo-climatic variable	
Altitude	Mean altitude in a circle of radius of 150 mts centered in sampling point
Slope	Mean slope in a circle of radius of 150 mts centered in sampling point
Precipitation	Mean annual precipitation in mm. (modelled to a resolution of 1 km^2)
Temperature	Mean annual temperature in ºC (modelled to a resolution of 1 km^2)
Radiation (insolation)	Mean annual potential solar radiation (Kj/m^2) in a circle of radius of 150 mts centered in sampling point

We defined two sets of predictive variables (table 1). The first set (vegetation) included 24 variables aimed to describe the land-cover (5 variables) and landscape structure (19 variables); the second set (topography and climate) included 5 variables descriptive of topography (3 variables) and climate (2 variables). We assume that the two sets convey partially different (but correlated) information about the environment around the point counts. We think that vegetation has a proximal effect on patterns of breeding bird occurrence at the scale of our study, while topography and climate may affect indirectly or, simply, their combination may reflect changes of vegetation cover at a finer grain than that of our land-cover map reflects: topography and climate may inform about microclimatic conditions and we therefore decided to join these two types of variables in a single set (topo-climatic).

Landscape structure variables estimated both the relationship between area and perimeter (AP-ratio) of the patches belonging to different land-cover categories, and the distance to the nearest patch of a given size (i.e.: d1X would be distance to nearest patch of land-cover X larger than 2 ha, d2X the same for the nearest patch larger than 10 ha, and d3X for the nearest patch larger than 100 ha). We account for size of patches because it affects occupancy patterns in a species-specific way (for an analysis in our geographical area, see: Tellería & Santos 1997; Santos & Tellería 1998). Vegetation variables (landscape structure and land-cover variables), except those related to riparian vegetation (see below), were extracted from the 1995 land-use/land-cover digital map of Andalusia (SinambA) provided by the Environmental Department of the Junta de Andalucía (Moreira & Fernández-Palacios 1995). Original data in vector format were rasterized to 50 m resolution. Topographic variables were obtained from a Digital Elevation Model (DEM) of Andalusia (50 m horizontal resolution). Mean precipitation and temperature data were obtained from the Instituto Nacional de Meteorología and interpolated by regression models and kriging at pixel resolution of 1 km^2 (own data, unpublished). Finally, a map of mean annual potential solar radiation was estimated from the DEM (following Ninyerola, Pons & Roure 2000). Published digital cartography of riparian vegetation was unsatisfactory. This type of vegetation occupies mostly narrow and fragmented patches in the study area, and thus small vegetated watercourses are likely to be disregarded and lumped with neighboring land-use/land-cover classes (land-use and land-cover patches smaller than 25 ha tend to be grouped in the vegetation map). Therefore, we elaborated a cartography of riparian vegetation through interpretation of IRS satellite images (sensor LISS III) aided by an overlay of watercourse information extracted from the DEM. All variables, except distances, were averaged for circles of radius 150 m centered in sampling points. Admittedly, the resolution at which define local variables should ideally be species-specific, but we have no reliable clues to select optimal resolutions for predictors (indeed, such clues are habitually inexistent for most species), so we choose to average in circles of radius 150 m to achieve a high resolution that is above expected georeferencing errors. Extraction of variables from the GIS was done using IDRISI 32 (Eastman 1999), IDRISI for

Windows (Eastman 1997) and MIRAMON (Pons 2000).

Statistical analysis

We performed Generalized Additive Models (Hastie & Tibshirani 1990) of presence/absence of each bird species using binomial errors and logit link. Explanatory variables for each model were selected from each set of potential predictors (table 1) by a forward-backward stepwise procedure (with the step.gam function of S-PLUS 2000 software, MathSoft 1999) that used an approximation of AIC (Akaike´s Information Criterion, Sakamoto, Ishiguro & Kitagawa 1986) as the criterion to enter or to remove variables. Predictors were allowed to enter the models as linear terms or as smoothing splines with 2 or 3 degrees of freedom (to achieve, respectively, a lower or higher degree of smoothing). The procedure we implemented tested first each predictor as a smoothing spline with 3 degrees of freedom, and then tried to simplify the model by testing the variables entered previously as smoothing splines with 2 degrees of freedom and, finally, as linear terms. Automated methods of variable selection such the one outlined above have been criticized (Burnham & Anderson 1998) because they can reveal spureous relationships (Flack & Chang 1987; Mac Nally 2000) or rend biologically implausible models (James & McCulloch 1990). However, they are frequently used in ecological analyses (Scott *et al.* in press) because they facilitate a rapid generation of models; moreover, automated models compare well with models that include expert opinion (Pearce *et al.* 2001; Seoane, Bustamante & Díaz-Delgado submitted), so we think our procedure is justified (at least as a heuristic comparison).

We built several models for each bird species that differed in the type of explanatory variables allowed to enter with the aim to answer several questions. First, in order to compare the predictive ability of vegetation *versus* topography and climate, we modelled species occurrence using only vegetation variables as predictors (models V), and then we tested if these models could be improved by the inclusion of topo-climatic variables (keeping the vegetation predictors that entered previously; models V-T). Analogously, we built models using only topo-climatic variables as predictors (models T), and then tested if vegetation variables could improve these models (models T-V). We also tried a complete model in which all of the variables were allowed to enter simultaneously. Second, to explore the relative relevance of the different vegetation variables, we built species predictive models with only vegetation variables reflecting land-cover at the sampling point (models C), and with only vegetation variables reflecting landscape structure (L), to finally test if the models with landscape variables could be improved with land-cover variables (L vs L-C), and if the models with land-cover variables could be improved with landscape variables (C vs C-L).

The set of potential vegetation predictors is considerably larger than the set of potential topographic and climate predictors (24 vs. 5, table 1), and thus the vegetation models could be better on average because they are considering a wider set of measures of environmental conditions (Elith 2000). To take into account this fact on the comparisons, we randomly distributed the set of vegetation variables in five groups of five variables (to be able to generate five groups of five predictors from 24 variables, the last group of four variables was completed with a 5th predictor –D1-F– selected at random from those already included in the other groups). Then, we built five vegetation models (VR1 to VR5) with each of those reduced sets of five potential predictors (the same number as in topo-climatic models). The set of landscape structure variables is also larger than the set of land-cover variables (19 vs 5); thus, as we did previously, we built four landscape structure models (LR1 to LR4) each one using a set of 5 randomly selected landscape variables (n=5, D3-R was randomly selected to appear in two groups).

To assess model accuracy, we estimated the area under the curve of ROC plots (the AUC, Swets 1988; Murtaugh 1996) with AccuROC 2.4 for Windows (Vida 1993). The ROC curve is built by plotting the sensitivity of a model (or true-positive rate) on the ordinate against 1-specificity (or false-positive rate) on the abcissa. This was made for every possible threshold value that can be chosen to convert the predicted probability of occurrence (a continuous value given by the models in the interval (0,1)) to predicted presence or absence (a dichotomous variable). The AUC summarizes ROC plots with a measure of overall accuracy independent of a threshold (Fielding & Bell 1997). AUC ranges between 0.5 (chance performance) to 1 (perfect discrimination), and can be interpreted as the probability of a model to render a higher predicted value of presence for a species in a site where the species exists than for a site where the species is not present (Zweig & Campbell 1993; Cumming 2000). AUC for models VR1 to VR5 and LR1 to LR4 were averaged to obtain a single estimate (VR and LR, respectively). Differences among model types were tested with a repeated measures factorial ANOVA with an error term due to species to control for the between-species variation, of no interest in this study.

RESULTS

It was possible to build predictive models better than a null model for every species and set of variables (except for Southern Grey Shrike *Lanius meridionalis* and topo-climatic variables). Mean AUC (Table 2) ranged from 0.69[SE=0.099] for models with land-cover predictors only (C) to 0.85[0.100] for models with topo-climatic and vegetation predictors (included in this order). Most of the specific models within each model type reached at least a moderate accuracy (we consider a subjective threshold of AUC>0.7 for the models to be considered potentially useful), except for models C, LR, and VR (table 2).

Vegetation models (V) were significantly more accurate than topo-climatic models (T) showing on the average a 6% difference in AUC (mean±SE, V=0.81±0.104, T=0.75±0.113; *F*=90.4, *p*<0.0001, table 3). Topo-climatic models were improved by the inclusion of vegetation variables (there was a significant increase in AUC: T vs T-V, *F*=250.84, *p*<0.0001, table 3), and vegetation models were improved by the inclusion of topo-climatic variables (V vs V-T, *F*=16.22, *p*<0.0001, table 3). The improvement in accuracy was relatively important (10%) when vegetation variables were allowed to enter in the topo-climatic model, but was relatively minor (3 %) when topo-climatic variables improved the vegetation models (T-V=0.85±0.100, V-T=0.84±0.104). However, mean AUC of vegetation models built with a reduced set of potential explanatory variables (VR) did not differ from mean AUC of topo-climatic models (VR=0.75±0.081; T vs VR, *F*=0.040, *p*=0.84, table 3).

Table 2. Bird prediction accuracy: mean AUC (and SE) values for the models generated with the different set of predictors. Models considered the following variables: 1) T, topography and climate; V, vegetation; T-V, topography and, afterwards, vegetation; V-T, vegetation and, afterwards, topography; All, all variables simultaneously; VR, a reduced set of five randomly-selected vegetation variables (AUC is the average of five VR1 to VR5 models). 2) C, land-cover; L, landscape structure; L-C, landscape structure and, afterwards, land-cover; C-L, land-cover and, afterwards, landscape structure; LR, a reduced set of five randomly-selected landscape variables (AUC is the average of four LR1 to LR4 models). It is also given the percentage of models with AUC >0.7 (a subjective threshold to consider models accurate enough to be of any use).

Model	AUC (SE)	%AUC > 0.7
T	0.75 (0.113)	70
V	0.81 (0.104)	94
T-V	0.85 (0.100)	99
V-T	0.84 (0.104)	96
All	0.84 (0.102)	99
VR	0.75 (0.081)	67
C	0.69 (0.099)	38
L	0.80 (0.084)	91
L-C	0.81 (0.082)	96
C-L	0.81 (0.104)	94
LR	0.78 (0.083)	67

Table 3. Results of repeated measures ANOVA testing the effect in model accuracy (AUC) of using vegetation or topo-climatic variables as predictors. Planned comparitions test if vegetation differs from topo-climatic variables in predictive accuracy (T vs V), if vegetation improves topo-climatic models (T vs T-V), if topo-climatic variables improve vegetation models (V vs V-T), and if mean predictive accuracy of vegetation variables differs from that of topo-climatic variables (T vs VR). Names of models as in table 2.

Variable	Df	SS	MS	F	P
Error: species					
Residuals	78	3.324	0.043	-	-
Error: within					
Vegetation vs topo-climatic variables	4	0.760	0.190	90.384	<0.0001
T vs V	1	0.199	0.199	94.438	<0.0001
T vs T-V	1	0.527	0.527	250.835	<0.0001
V vs V-T	1	0.034	0.034	16.221	<0.0001
T vs VR	1	0.000	0.000	0.040	0.84
Residuals	312	0.656	0.002		

Table 4. Results of repeated measures ANOVA testing the effect in model accuracy (AUC) of using land-cover or landscape variables as predictors. Planned comparitions test if landscape models differ in accuracy from land-cover models (L vs C), if landscape variables improve land-cover models (C vs C-L), if land-cover variables improve landscape models (L vs L-C) and if mean predictive accuracy of a landscape variable differs from mean predictive accuracy of a land-cover variable (C vs LR). Names of models as in table 2.

Variable	Df	SS	MS	F	P
Error: species					
Residuals	78	2.628	0.037	-	-
Error: within					
Vegetation structure vs landscape	4	0.888	0.222	119.330	<0.0001
L vs C	1	0.275	0.275	148.070	<0.0001
C vs C-L	1	0.408	0.408	239.398	<0.0001
L vs L-C	1	0.008	0.008	4.418	0.036
LR vs C	1	0.196	0.196	105.436	<0.0001
Residuals	312	0.580	0.002		

Models built using only landscape structure variables (L) were significantly more accurate than models built using only land-cover variables (C), showing on average a 11% difference in AUC (mean±SE, L=0.80±0.084, C=0.69±0.099; *F*=148.1, *p*<0.0001, table 4). The inclusion of landscape variables improved greatly (12% on average) and significantly the land-cover models (C vs C-L, *F*=239.4, *p*<0.0001, table 4), but the inclusion of land-cover variables improved only sligthly the landscape models (1% on the average) and this difference was only slightly significant (L=0.80±0.084, L-C=0.81±0.082; L vs L-C, *F*=4.4, *p*=0.04, table 4). Mean AUC of landscape models built with a reduced random set of potential predictors (LR) was significantly higher (LR vs C, *F*=105.4, *p*<0.0001, table 4) than that of land-cover models (a 9% of average difference).

The order in which each general set of variables (vegetation and topo-climatic variables) was added did not clearly affect the prediction ability of the resulting models, though there was a slight significant improvement (1%) for models in which topography was added first (T-V vs All variables, *F*=10.3, *p*=0.002; V-T vs All variables, *F*=0.07, *p*=0.791).

DISCUSSION

Our analysis show correlational relationships between breeding bird distribution and some coarse explanatory variables typically available from common cartographical data. By providing breeding substrates and foraging grounds, vegetation is likely to have an effect on breeding bird distribution at a fine scale closer to causality than topography and climate. Therefore, vegetation variables may be more promising to build accurate predictive models at the scale of this present study. Accordingly, our vegetation models (V) have a greater predictive ability than topo-climatic models (T), and the mixed models (T-V, V-T, and All variables) only improved conspicuosly topo-climatic models. However, this relative improvement seems to be due to the number of potential predictors tested to enter the models, because there were no differences between vegetation and topo-climatic models when controlling for the number of the potential predictors in the initial set. A larger set of potential predictors may contain more information about the environment, and is likely to include more variables that correlate with the presence/absence of a species. This is possibly the reason why the vegetation models here developed were more accurate than topo-climatic models. Vegetation, climate and topography are expected to be correlated (Woodward 1987; Brown 1995); for example, in our study area the more xeric, low-altitude and flat zones are mainly covered by cereal crops. However, our results suggest that both sets of potential predictors have some degree of independent information about the environment, because mixed models reached the higher predictive abilities and, in particular, the inclusion of vegetation variables notably improved the predictive ability of topo-climatic models. This pattern is in agreement with a previous study by Beard et al. (1999), who found similar results in a coarser-scale study that considered other climate and land-cover variables (but not including landscape structure) and analyzed with a different modelling approach data from the Breeding Bird Survey at Idaho (area of study ~200000 km^2). This agreement in the results of two disparate analysis further support our feeling that topographic and climatic data are a source of potential predictors as adequate for breeding bird distribution modelling as vegetation data. Mixed models (vegetation plus topo-climatic variables) somewhat improve predictive ability but, what is more important, these models generates reasonably accurate predictions (AUC>0.7) for almost every species (>95%).

Within vegetation variables, landscape structure had a greater predictive ability than land-cover categories as predictors. This is so even when controlling the number of the potential predictors in the initial set, what means that, in the average, a single landscape variable is more useful for modelling than a single land-cover variable. Landscape

Table 5. Results of repeated measures ANOVA testing the effect in model accuracy (AUC) of the order of inclusion of topo-climatic or vegetation variables. Planned comparitions test if including topo-climatic variables first renders models that differ in accuracy from those in which all variables are tested simultaneously (T-V vs All), and if including vegetation variables first renders models that differ in accuracy from those in which all variables are tested simultaneously (V-T vs All). Names of models as in table 2.

Variable	Df	SS	MS	F	P
Error: species					
Residuals	78	2.410	0.031	-	-
Error: within					
Order of inclusion of variables	2	0.0023	0.0011	5.191	0.007
T-V vs All	1	0.0023	0.0023	10.312	0.002
V-T vs All	1	0.0000	0.0000	0.070	0.791
Residuals	156	0.0343	0.0002		

characteristics and land-cover categories are well known to be spatially correlated (Mac Garigal & Mac Comb 1995), but at our study scale this two sets of potential predictors are not totally redundant, since the inclusion of landscape variables greatly improved land-cover models. Therefore, our results suggest that landscape may have indeed a profound effect on breeding bird distribution, what could be of particular concern in heterogenous areas. A caveat to made is that we did not thoroughly explore individual models, so there may be some species for which land-cover predictors are as good as (or even better than) landscape, since species differ in their sensibility to landscape features (Knick & Rotenberry 1995; Bolger, Scott & Rotenberry 1997; Santos & Tellería 1998).

The relative importance of landscape configuration and site-specific vegetation variables in bird species distribution is open to discussion. So, some studies have found a relevant and direct influence of simple landscape patterns (e.g., distance to borders) on bird species distribution (Bolger, Scott & Rotenberry 1997; Sánchez-Zapata & Calvo 1999), while others have found more moderate and complex effects (Mac Garigal & Mac Comb 1995). Landscape may be relevant in explaining bird distribution, as our results suggests, for two reasons. First, according to a hierarchical view of habitat selection (Johnson 1980), landscape patterns provide environmental clues that are used for birds to select their home range, so that potential resourceful areas within the range of a species may remain unoccupied or sub-occupied if they lack those clues (Rolstad, Loken & Rolstad 2000). Second, the adequacy of apparently homogenous habitats for a particular species may not be spatially constant, for example by changing with distances to the limits between suitable and unsuitable habitats (Bolger, Scott & Rotenberry 1997). Indeed, there is some evidence of negative effects of landscape quality on birds physiology (individuals with feathers growing slower were found in small fragments of forests, Stratford & Stouffer 2001).

If the relevance of landscape on animal distribution is prevalent among different communities and taxa, then the regional programmes that (courageously) aim to model distributions at a high spatial resolution, such as the GAP in USA (Scott *et al.* 1993), LANDSPOT in Switzerland (Guisan *et al.* 2000), or the NFBS in Australia (see Pearce & Ferrier 2000; Pearce & Ferrier 2001) should consider landscape among their potential predictor variables (or, at least, in what concerns bird distribution). To our knowledge, only the latter explicitly includes explanatory variables related to landscape configuration (e.g., the probability of certain vegetation types in a surrounding area), and their models have proven useful and accurate for many taxa (Pearce & Ferrier 2001).

To conclude, our results have two implications in the modelling of bird-habitat relationships. First, the selection among sources of potential explanatory data (if any) should be done on the grounds of data availability, since model accuracy is likely to be similar for models derived from general land-cover and land-use vegetation maps, and from models derived from topographic and climatic information. However, we would recommend using the two sources of information. Second, local models that do not take into account landscape parameters are probably missing a relevant source of variation because the many implications of such variables on bird distribution here mentioned.

ACKNOWLEDGEMENTS

This work is a contribution to the project “predictive cartography of land birds: a pilot study in western Andalusia”, funded by the Dirección General de Enseñanza Superior e Investigación Científica (Ministry of Science and Technology) and FEDER funds from the EU, project # 1DF-97-0648. during the work, J.S. had a predoctoral fellowship from the Ministry of Education and Culture. The extensive field work presented in this paper could not have been done without the help and sense of humour of Daniel López Huertas, Luis M. Carrascal, and Mario Díaz who also brought intellectual insight to the project.

NOTE

A version of this chapter has been submitted to *Conservation Biology* with J.Bustamante and R.Díaz-Delgado.

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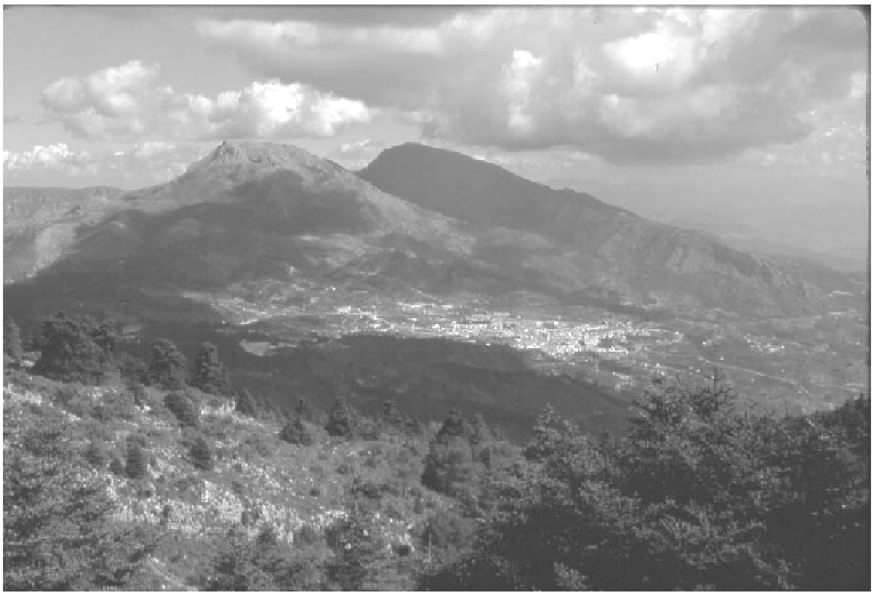


SECCIÓN TERCERA

Puesta en práctica: aplicaciones de la cartografía de especies

There is not one correct way to do ecology. Mathematical models, model ecosystems, field manipulation experiments and the search for large-scale patterns are all valid approaches, and all have their strengths and weaknesses.

—John Lawton, OIKOS 75: 145-147, 1996.

CAPÍTULO VII: Modelos aditivos generalizados y SIG para predecir la adecuación del hábitat de rapaces forestales en el sur de España

RESUMEN

Los gestores de recursos naturales necesitan predecir la distribución y abundancia de las especies y la adecuación de los hábitats existentes. En este trabajo se comprueba la efectividad de las variables topográficas y de vegetación, medidas con un Sistema de Información Geográfica (SIG), para predecir la distribución del Busardo ratonero *Buteo buteo*, Culebrera europea *Circaetus gallicus*, Aguililla calzada *Hieraaetus pennatus* y Milano negro *Milvus migrans* en el sur de España. Se realizaron censos por carretera en cuadrículas de 10x10 km para muestrear la distribución de esas rapaces y se ajustaron modelos aditivos generalizados (GAM, del inglés "Generalised Additive Models") con un procedimiento de selección de variables automático por pasos. En la mayor parte de las circunstancias, y usando sólo variables topográficas o de vegetación, fue posible construir modelos predictivos que mejoraron significativamente una clasificación al azar, pero los modelos no fueron precisos. Los modelos mejoraron su capacidad predictiva si se incluían las variables de ambos conjuntos y, además, en tres de las cuatro especies la inclusión de las coordenadas espaciales mejoró los modelos. Los mejores modelos, en cuanto a su capacidad predictiva, fueron los de la Culebrera europea y los de la Aguililla calzada; pero estos modelos incluyeron algunas variables de difícil interpretación ecológica. Los modelos para el milano negro alcanzaron altas tasas de clasificación correcta pero no fueron robustos. La distribución del Busardo ratonero resultó la más difícil de modelar probablemente debido a que esta especie está muy extendida y el hábitat parece no tener una calidad demasiado heterogénea a la escala en que fue medido. Nuestros resultados indican que es posible construir satisfactoriamente modelos predictivos para las rapaces usando predictores derivados de la cartografía temática digital disponible, e integrar tales modelos en un SIG para producir mapas precisos de la distribución del hábitat adecuado para cada especie.

CHAPTER VII: Using Generalised Additive Models and GIS to predict habitat suitability for forest raptors in Southern Spain

ABSTRACT

Resource managers need to be able to predict the distribution and abundance of species and the suitability of available habitats. We test the effectiveness of topographic and vegetation variables estimated with a Geographic Information System (GIS) to predict the distribution of the common buzzard *Buteo buteo*, short-toed eagle *Circaetus gallicus*, booted eagle *Hieraaetus pennatus* and black kite *Milvus migrans* in Southern Spain. We used road census in 10x10 km squares to sample raptor distribution and adjusted Generalised Additive Models with a stepwise variable selection procedure. In most cases it was possible to build predictive models that improved significantly a classification by chance with only topographic or only vegetation variables, but models were not accurate. Models improved their predictive ability if variables from both sets were included, and, further, in three out of four species the inclusion of spatial co-ordinates to account for neighbourhood effects improved these models. The best models considering their predictive ability were those for the short-toed eagle and for the booted eagle; but they included some variables difficult to interpret from an ecological point of view. Models for the black kite gave high correct classification rates but were not robust. The distribution of the buzzard resulted the most difficult to model probably because the species is very widespread and the habitat seems not very heterogeneous in quality at the scale we measured it. Our results indicate it is possible to build accurate predictive models for raptors using predictors derived from the digital environmental cartography available, and to integrate these models in a GIS to render accurate distribution maps of habitat suitability for each species.

1. INTRODUCTION

Resource managers need to know how species are distributed, how abundant they are in the landscape and how suitable for a certain species different habitats are. Distribution maps in books and field guides have been compiled traditionally from the records of localities were a species is known to be present plus a certain degree of interpolation and expert knowledge guess, usually in unknown proportions (see e.g. Harrison 1982). Atlas works provide distribution maps that are built in a more systematic way, but data are costly to obtain and are usually not detailed enough for all applications (see e.g. Hagemaijer & Blair 1997). In most Atlas it is not possible to distinguish between real absences and areas that have not been well covered with field work. Also, areas were the species is abundant tend to appear indicated in the same way as areas where the species is rare or accidental (Purroy 1997).

Predictive models provide an alternative way to build distribution, abundance and/or habitat suitability maps for a species (Austin *et al.* 1996; Morrison, Marcot & Mannan 1998; Beard, Hengartner & Skelly 1999; Brito, Crespo & Paulo 1999; Osborne, Alonso & Bryant 2001). They are based on the knowledge that species are habitat selective (Cody 1985), and they assume it is possible to find environmental variables that are good predictors of their distribution or abundance (Nicholls 1989; Buckland & Elston 1993). Considering that abundance is in many instances a good indicator of habitat suitability (but see Van Horne 1983; Vickery, Hunter & Wells 1992) it is possible to build habitat suitability maps with predictive models.

Geographic Information Systems (GIS) provide tools that allow to measure easily environmental variables that are available in a digital format for any point where the distribution of the species has been surveyed. These variables measured in a GIS can be tested statistically as prospective predictors of the distribution of the species. The resulting statistical models can generate predictive maps of the distribution of the species with the help of a GIS, provided that we have digital maps for the predictors for the study area (Pereira & Itami 1991; Guisan, Theurillat & Kienast 1998; He *et al.* 1998; Rico Alcázar *et al.* 2001). It is desirable that the causal relation between predictors and the distribution of the species is known, as this would allow experts to know when the extrapolation to other areas is possible. Also, is important that a detailed cartography for the predictors is available and that it can be updated easily and at low cost. Models based on predictors that are as difficult to update as the distribution of the species itself are of limited use for a resource manager.

It is expected that vegetation will be a better predictor of bird distribution than topography, because bird species tend to be associated with certain vegetation types more than with certain topographic features (Cody 1985). On the other hand, it is easier and cheaper to generate a Digital Elevation Model (DEM) for an area than a vegetation map that is up to date. Also land-use/land-cover maps are very dependent on the criteria used to generate them, so that two land-use/land-cover maps of the same area can be very different if they have been generated for different purposes or by different agencies (Cherrill &

McClean 1999). As vegetation and land-use over a territory is not independent of topography, we expect that topographic variables measured on a DEM would have a certain predictive ability of bird distribution. We want to know: (1) if the information contained in a DEM is enough to predict the distribution of some bird species, (2) if the models derived from a DEM are better or worse than those derived from a vegetation map, (3) if models derived from one group of variables (topography or vegetation) can be improved with variables from the second group, and (4) if considering neighbourhood effects we can improve the predictive ability of habitat models.

In this paper we have tested the possibility of predicting the distribution of four species of forest raptors: common buzzard *Buteo buteo* Linnaeus, booted eagle *Hieraaetus pennatus* Gmelin, short-toed eagle *Circaetus gallicus* Gmelin and black kite *Milvus migrans* Boddaert, in Southern Spain using as predictors topographic variables derived from a DEM, vegetation variables derived from a land-use/land-cover digital map and spatial co-ordinates to correct for neighbourhood effects.

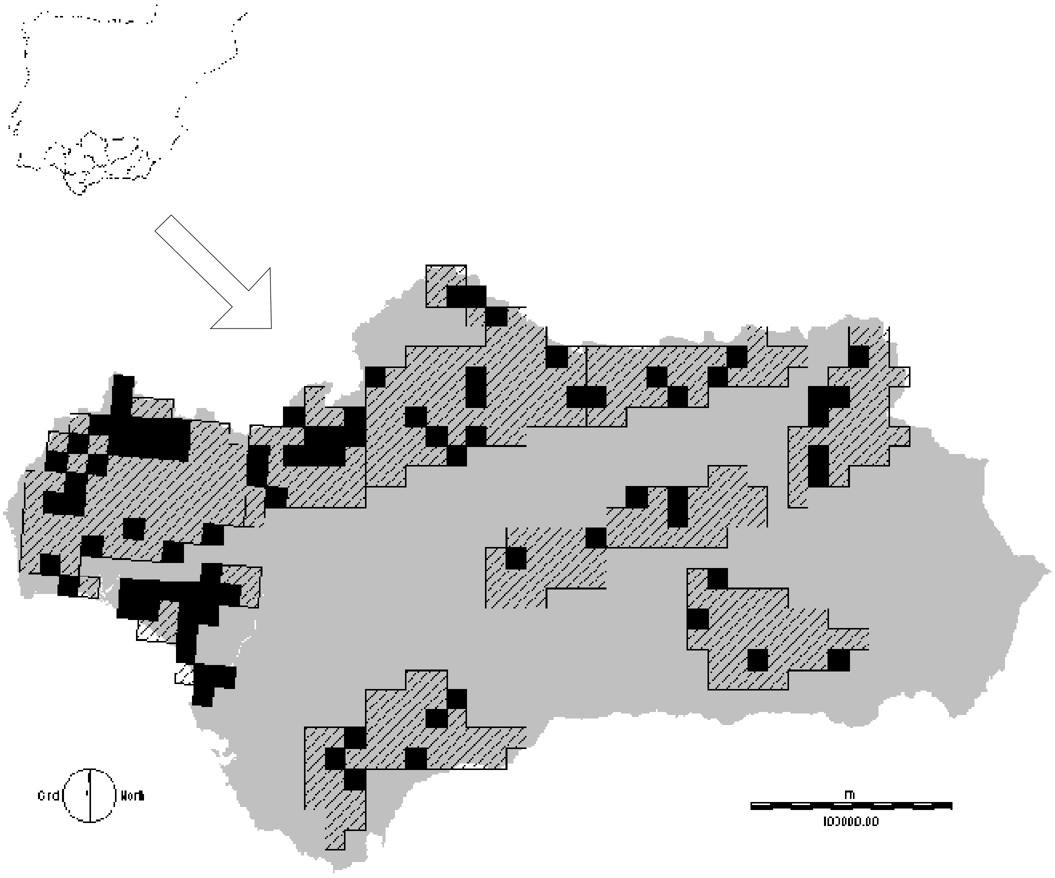


Figure 1. Location of study area (black striped polygons) and censused squares (solid squares) in the Autonomous Community of Andalusia (Spain).

2. METHODS

2.1. Study area

We restricted our study to the Autonomous Community of Andalusia (Southern Spain) and divided the area in 10x10 km squares using the UTM grid. We selected all continuous squares where dominant vegetation was Mediterranean forest or Mediterranean scrubland. The study area was divided in 9 zones that covered a surface of 37,700 km^2 . We selected a sample of 10x10 km squares in each zone to be censused for raptors (Fig. 1). Census work was initially designed to estimate red kite *Milvus milvus* breeding population –a species not considered in this paper–, so the sample was stratified between zones, and the number of squares sampled within each zone was proportional to expected breeding density of red kites. Within each zone the squares to be censused were selected at random. After the censuses were carried we selected the four species of forest raptors that resulted more abundant: common buzzard, booted eagle, short-toed eagle, and black kite, and tried to build predictive models for them. As we had excluded *a priori* those continuous zones were dominant land-use is agriculture we did not made predictions from our models in those areas.

2.2. Raptor census

A total of 88 squares of 10x10 km were censused (23% of the study area, Fig. 1). In each square we performed approximately 40 km of road census with a vehicle, using dirt roads or roads with low traffic that allowed us to census at a speed of 20 km/h. Two persons carried out each census, one driving and the other recording all raptors. All squares were censused in spring 1996, between May and July. Although observers recorded number of individuals of each species and the co-ordinates of each contact with a raptor, for our models we only used the presence/absence of each species in each square. Prevalence (the ratio of positive squares to total sample) was similar for the four species: common buzzard (0.45), short-toed eagle (0.43), booted eagle (0.42), and black kite (0.39)

2.3. Predictive variables

Estimates of all environmental variables within each square were performed in a GIS, using IDRISI for Windows v.2.0 (Eastman 1997) and IDRISI32 v.1.01 (Eastman 1999). Topographic variables (T) were estimated from a DEM of the study area (50 m horizontal resolution, 20 m vertical resolution), that had been derived from interpolation of 1:50.000 topographic maps. Overall DEM accuracy was checked by comparing a random sample of point co-ordinates with the altitude measured from 1:50.000 topographic maps. This gave an error of less than 20 m (or one contour line). The DEM was checked for errors at the joints of different map sheets, as these errors could affect our estimates of slope. Pixels that gave unreliable slopes were excluded from the estimates of slope for each square. Topographic variables tested as predictors in the models are given in Table 1. Land-use/land-cover variables (U) were estimated from the SinambA 1995 digital land-use/land-cover map for Andalusia (Consejería de Medio Ambiente, Junta de Andalucía, unpubl. data). The map has 112 land-use/land-cover classes that have been updated with satellite image and aerial photographs and records all land-use/land-cover polygons that have more than 25 Ha. We rasterised the original Arc-Info coverage at a 50 m resolution, and all our variables were estimated on this raster image. The estimated Vegetation Index for each square was derived from the Experimental Calibrated Global Vegetation Index from NOAA-AVHRR (NOAA 1992). Land-use/land-cover variables tested as predictors in the models are given in Table 1.

2.4. Stastistical models

We used Generalised Linear Models (GLM) (Nelder & Wedderburn 1972; Dobson 1983; McCullagh & Nelder 1989) and Generalised Additive Models (GAM) (Hastie & Tibshirani 1990) with a binomial error and a logistic link to model the presence/absence of each raptor species in each 10x10 km square. We used as predictors a set of topographic variables (T models), a set of vegetation, land-use/land-cover variables (U models), both sets of variables (TU models), and both sets of variables plus spatial co-ordinates to correct for possible neighbourhood effects (TUC models). These final TUC models were also simplified with more stringent statistical criterion looking for possible causal relationships between environmental variables and species distribution (TUCS models)

GLM are mathematical models in which a relation is stablished between a response variable and a linear combination of explanatory variables using an error distributions and a link function adequate to the nature of the response variable. Their use is well stablished in ecology (Crawley 1993) and have been previously used to model raptor distribution and habitat

Table 1. Description of explanatory variables tested in predictive models

Acronym	Description and source
Topograhic variables	
Altitude	Mean altitude a.s.l. estimated from a DEM⁽¹⁾ of the study area.
Slope	Mean slope (%) in the 10x10 km square for a 50 m pixel as estimated from the DEM using the SURFACE module of IDRISI32 that uses a rook's case procedure (Monmonier 1982; Eastman 1999)
Southern Orientation	Fraction of 50 m pixels showing a South-east to South-west orientation in the 10x10 km square. Orientation calculated from the DEM with SURFACE module of IDRISI32. Flat pixels are considered to have a southern orientation
Rivers	Fraction of 50 m pixels that are crossed by a river or a stream obtained converting from vector to raster the 1:50.000 hydrology coverage of Andalusia (2)

(1) Digital Elevation Model of Andalusia obtained by interpolation of 20 m contours from the 1:50.000 topographic maps. Horizontal resolution 50 m. Source: SinambA (1999), Consejería de Medio Ambiente, Junta de Andalucía., unpubl. data.

(2) Hydrology cover of Andalusia digitised from 1:50.000 topographic maps. All permanent rivers and streams are considered irrespective of their size. Source: SinambA (1999), Consejería de Medio Ambiente, Junta de Andalucía, unpubl. data.

Table 1 (Cont.). Description of explanatory variables tested in predictive models

Acronym	Description and source
Land-use/land-cover variables	
Urban	Fraction of 50 m pixels classified in the land-use/land-cover raster map(3) in the urbanised and infrastructure classes.
Agricultural	Fraction of 50 m pixels classified in the land-use/land-cover raster map in the agricultural classes.
Natural	Fraction of 50 m pixels classified in the land-use/land-cover raster map as natural vegetation.
Dense Forest	Fraction of 50 m pixels included in classes with tree coverage >50 % in the land-use/land-cover raster map.
Dispersed Forest	Fraction of 50 m pixels included in classes with tree coverage from 5 to 50% in the land-use/land-cover raster map.
Dense Scrubland	Fraction of 50 m pixels included in classes with a scrub coverage >50 % in the land-use/land-cover raster map.
Disperse Scrubland	Fraction of 50 m pixels included in classes with a scrub coverage from 20 to 50% in the land-use/land-cover raster map.
Pine Forest	Fraction of 50 m pixels included in classes of natural or planted coniferous forest (tree coverage > 5 %) in the land-use/land-cover raster map.
Eucalyptus Forest	Fraction of 50 m pixels included in classes of planted Eucalyptus spp. Forest (tree coverage > 5 %) in the land-use/land-cover raster map.
Broad-leaved Forest	Fraction of 50 m pixels included in classes of natural broad-leaved forest (mostly Quercus spp. forest, tree coverage > 5 %) in the land-use/land-cover raster map.
Olive/fruit Groves	Fraction of 50 m pixels included in classes of cultivated trees (mainly olive, fruit and almond groves) in the land-use/land-cover raster map.
Forest Perimeter	Border in meters between forested and non-forested classes divided by number of 50 m pixels with land-use information.
MSSVI	Mean Spring-Summer Vegetation Index (March to August). First a mean image for each month for the period April 1985-August 1991 was obtained from monthly values of the Experimental Calibrated Vegetation Index (version 2, monthly values from the U.S. Geological Survey) (NOAA 1992). Then the Mean Index was computed from mean monthly values. The NDVICOMP module of IDRISI32 was used to compute mean values as quadratic means of original values according to the formula $x' = \sqrt{\Sigma x_j^2 / n}$. The mean index (original data at approximate 15 km resolution) was reprojected to UTM co-ordinates at 1 km resolution, filtered tree times with a 3x3 mean filter, and mean values were extracted for 10x10 km squares

(3) Land-use/land-cover 1995 digital map of Andalusia. Source: SinambA (1999), Consejería de Medio Ambiente, Junta de Andalucía, unpubl. data, but see Moreira and Palacios (1995) for a description of land-use/land-cover 1991 digital map.

selection(Donázar, Hiraldo & Bustamante 1993; Austin *et al.* 1996; Bustamante 1996; Bustamante 1997; Sánchez-Zapata & Calvo 1999; Suárez, Balbontín & Ferrer 2000). Generalised Additive Models (GAM) are a more general class of models from which GLMs constitute a particular case (Hastie & Tibshirani 1990). In GAMs the relation between the response and the explanatory variable is replaced by a scatterplot smooth function of the data (s).

$y = \mathrm{s}(x)$ eqn 1

As linear functions can be seen as particular cases of scatterplot smoothing when span = 1, GLM models can be seen as a restricted subset of GAM models (Hastie & Tibshirani 1990).

Model fitting was performed using S-Plus 2000 (MathSoft, 1999). To find the best T, U, TU model for each species, we chose an automatic forward-backward stepwise variable selection procedure (procedure step.gam) testing in turns polynomial fits of all the explanatory variables in a set up to third degree. The step.gam procedure uses a stepwise search to select the best model in terms of Akaike's Information Criterion (AIC), given a range of models to consider. The AIC statistic has into account both the information explained by the model and its complexity, according to the expression:

AIC = Deviance + 2 * Scale * residual degrees of freedom (eqn 2)

where the scale is the scaled Chi-squared (Sakamoto, Ishiguro & Kitagawa 1986). The gam procedure in S-Plus allows to fit all models even those in which the scatterplot smoother is a linear or polynomial function. The particular stepwise procedure that we implemented starts from a null model and builds all possible univariate models containing the predictor as a first degree polynomial. It compares all these univariate models and the null model and keeps the one with a lower AIC. In a second step it tests including in the model previously selected each of the remaining predictors as first degree polynomials or transforming to a second degree polynomial the predictor included in the previous step. The model with the lowest AIC is selected at each of the steps. In a third step the program tests excluding all the predictors included, one at a time, or reducing the degree of the polynomials included. The procedure cycles these steps until the AIC can not be decreased.

As the procedure does not test automatically a second order polynomial if the first order polynomial is not significant in the first case, we also run the procedure a second time eliminating all non-significant first-order terms, and a third time eliminating all non-significant second-order terms. Using this procedure we obtained for each species (i) the best predictive model derived from the topographic variables set (T model), (ii) the best predictive model derived from the land-use/land-cover variable set (U model), and the best predictive model derived from all topographic or land-use/land-cover variables (TU model).

The best TU model was corrected for neighbourhood effects (Legendre 1993) fitting a nonparametric surface of latitude and longitude (a bivariate local regression surface, LOESS, with span equal to 0.5), and then we tested by removal (procedure step.gam) if T variables, U variables and the spatial surface remained significant. The resulting model was the TUC model. We decided to use linear models with a maximum 3 df instead of scatterplot smoothers for topographic and land-use/land-cover variables both because polynomials are easier to implement in a GIS than scatterplot smoothers (Guisan, Theurillat & Kienast 1998), and in order to keep low the model degrees of freedom considering our sample size (see a similar approach inPreisler, Rappaport & Wood 1997). We used a smoother for spatial co-ordinates because we had no a priori expectation of spatial trends and we wanted to be strict in checking if environmental variables remained significant after correcting for any possible neighbourhood effects.

In order to avoid overparametrization and to obtain a simpler model, we further modified the TUC model by a backward stepwise procedure using the χ^2 statistic (more conservative than AIC Ludden, Beal & Sheiner 1994; Burnham & Anderson 1998) and produced the TUCS models. We only kept variables (or terms of variables) when removing them yielded a significant increment of residual deviance. A variable was removed from the model if $P > 0.01$, but the order of a polynomial was only reduced if $P > 0.05$. We believe that the TUCS models although having lower predictive power than the TUC models provide us with more appropriate cues of actual habitat selection by the species.

Predicted probabilities of appearance given by the models were converted to 1 (presence) or 0 (absence) values by choosing a threshold value for each species so that the number of predicted and actual presences were equal. Success of predictions was then measured by the correct classification rate and by the Kappa statistic which measures the correct classification rate corrected by chance (Titus, Mosher & Williams 1984; Fielding & Bell 1997).

Stability of models was studied using a Leave-One-Out (LOO) resampling technique (each square was left out in turns and the model was refitted with the remaining 87 squares, the probability of the square left out was estimated from the model not containing it), and we compared presence/absence predictions of the original model with those of the models generated by resampling.

3. Result

3.1. Common buzzard

The models that contained both topographic and land-use variables (TU model) predicted significantly better that those based on one type of variables (T or U models) (Table 2). The spatial co-ordinates did not improve the TU model, so TU and TUC models are actually the same model. All models except the T model predicted significantly better than chance. The value of Kappa was poor for the U model (0.24) (Landis & Koch 1977) that consider poor predictive models those with Kappa < 0.4) but good for TU and TUCS models (0.45 and 0.50 respectively) (Fig. 2). Models were quite stable, as measured by a the percentage of coincidences with LOO models, that were above 90% in every case (Fig. 3). The spatial predictions of U, TU, TUC and TUCS models were similar (only the TUC model is represented in Fig. 4) while the T model was the one giving a more different location for suitable areas.

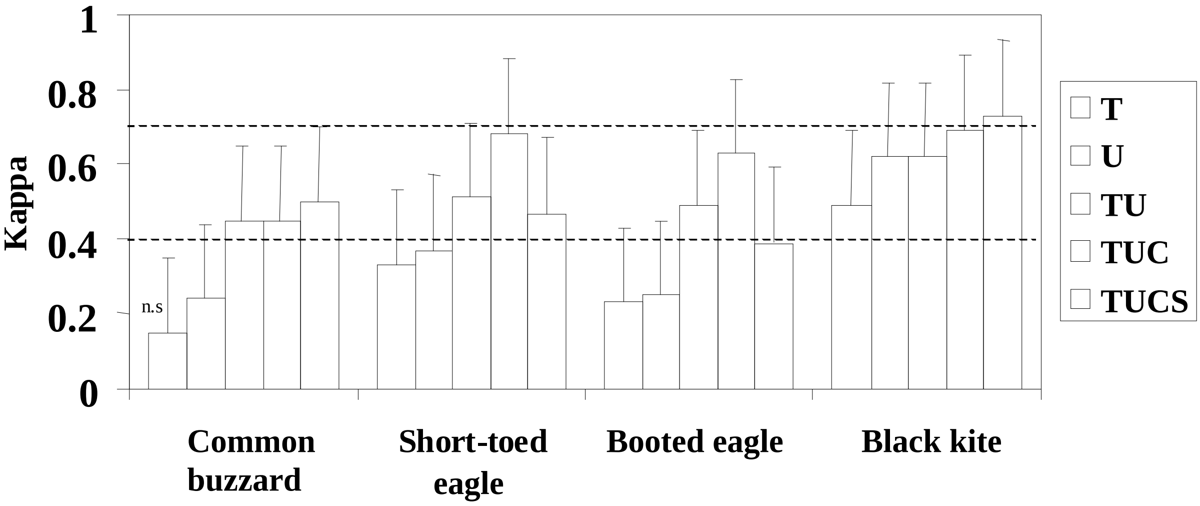


Figure 2. Classification improvement over chance (Kappa statistics) for all models. Variable sets used in each model: Topography (T), land-use/land-cover(U), topography and land-use/land-cover (TU), topography, land-use/land-cover and co-ordinates (TUC), and simplified TUC model (TUCS). Standard Error for kappa is 0.1 in all cases. n.s. = not significant. Dashed lines are suggested boundaries for poor, good and excellent agreement according to Landis and Koch (1977)

According to the TUCS model the probability of presence of the common buzzard increases with the variables *Dense Forest* and *Forest Perimeter* while decreases with *Slope* and *Eucalyptus Forest*. These four variables were present in all the mixed models (TU and TUC model), but *Altitude* entered instead of *Slope* in the T model, and *Pine Forest* entered instead of *Eucalyptus Forest* in the U model. However, within these pairs of variables the relationship with the response was very similar (a strong linear decrease in both cases). *Altitude* is positively correlated with *Slope* and *Eucalyptus Forests* are to a great extent correlated with *Pine Forests* so these pairs of explanatory variables probably indicate the same habitat and land-use features.

3.2. Short-toed eagle

The models that contained both topographic and land-use variables (TU and TUC models) predicted significantly better that those based on one type of variables (T or U models) (Table 2). All models predicted significantly better than chance, having significant Kappas varying from a poor (T and U model, 0.33 and 0.37 respectively) to a good agreement (TU, TUC and TUCS models, 0.51, 0.68 and 0.47 respectively, Fig. 2). The model with highest corrected classification rate was the TUC model (Fig. 5). Coincidence of prediction between each model and those generated by the LOO procedure were above 95% for the T and U models, and between 84 and 92% for the mixed TU, TUC and TUCS models (Fig. 3). The spatial predictions derived from all models showed a good spatial agreement

Table 2. Best models for each species, based on topography (T), land-use/land-cover(U), topography and land-use/land-cover (TU), topography, land-use/land-cover and co-ordinates (TUC), and simplified TUC model (TUCS)

Species	Model	Variables	(%) correct classification	AIC (deviance, df)
Common buzzard	T	Altitude + Rivers	58	118.1 (112.1, 85)
	U	(Dense Forest)^2 + (Disperse Scrubland)^2 + Pine Forest	63	113.6 (101.6, 82)
	TU	Slope + (Dense Forest)^2 + Dense Scrubland + Eucalyptus Forest + Forest Perimeter + MSSVI	73	96.6 (80.6, 80)
	TUC	Slope + (Dense Forest)^2 + Dense Scrubland + Eucalyptus Forest + Forest Perimeter + MSSVI	73	96.6 (80.6, 80)
	TUCS	Slope + Dense Forest + Eucalyptus Forest + Forest Perimeter	75	- (90.6, 83)
Short-toed eagle	T	(Altitude)^2 + (Rivers)^2 + Southern Orientation	67	109.8 (97.8, 82)
	U	(Dense Forest)^2 + (Pine Forest)^2 + (MSSVI)^2	69	111.3 (97.3, 81)
	TU	(Rivers)^2 + Southern Orientation + (Dense Forest)^3 + (Pine Forest)^2 + (Eucalyptus Forest)^2 + (MSSVI)^2	76	99.7 (73.7, 75)
	TUC	(Rivers)^2 + Southern Orientation + (Dense Forest)^3 + (Pine Forest)^2 + (Eucalyptus Forest)^2 + (MSSVI)^2 + LOESS(Latitude, Longitude)	84	98.3 (56.3, 67)
	TUCS	(Rivers)^2 + MSSVI + LOESS(Latitude, Longitude)	74	- (81.0, 76)
Booted eagle	T	Slope + Southern Orientation	63	118.8 (112.8, 85)
	U	(Dense Forest)^2	64	115.3 (109.3, 85)
	TU	Southern Orientation + (Dense Forest)^2 + (Disperse Scrubland)^2 + (Broad-leaved Forest)^2	75	105.7 (89.7, 80)
	TUC	Southern Orientation + (Dense Forest)^2 + (Disperse Scrubland)^2 + (Broad-leaved Forest)^2 + LOESS(Latitude, Longitude)	82	105.1 (72.4, 72)
	TUCS	(Dense Forest)^2 + Disperse Scrubland + Southern Orientation	70	- 96.6, 83)
Black kite	T	(Slope)^3	76	98.4 (90.4, 84)
	U	(Agricultural)^2 + (Natural)^2 + Disperse Scrubland + Olive/fruit Groves + (Pine Forest)^3 + (Eucalyptus Forest)^3	82	88.7 (62.7, 75)
	TU	Slope + (Natural)^2 + (Disperse Scrubland)^2 + (Pine Forest)^3	82	87.7 (69.8, 79)
	TUC	(Natural)^2 + (Pine Forest)^3 + LOESS(Latitude, Longitude)	85	83.4 (55.5, 74)
	TUCS	Natural + (Pine Forest)^2 + LOESS(Latitude, Longitude)	88	- (57.1, 76)

The TUCS model retained only two of the six topographic and habitat variables of the TU and TUC model (Table 2): *Rivers* and *MSSVI*, that entered, respectively, as a quadratic and a positive linear function. Both entered with a similar form in the single T and U models. Co-ordinates entered the TUC model without removing variables or modifying noticeably their form in the TU model. The shape of the spatial surface in the model indicates a contagious distribution and that the probability of presence of short-toed eagle increases in the north and central parts of the study area.

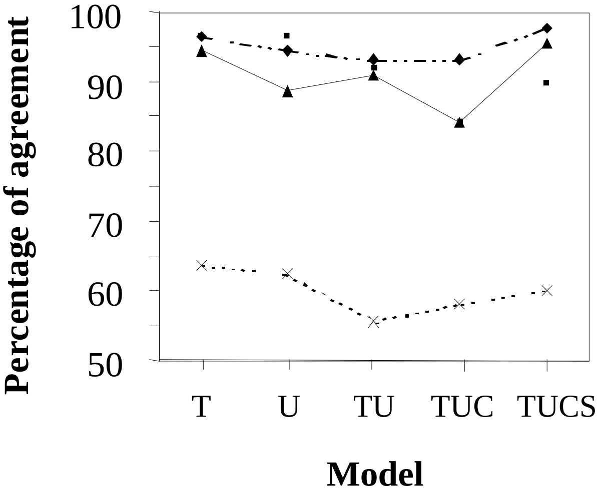


Figure 3. Percentage of agreement between predictions of the original models and those generated by the Leave-One-Out procedure. Diamonds, Common buzzard; squares, Short-toed eagle; Triangles, Booted eagle; Crosses, Black kite.

3.3. Booted eagle

The models that contained both topographic and land-use variables (TU and TUC models) predicted significantly better that those based on one type of variables (T or U models) (Table 2). All models predicted significantly better than chance, but Kappas were only good for the TU and TUC models (0.49 and 0.63 respectively) (Fig. 2). Coincidences with predictions of LOO models varied between 84 (TUC) and 95% (TUCS, Fig. 3). The spatial predictions derived from the different models agree in some areas but disagree in others. Spatial prediction from the best model in terms of predictive ability (TUC model) are given in Fig. 6.

The explanatory variables *Southern Orientation* and *Dense Forest* that were included in the simplified TUCS model, were the more stable of all the variables entering models for this species (single and mixed, Table 2). The probability of presence of the eagle increased with *Southern Orientation* following a positive linear function and also increased as a quadratic function of *Dense Forest* . The TUCS model also indicated an increase in the probability of presence with *Disperse Scrubland* that had not entered in U model. The spatial co-ordinates surface of the TUC model indicated a higher probability of presence in the north of the study area but it was no longer significant in the TUCS model. The co-ordinates entered the TUC model without removing or changing the form of the variables that were previously in the TU model.

3.4. Black kite

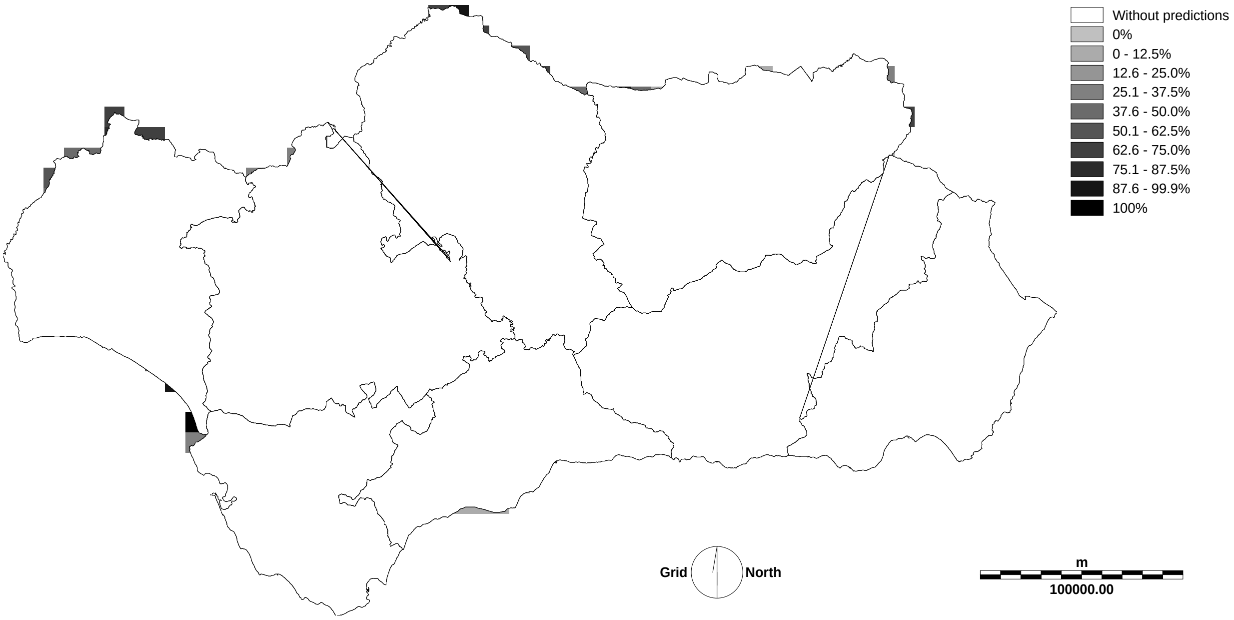
Models for the black kite had AIC statistics below 98, what is similar or lower than the best achieved for the rest of the species. The models that contained both topographic and land-use variables (TU and TUC models) performed better than those based on one type of variables (T and U models), although the difference between the U and the TU model was only slight (Table 2). Correct classification rates were over 75% for all models (Table 2). They were significantly better than chance and showed a good agreement with original data (Fig. 2). However, the stability of the models was low, as coincidences with predictions of LOO models were only between 55-65 % (Fig. 3). The spatial predictions from the TUC model are given in Fig. 7.

The explanatory variables *Natural* and *Pine Forest* were present in both the single and the mixed models. In the TUCS model the probability of presence of the black kite decreased linearly with *Natural* and increased with *Pine Forest*. The spatial co-ordinates surface improved the TU model and indicated an increase in the probability of presence to the north and west of the study area.

4. DISCUSSION

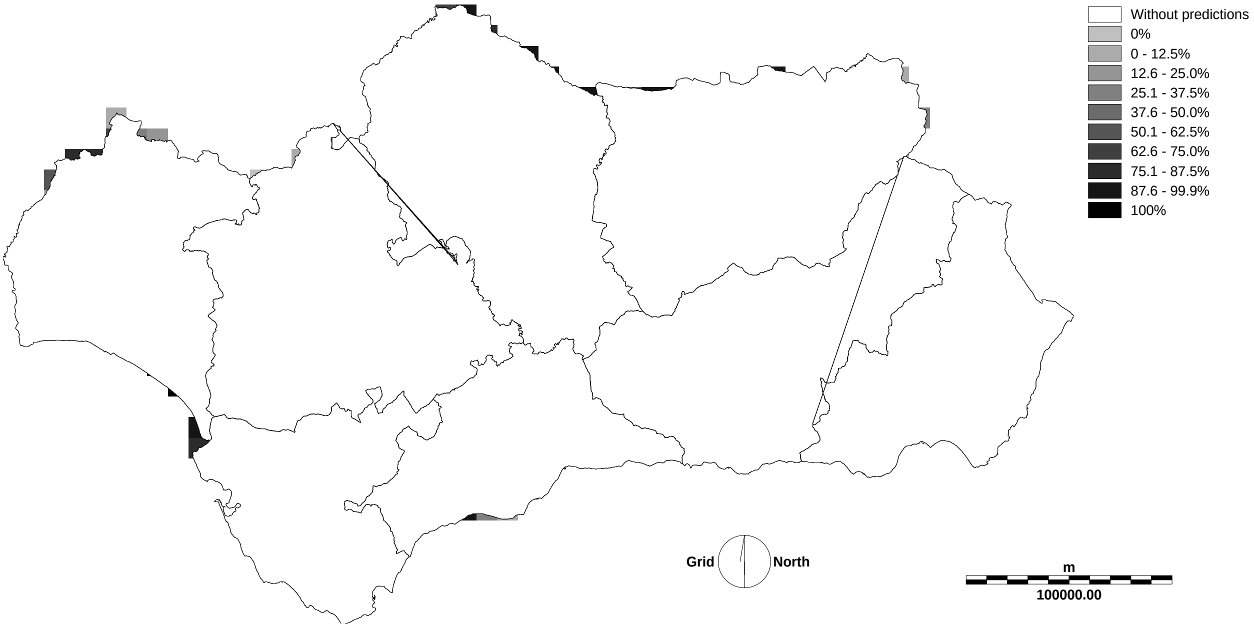
4.1. Common buzzard

The models we were able to build for the common buzzard had a poor performance. The best models (TU and TUCS models), although significantly better than chance were only 45 to 50% better. This is not too high if we consider that models under 40% are considered poor models (Landis & Koch 1977). This could be due to an incorrect selection of either the explanatory variables or the scale to which those and the response are analysed. Indeed, there are several reasons to think that scale is precluding an accurate prediction. First, we believe that the selected pool of variables was wide enough to cover, direct or indirectly, most of the ecological needs of buzzard (and the other raptors in general). The variables that entered in the simplified TUCS model are easily interpreted and are in agreement with what we expected before building the models: the common buzzard seems to favour forested areas interdigitated with other open habitats, and avoids poor homogeneously reforested land (areas dominated by eucalyptus and pine trees). This kind of habitat is most common at low and medium altitude (where *Slope* tends to be moderate). This preference with forested habitat has also been seen in other Mediterranean areas in Spain (Sánchez-Zapata & Calvo 1999), and a strong relationship between breeding distribution and border between forest and open habitats was also apparent in the previous study and in another study in Scotland (Austin *et al.* 1996). Co-ordinates did not enter in TUC model, suggesting that the common buzzard is widespread within the study area and has no clear spatial trend. Moreover, the low average influence of a single sample square in the models (the percentage of agreement with LOO models was very high) is in support of this view. It could be that within the limits of the study area chosen and with the resolution of our 10x10 km sampling squares there are not big differences in suitability for the buzzard. That would explain why our best model only improves slightly over a null model that gives equal probabilities to all squares. In order to build better models for this species it would be necessary to extend the study area to increase the range of environmental conditions met by the species, or to work at a finer resolution so that sampling units would be more variable in relation to habitat suitability for the buzzard. Austin et al.(1996) working at a finer resolution were able to find adequate predictive models for the buzzard in an area of Scotland.



common buzzard

Figure 4. Spatial predictions of the best model for the common buzzard (TUC) White areas indicate where the model is not applicable.



short-toed eagle

Figure 5. Spatial predictions of the best model for the short-toed eagle (TUC) White areas indicate where the model is not applicable.

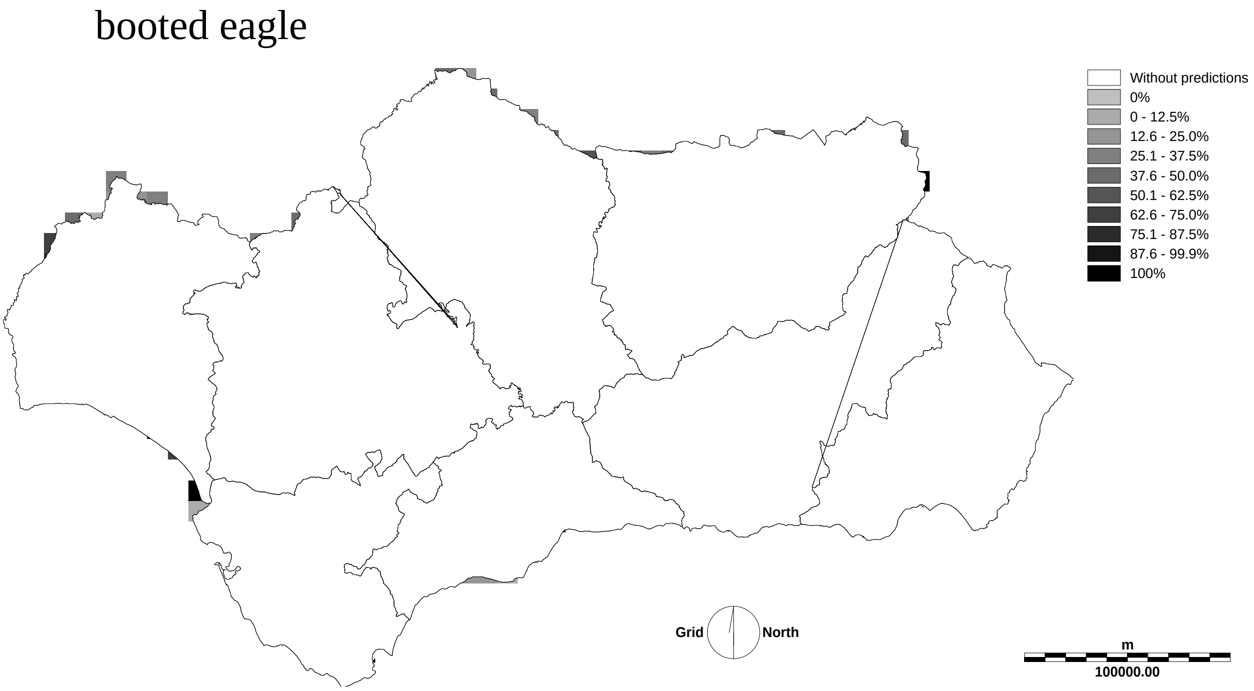


Figure 6. Spatial predictions of the best model for the booted eagle (TUC) White areas indicate where the model is not applicable

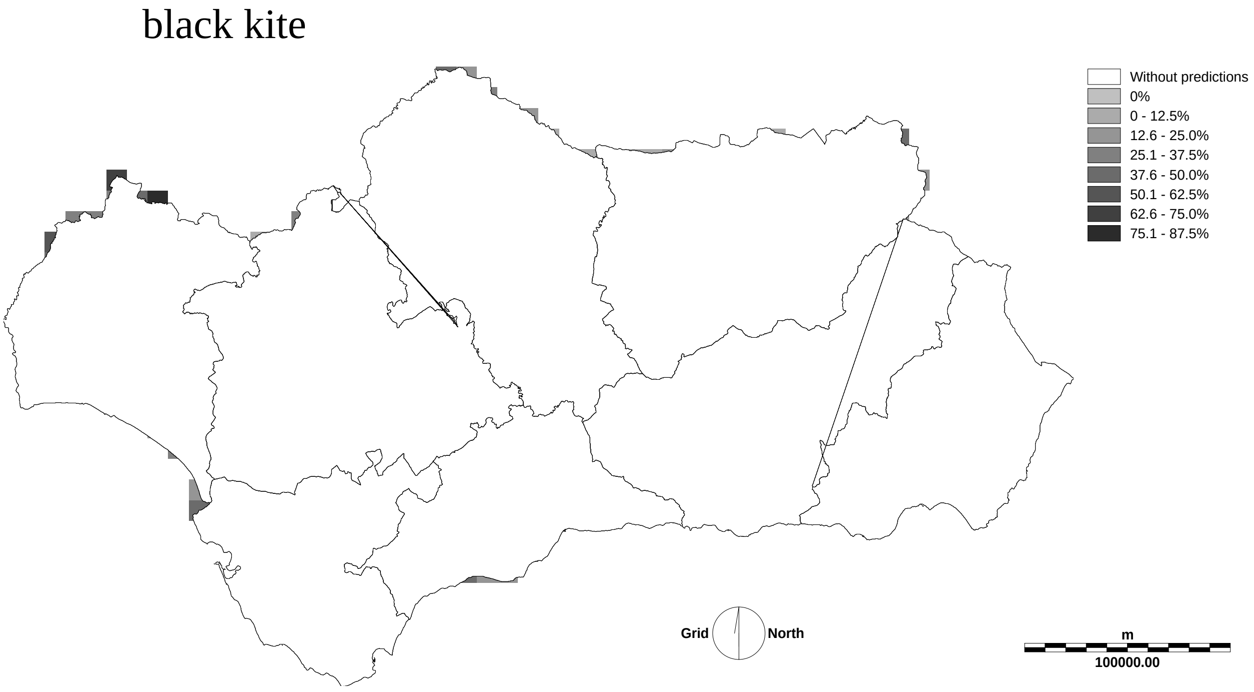


Figure 7. Spatial predictions derived from the best model for the black kite (TUC) White areas indicate where models are not applicable

4.2. Short-toed eagle

Mixed models for this species are satisfactory in terms of predictive ability. However, the best models (the TU and TUC models) have numerous variables and are difficult to interpret. Some of these may have entered by chance, since our more strict procedure of variable removal led to a very simplified TUCS model. This simple model is still difficult to interpret from the point of view of the ecology of the species. It suggests a selection for the more productive areas regarding vegetation and a noticeable neighbourhood effect identified by the significance of the spatial co-ordinates, but we have no interpretation for the strong apparent avoidance of squares with intermediate levels of *Rivers*

4.3. Booted eagle

Similarly to what happened with the short-toed eagle, the mixed models for the booted eagle were satisfactory in terms of predictive ability but difficult to interpret. They suggest a slight neighbourhood effect, since co-ordinates entered the TUC model (but were rejected in the stricter TUCS model). TUCS model suggest also an expected preference for more forested squares and a positive relation (although slight) with *Disperse Scrubland* and *Southern Orientation*. A similar preference for forested areas and areas of scrubland was found by Sánchez-Zapata & Calvo (1999) in South-eastern Spain.

4.4. Black kite

Models for this species, both single and mixed, have the greatest predictive ability among those generated in this work. This was to be expected since the black kite is the species with a more localised distribution in the west of the study area (it is abundant mainly in the Doñana National Park and surrounding areas), and thus it is *a priori* easy to model: any variable that identifies the clumped zone of distribution will have a high predictive ability. This seem to be the case for the positive relation between the presence of the species and *Pine Forest* (TUCS model), since the habitat the black kite occupies in Doñana is mainly pine-tree forest. On the other hand, TUCS model shows a negative relation with *Natural* that could be closer to the actual habitat selection of this species, known to breed and feed in humanised areas more frequently than the rest of the raptors analysed in this work.

4.5. General conclusions

Topography and vegetation (as derived from a land-use/land-cover map) have a certain predictive ability on the distribution of forest raptors, but neither of them alone seem to be able to provide accurate predictions of the distribution of the species we studied. Considering the extreme results, topography was not able to predict better than chance the distribution of the buzzard but, on the other hand, topography or vegetation alone gave relative good predictive models (> 40% better than chance) for the black kite. Models derived from vegetation variables had a slightly higher predictive ability and they were better (in terms of AIC) than topographic models, but we cannot exclude that this could be a consequence of the former having a more numerous set of variables from which to choose. Mixed models were needed to obtain a fair (40-75%) improvement over chance in predictions, what shows that both set of variables provide a different information content. Probably topographic variables complement the information on changes in habitat/vegetation that are not adequately covered in the land-use/land-cover map. Our results are in agreement with those of Beard et al.(1999) who found that models based on vegetation, climate or spatial autocorrelation were better than null models to predict the distribution of birds in Idaho, but that the best predictive models were those combining variables from two sets.

As has been shown in other studies (Smith 1994; Augustin, Mugglestone & Buckland 1996; Chou & Soret 1996; Lennon 1999; Merrill *et al.* 1999; Osborne, Alonso & Bryant 2001) there is much to gain in incorporating terms in the model building that take account of neighbourhood effects. These can arise because of habitat being more similar between neighbouring areas or because the probability of finding a individual in a place may not be independent of the probability of finding individuals in neighbouring places (Augustin, Mugglestone & Buckland 1996). Raptors are very mobile and their distribution may be less influenced by local habitat features than in other animal groups(Chou & Soret 1996). If the presence of raptors in 10x10 km squares is autocorrelated, the “spaceless” models T, U and TU may be formed by the more autocorrelated variables (Lennon 1999) and then a biologically meaningful interpretation of the models could be precluded. This does not seem to be the general case in our study, since the incorporation of co-ordinates (TUC) improved the prediction ability but did not remove any variables that had entered previously. The only exception to this rule were the models for the black kite, whose distribution is clearly contagious, with peak numbers around the Doñana National Park, and in which variables like *Slope* and *Disperse Scrubland* were no longer significant when co-ordinates entered the models.

Our study was able to produce predictive maps for all four species that where significantly better than chance (TUC maps Figs 4-7). These maps can be useful for pointing out the best areas for each species. Although maps produced are statistically accurate it is difficult to know how reliable will be the predictions if the models are extrapolated to other areas. The models for the short-toed eagle and the booted eagle were relatively good, although some of the variables that entered the models probably do not have a direct causal relation with the distribution of the species and are difficult to interpret ecologically. The distribution of the black kite in the study area was relatively easy to predict but models proved to be very unstable. These models probably can provide a very limited insight to which factors affect the distribution of the species and we do not expect that they can make accurate predictions outside the study area. The fact that the inclusion of the spatial co-ordinates modifies the previous model indicates that the significance of some variables can be attributed, at least partially, to a neighbourhood effect. On the other hand, the models for the buzzard had a poor predictive performance at this scale but the selection of variables was relatively stable and coincident with variables that have shown to affect the distribution of the species in other areas or at other spatial scales. In a similar study in Argyll (Scotland) --in which the extent of the study area (140 km^2) was similar to our resolution (100 km^2)-- Austin et al. (1996) were able to build good predictive models for the distribution of common buzzard nesting sites in 0.5x0.5 km squares. All this supports our conclusion that our study area is too homogeneous for the common buzzard at the scale of 10x10 km squares. Still the map produced by our model probably reflects some subtle differences in suitability across the study area, and could be useful as a management tool for the species.

Finally, our results show it is possible to produce accurate predictive maps for the distribution of raptors using available environmental cartography elaborated for other purposes. But caution should be taken when using these models as good predictive accuracy does not necessarily imply that they are good explanatory models of the habitat selection of each species (Mac Nally 2000) .

ACKNOWLEDGEMENTS

Data for this study were collected while conducting a red kite survey financed by the Consejería de Medio Ambiente, Junta de Andalucía and directed by F. Hiraldo. We thank E. López, F. Gavilán, R. Cañete, J.M. Pérez, E. Urbano, F. Buenestado, S. Buenestado, F. J. Ávila, A. Matos, J. Bustamante, F. Hiraldo, J. Ballester, J. Royo, J.C. Nevado, A. Montalban, J. L. Barroso, M. A. Pineda, J. R. Benítez, L. García, J. A. Oña, M. Carrasco, J. López, M. de la Riva, J. A. Sánchez-Zapata, M. Moral, S. Moreno, J. M. Sayago, P. Moreno, P. Córdoba, R. Pulido, M. López and R. López for conducting or helping with the road census. Y. Menor de Gaspar and M. de la Riva helped with database management. The SinambA, Consejería de Medio Ambiente, Junta de Andalucía provided GIS data coverages. J. S. acknowledges a predoctoral fellowship of the Ministerio de Educación y Cultura. The analysis of these data and writing of this paper was funded by project # 1DF97-0648 to J. B. from the Dirección General de Enseñanza Superior e Investigación Científica.

NOTES

A version of this manuscript has been submitted to *Ecography* with J.Bustamante.

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CAPÍTULO VIII: El uso de modelos regionales para identificar factores limitantes y áreas con problemas de conservación: la distribución y abundancia del milano real en la península Ibérica

RESUMEN

Los modelos predictivos de hábitat generan hipótesis acerca de los requerimientos ecológicos de las especies y de los factores que afectan a su distribución, por lo que pueden guiar la práctica de la conservación. En este trabajo se presenta un modelo regional de la distribución y abundancia de milano real *Milvus milvus* en la península Ibérica. La distribución y abundancia de milano real en cuadrados UTM de 100 km^2, que se estimó mediante censos en carretera, se modela con variables explicativas de grano grueso obtenidas de imágenes de satélite, cartografía temática digital, datos meteorológicos y coordenadas espaciales. El modelo de distribución incorporó principalmente variables climáticas y alcanzó una gran capacidad discriminatoria en un conjunto de datos independiente (Kapa=0.48[SE=0.07], AUC=0.92[0.01]). Por el contrario, el modelo de abundancia incorporó en mayor medida variables de cobertura de vegetación y tuvo un menor poder explicativo (r^2=0.14). Las predicciones subestimaron algo los datos registrados, lo que está de acuerdo con el declive de la población y del rango areal que se ha observado para esta especie en el área de estudio. Los modelos son relevantes para la conservación del milano real por dos razones principales: primero, sugieren los factores limitantes para el milano real en la península Ibérica, y segundo, generan mapas predictivos que destacan tanto los lugares donde existen serios problemas de conservación (aquellas en las que áreas óptimas están desocupadas), como los lugares de los que se carece de datos pero donde es probable que la especie esté presente.

CHAPTER VIII: Use of regional models to identify limiting factors and areas with conservation problems: the distribution and abundance of the Red kite in the Iberian peninsula

ABSTRACT

Predictive habitat modeling render insights into the ecological requirements of the species and the factors affecting its distribution, and so can guide conservation practice. In this work we present a regional model for the distribution and abundance of breeding red kite *Milvus milvus* in the Iberian peninsula. Red kite occurrence and estimated abundance in 100 km^2 UTM squares resulting from road census was modeled with coarse explanatory variables obtained from satellite imagery, thematic digital cartography, meteorological data and spatial coordinates. The occurrence model incorporated mainly climatic variables and, assessed in a independent data set, have good discrimination ability (Kappa=0.48[SE=0.07], AUC=0.92[0.01]), while the abundance model incorporated mainly land-use variables and had a lower explanatory power (r^2=0.14). The predictions somewhat underestimate actual outcomes, what agrees with the declining of population size and range observed for this species in the study area. These models are relevant in the conservation of the species for two main reasons: first, they suggest the limiting factors for red kite in the Iberian peninsula, and, second, they generate predictive maps that point out both areas in which conservation problems may be acute (suitable locations are unoccupied), and areas where no data is available but red kite is likely to be present.

INTRODUCTION

The development of effective conservation programs for a given species requires clear understanding of its ecological requirements, and of the factors determining its distribution and abundance. However, regional-scale studies on the abundance and distribution of species are difficult to perform, and results from regional-scale census are rarely analyzed in detail for conservation purposes. The wider availability of digital cartography and environmental data derived from sensors onboard of satellites, plus recently developed methods based on the use of GIS (Geographical Information Systems) and statistical modeling techniques such as GLM (Generalized Linear Models) or GAM (Generalized Additive Models), provide powerful tools that can be used to model the distribution and abundance of species (see a review in Guisan & Zimmermann 2000) considering relevant variables, such as climate, topography, habitat type or structure, or human pressure (e.g.: Austin *et al.* 1996; Lavers & Haines-Young 1996; Corsi, Duprè & Boitani 1999; Sánchez-Zapata & Calvo 1999; Osborne, Alonso & Bryant 2001). These models may then be used to evaluate if the census has covered adequately all potential areas for the species and indicate where coverage should be improved. Models can also detect suitable areas for the species but currently unoccupied, and consequently, may give insight into conservation problems at regional or local scales, indicating areas where conservation actions should be prioritary (e.g.: Lawton & Woodroffe 1991; Donázar, Hiraldo & Bustamante 1993; Sánchez-Zapata & Calvo 1999; Osborne, Alonso & Bryant 2001; Teixeira, Ferrand & Arntzen 2001) .

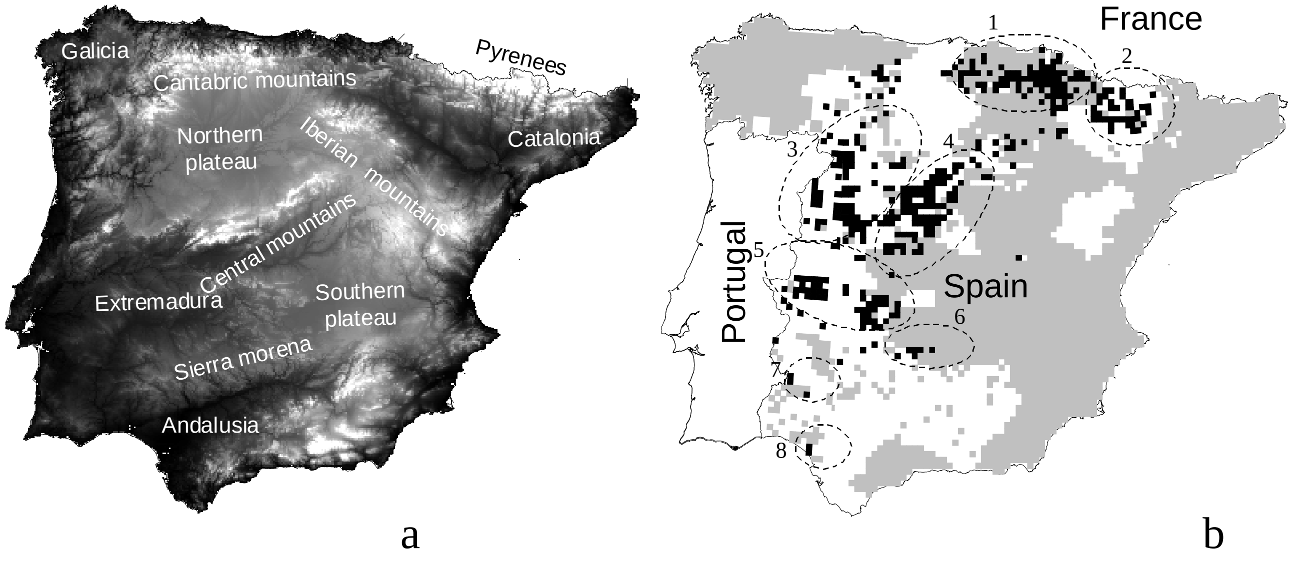


Figure 1. (a) Study area. Topography of the Iberian peninsula with geographical names as used in the text. Darker shades correspond to lower altitudes. (b) Location of 10x10 UTM squares with red kite presence (black squares), absence (grey squares) or no data available (but presumably absence in most cases, white squares). The main breeding areas are highlighted: 1. southwestern Pyrenees, 2. central Pyrenees, 3. Northern Plateau (nucleus of Salamanca-Zamora), 4. Central Mountains, 5. Extremadura , 6. Eastern Sierra Morena, 7. Western Sierra Morena, 8. Doñana marshland.

The red kite (*Milvus milvus*) is the only species of raptor that may be considered as almost exclusively european (Cramp & Simmons 1980). With the exception of some small relict populations of uncertain status in Mediterranean Northern Africa (Viñuela 1996), the Iberian peninsula is the southern edge of the distribution of the species. Red kite populations disappeared or were strongly reduced over all its range during the XIX and first half of XX centuries, mainly due to human persecution, and thus it was considered a globally endangered species up to the 80s (Collar & Andrew 1988; Evans & Pienkowski 1991). After implementation of protection laws of raptors during the 60s-70s, populations of red kites in central Europe quickly recovered, and the species even recolonized countries where it had become extinct long time ago (Evans & Pienkowski 1991; Tucker & Heath 1994). As a consequence, the red kite was removed from the list of endangered birds by the early 90s (Tucker & Heath 1994). However, by that time the species had still a poor conservation status in the southern edges of its range (Viñuela 1996), and during the last 10 years alarming population declines have been detected in the three main strongholds of the species, Germany, Spain, and France (Viñuela, Martí & Ruiz 1999; Mammen 2000; Mammen & Stubbe 2001; Thiollay 2001). The causes of these declines might be at the breeding areas (Hille 1995; Mammen 2000; Thiollay 2001), but also at the main wintering area, Spain, where most German and French red kites spend about half their lives, and where serious conservation problems for the species have been detected in the last decade (Viñuela, Martí & Ruiz 1999; Viñuela & Contreras 2001; Viñuela & Villafuerte in press). Spain held the second most important European breeding population of the species in 1994, estimated to be 3300-4100 breeding pairs (Viñuela, Martí & Ruiz 1999), but by that time most populations for which data were available were declining, apparently due to illegal predator control by hunting and poisoning (Villafuerte, Viñuela & Blanco 1998).

The red kite is considered a relatively eclectic species, with no important habitat requirements, and able to breed in a wide range of climates (Cramp & Simmons 1980; Carter 2001). The only requirement often cited for this species is a mixture of forest patches to breed and open areas to search for food. It has been suggested that human landscapes created in some agricultural areas, with a mixture of forest patches and open croplands, probably favoured the expansion of the species in the past (Carter 2001). However, only partial and local data about the factors determining distribution and abundance of the species have been published (reviewed in Viñuela, Martí & Ruiz 1999; Carter 2001), and it has been suggested that habitat alterations induced by regional-scale land-use changes may strongly affect its breeding success, abundance, and distribution (George 1995; Hille 1995; Mammen 2000; Thiollay 2001). Furthermore, the distribution of red kites in France, Germany and Spain is highly fragmented, but the reasons for that irregular distribution are poorly known (Cramp & Simmons 1980; De Juana 1989). It has been suggested that this irregular pattern of distribution may be explained by human factors, such as small populations persisting where persecution levels are lower (De Juana 1989; Villafuerte, Viñuela & Blanco 1998; Carter 2001). However, natural factors such as habitat or climate could contribute to explain that irregular distribution. This is why it is relevant to identify the biological or ecological factors determining red kite distribution, in order to improve the identification of human-related conservation problems (e.g., poisoning or hunting).

In this paper we present regional-scale predictive models of distribution and abundance of breeding red kites for the Iberian peninsula (~600000 km^2). The models consider climatic, topographic, and habitat factors, with the aim of improving our understanding of which are the main natural factors determining the occurrence and abundance of the species. The Iberian peninsula may be particularly adequate for this study, because it is the southern edge of the range of red kites, and then presumably the factors affecting its distribution are probably more easily identified than at the core of its range, where some limiting factor may be overlooked. Furthermore, we develop a predictive model of the occurrence and abundance of red kites in Spain, with the aim of identifying areas suitable for red kites but currently unoccupied, and that thus may give a clue about which are the areas where conservations problems are acting more strongly, and where conservation programs should have priority.

METHODS

Red kite data and variables considered

Our basic data are the results of the national red kite census performed in 1994 for most of Spain (Viñuela, Martí & Ruiz 1999), plus data of a more detailed census of Andalusia performed in 1996 (Bustamante, Donázar & Hiraldo 1997). In both censuses an average of 40 kilometers of road transects were driven at a low speed in each of a number of 10x10 km UTM squares. For the 1994 census, the study area was stratified following habitat and topographic criteria, and the census was conducted by > 500 volunteer observers and regional ornithologists. Every stratum was sampled completely when possible, but if there were insufficient observers, a random sample of squares was selected trying to cover a minimum of 50 % of the area of each stratum. In a sample of 61 10x10 km UTM squares, red kite populations were surveyed simultaneously by road transects and nest searching/detection of territorial pairs by standardized observation (Viñuela 1997; Viñuela, Martí & Ruiz 1999) . Within this sample we calculated an index of relative density (IRD, no of kites /100 km of transect) for each square sampled. A linear regression of IRDs on estimated populations through nest detection for those squares explained > 85 % of the variance in IRDs, and thus road transect proved to be an adequate method to census this species in most of the Iberian peninsula (Viñuela 1997). For the 1996 census, the Andalusia Autonomous Community was stratified in nine zones that covered all historical and potential breeding areas for red kite. The UTM sampled squares were those known to have had at least one breeding pair the previous years and a set selected randomly within each zone in a number proportional to the *a priori* expected breeding density (thus the known core zones for breeding had more squares sampled than the zones with a lower density of kites). About a 25% of total potential area was finally sampled. Some squares where no kites were seen in road transects, were additionally surveyed by nest searching/detection of territorial pairs, because road transects may be not an adequate method to detect this species when breeding densities are low (< 3 pairs/100 km^2; Viñuela, 1997). Some areas of Spain were not exhaustively sampled, but enough previous information existed to assume that no kites bred there; these squares were included in the analysis as squares where the species was absent (Fig. 1). Thus, we had information about the occurrence of the species in 2990 10x10 km UTM squares (386 with presence of red kite and 2604 with absence) and an estimate of breeding pairs for each sampled square.

To build models to predict the distribution and abundance of the species, we tested as predictors 11 variables: six land-use/land-cover variables derived from CORINE digital map (CORINE 1991), two topographic variables (altitude and slope) derived from a digital elevation model (DEM, a computerized representation of altitude curves), two climatic variables (rainfall and temperature), and an index of interannual plant productivity derived from satellite imagery (PPI, Table 1). The raw data for the latter is a monthly maximum value composite (an image) of a radiometric vegetation index

(NDVI) from the sensor AVHRR of the NOAA satellite (Mather 1999; Díaz-Delgado & Pons 2001). We performed a principal component analysis on 166 images dated between 1984 and 2000, and selected the first component (our index PPI), which explained 95.8% of variation in data (see for details Eastman & Fulk 1993; Lillesand & Kiefer 1994; Osborne, Alonso & Bryant 2001). Predictors were in origin at different resolutions (from DEM at 100 m to Corine at 250 m and NOAA imagery at 10x10 km) and data were averaged within 10x10 km UTM squares (Table 1).

Statistical analysis

We built Generalized Additive Models (GAM, Hastie & Tibshirani 1990) of occurrence and abundance of breeding red kites in 10x10 km UTM squares. For the first type of model the response variable was the presence/absence of red kite in each square, and we used a binomial error and a logistic link, that is equivalent to logistic regression. To model the breeding abundance the response variable was the estimated number of breeding pairs per square, and we used a Poisson error with a log link that is equivalent to Poisson regression. In the abundance model we included only the squares with one or more kites (n=386). We started building full models that included all the predictors as smooth terms (a smoothing spline with 3 degrees of freedom) and performed a backwards stepwise search of a best subset model. In every step, we tested the significance of variables by a likelihood ratio test of the current full model *versus* the reduced model without each particular variable (Crawley 1993). Non-significant variables (p>0.05) were tested with a simpler form (that is, with less degrees of freedom) and, if the effect was non-significant, they were excluded from the model. We aimed to obtain a parametric model to facilitate the transfer of results to a GIS for the generation of maps, and because parametric models may

Table 1. Predictive variables tested in the models for occurrence and abundance of breeding red kite in the Iberian peninsula. A single mean value was obtained for each 10x10 km UTM square in the analysis.

Predictor	Description	Source
FOR	Percentage of forest	Modified from CORINE[1]
DEH	Percentage of *dehesas* (sparsely forested areas, mainly of *Quercus ilex* subsp. *ballota* and *Q. suber*.	Modified from CORINE[1]
PAS	Percentage of pastureland	Modified from CORINE[1]
TRE	Percentage of tree cultures (mainly olive groves)	Modified from CORINE[1]
IRR	Percentage of irrigated cultures	Modified from CORINE[1]
NIC	Percentage of non-irrigated cultures	Modified from CORINE[1]
ALT	Mean altitude (m)	Digital Elevation Model[2]
SLO	Mean slope (degrees)	Digital Elevation Model[2]
TEMP	Mean annual temperature (10^{-1} ºC)	Meteorological stations[3]
RAIN	Mean annual precipitation (mm)	Meteorological stations[3]
PPI	Plant productivity index	Satellite imagery[4]

[1] Variables obtained by pooling the original 54 categories of the CORINE land cover cartography as follows: FOR is Forests category; DEH, Agro-forestry areas; PAS, Pastures and Natural grassland; TRE, Permanent crops; IRR, Permanently irrigated land and Rice fields; and NIC, Heterogeneous agricultural and non-irrigated areas (except Agro-forestry areas). Resolution is 250 meters.

[2] Variables obtained from a Digital Elevation Model of the Iberian peninsula at 100 meters horizontal resolution.

[3] Raw data provided by the Spanish Instituto Nacional de Meteorología and spatially modeled at resolution 1km^2 (own data, unpublished).

[4] Raw data provided by the LATUV (Laboratorio de Teledetección de la Universidad de Valladolid) is a monthly maximum value composite of a radiometric vegetation index (NDVI) from the sensor AVHRR of the NOAA satellite at resolution 10x10 km (see text for details).

be more interpretable than complex non-parametric curves (Guisan & Zimmermann 2000). So we finally transformed all the smoothed variables to suitable parametric terms guided by visual inspection of partial residual plots (see a similar approach in Brown 1994; Franklin 1998). For example, we transformed curvilinear forms that showed a maximum either to quadratic polynomials (see ALT in Fig. 2b) or to piecewise linear functions with a threshold beyond which the response is constant (see PAS in Fig. 2d). These models will be called hereafter *environmental models*.

We converted the environmental models into *autologistic models* (Augustin 1996) to take into account the possible spatial autocorrelation of the squares (Legendre 1993; Smith 1994), that is, the fact that neighbouring squares are likely to have similar environmental characteristics or that high red kite density in a given square may influence density in neighbour, less favourable squares. To this aim, we estimated the predicted probabilities of the models for each 10x10 km UTM square in the Iberian peninsula, then we took the average of predicted probability in each group of 9 adjacent squares and included this new variable —an autocovariable— within the environmental models (Wu & Huffer 1997; Merrill *et al.* 1999; Araújo & Williams 2000). Finally, we modeled the amount of unexplained variation in the autologistic models with the cartesian coordinates (latitude, longitude and their interaction) in UTM projection to account for regional trends in the pattern of distribution (Legendre 1993; Preisler, Rappaport & Wood 1997). We entered coordinates as non linear terms (natural cubic splines with 3 knots in the 0.1, 0.5 and 0.9 quantiles, Harrell 2001).

There is not an unanimously accepted measure of performance for logistic models such as the coefficient of determination R^2 in linear regression (but see Ash & Shwartz 1999). Therefore, we assessed the discrimination ability (Pearce & Ferrier 2000) of the occurrence models with three different measures. First, the commonly used correct classification rate, which is affected by both the unbalance between presences and absences and the need to choose a threshold to convert the estimated probabilities in presences or absences (Fielding & Bell 1997). Second, the Cohen’s Kappa statistic, which estimates the correct classification rate adjusting by chance (Titus, Mosher & Williams 1984). In this case we chose the threshold to be the mid-point between the mean estimate for presence and the mean estimate for absence (Fielding & Haworth 1995). And third, the Area Under the Curve (AUC) of a Receiver Operating Characteristic (ROC) plot (Swets 1988; Cumming 2000), which is an index of rank correlation between predicted probability of presence and actual observations (Harrell 2001). From all possible pairs of squares, one with and the other one without breeding kites, the AUC measures the proportion of such pairs in which the occupied square has a higher probability of presence than the unoccupied square (Centor 1991; Zweig & Campbell 1993). AUC does not require to choose a threshold to convert probabilities in presences or absences, and it is unaffected by the unbalance between them (Manel, Williams & Ormerod 2001). Finally, we used Spearman correlation (r_s) to analyze the agreement of predicted and actual abundance, but Pearson correlation (r) to measure the amount of explained variation in both the occurrence and abundance models (Mittlböck & Schemper 1996).

To evaluate the models we followed a data-splitting strategy (Verbyla & Litvaitis 1989; Picard & Berk 1990), developing the models with a random selection of 75% of the squares (the *training* set) and holding the rest of data to evaluate the models (the *test* set). The correct estimates of discrimination ability of the models in new scenarios are those for the test set, that will be reported here. Final estimates of model coefficients were obtained with the complete dataset, and predictions were produced for all squares in the Iberian peninsula, including Portugal and the unsampled Spanish areas.

Models were developed with S-PLUS 2000 (MathSoft 1999) and AUC calculated non-parametrically with AccuROC 2.5 (Vida 1993).

RESULTS

Occurrence model

The environmental model was highly significant ($p<0.0001$) and included 8 of the original set of 11 variables (Table 2). The variable PPI (plant productivity) generated the major change in deviance (about 30% of the total), and was included in the model as a quadratic polynomial (Fig. 2a). Red kite occurrence showed a maximum at a value of 1896 units of our index (range 0-2500). The topographic variables accounted for a further 25% of the model change in deviance (Table 2). Red kite probability of occurrence had a quadratic relationship with ALT and a piecewise linear relationship with SLO, with maximum probability of occurrence for altitudes around 850 m, and decreasing probability of occurrence with topographic ruggedness (Figs. 2b and 2d). The most important land-use/land-cover variable related to red kite occurrence was PAS, so that an increasing coverage of pasturelands was associated with increasing probability of occurrence (Fig. 2c). Other land cover and climatic variables had less importance, in terms of change in deviance (Table 2). The model showed a linear decrease in probability of occurrence with increasing TRE, a slight linear increase with increasing NIC, a small maximum for intermedious values of FOR (65%) and, finally, a stairway-like decrease with TEMP (Figs. 2f-2h).

Table 2. Deviance table of the environmental model for occurrence of red kite in 10x10 km UTM squares. Change in degrees of freedom and change in deviance associated with each variable is estimated by comparison of the reduced model without each particular variable against the saturated model. Names of variables as in table 1.

Term	Coefficient	SE	Residual df	Change in df	Residual deviance	Change in deviance	*P*-value
Null			2416		1882		
Saturated			2403	13	1289	593	
Intercept	-17.406	2.346					
PPI	0.022	0.002		-2		-168	<0.0001
PPI^2	$-5.8*10^{-6}$	$-5.9*10^{-7}$					
SLO*	-0.851	0.117		-1		-89	<0.0001
PAS*	0.068	0.008		-1		-87	<0.0001
ALT	0.007	0.001		-2		-58	<0.0001
ALT^2	$-4.1*10^{-6}$	$6.2*10^{-7}$					
TEMP$_1^*$	-5.634	1.133		-3		-44	<0.0001
TEMP$_2$	-4.868	1.031					
TEMP$_3$	-7.032	1.252					
TRE	-0.061	0.019		-1		-8	0.005
NIC	0.047	0.004		-1		-8	0.005
FOR	0.026	0.012		-2		-7	0.029
FOR^2	$-2.0*10^{-4}$	$1.6*10^{-4}$					

*SLO, PAS and TEMP modeled as piecewise linear functions (see Figs. 2c, 2d, and 2h).

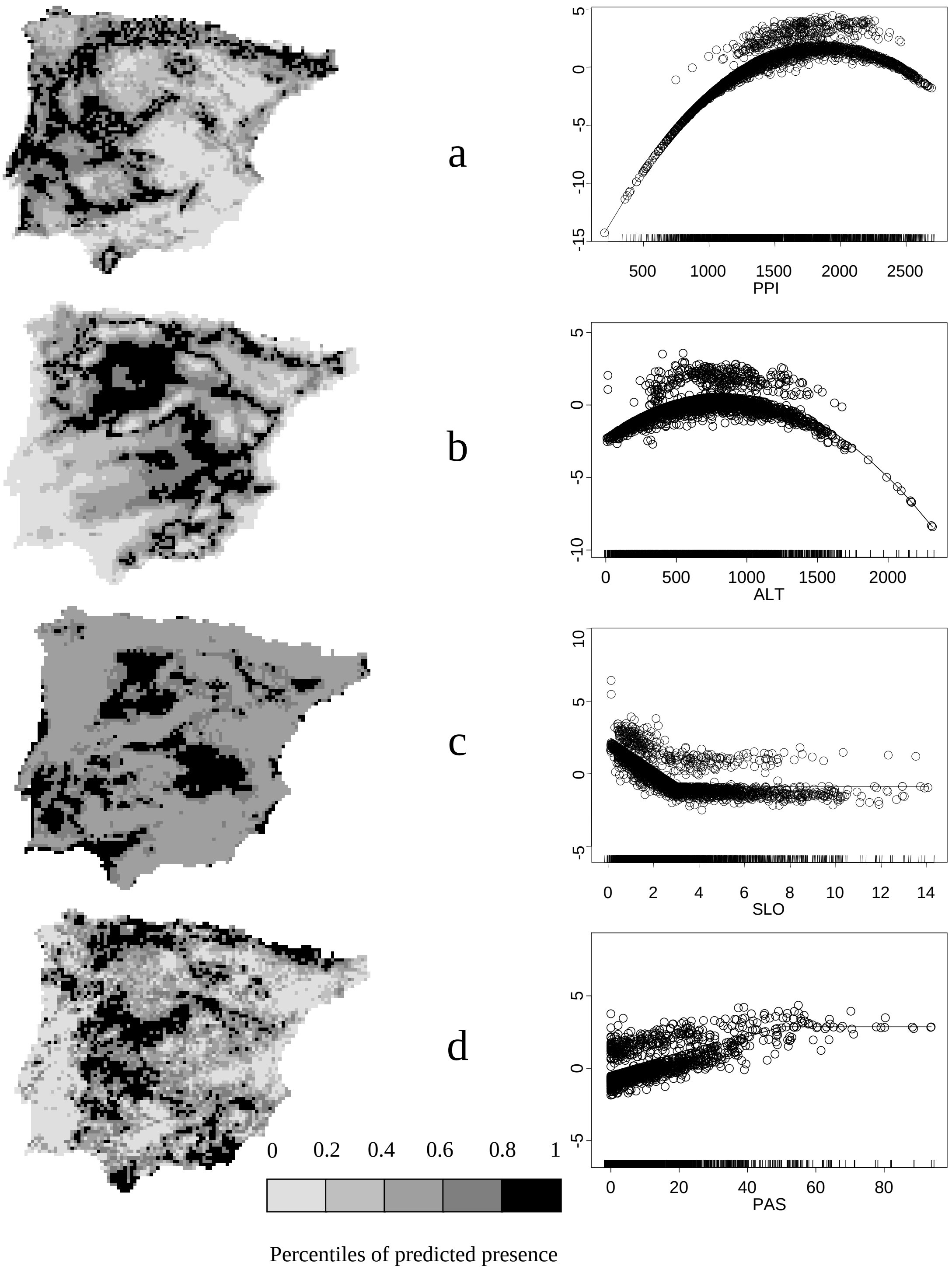


Figure 2. Partial residual plot for the individual predictors in the occurence model and their corresponding map. The partial residual plot is a plot of $r_i+b_kX_{ik}$ versus X_{ik}, where r_i is the deviance residual for the i-th observation, X_{ik} is the value for the k-th predictor and the i-th observation, and b_k is the regression coefficient for the k-th predictor (Hastie and Tibshirani 1990). Lines show the relationship between each predictor and the response variable (probability of red kite presence, vertical axes), keeping constant the rest of predictors. Circles correspond to partial residuals for each observation. To have a spatial representation of the effect of each variable, we show maps of predicted values for each term (in the predictor scale) categorized in five 20-quantile levels. Darker squares indicate a higher predicted probability of presence. PPI: plant productivity index, ALT: mean altitude (m), SLO: mean slope (degrees), PAS: percentage of pastureland, TRE: percentage of tree cultures, NIC: percentage of non-irrigated cultures, FOR: percentage of forest, TEMP: mean annual temperature (10^{-1} ºC).

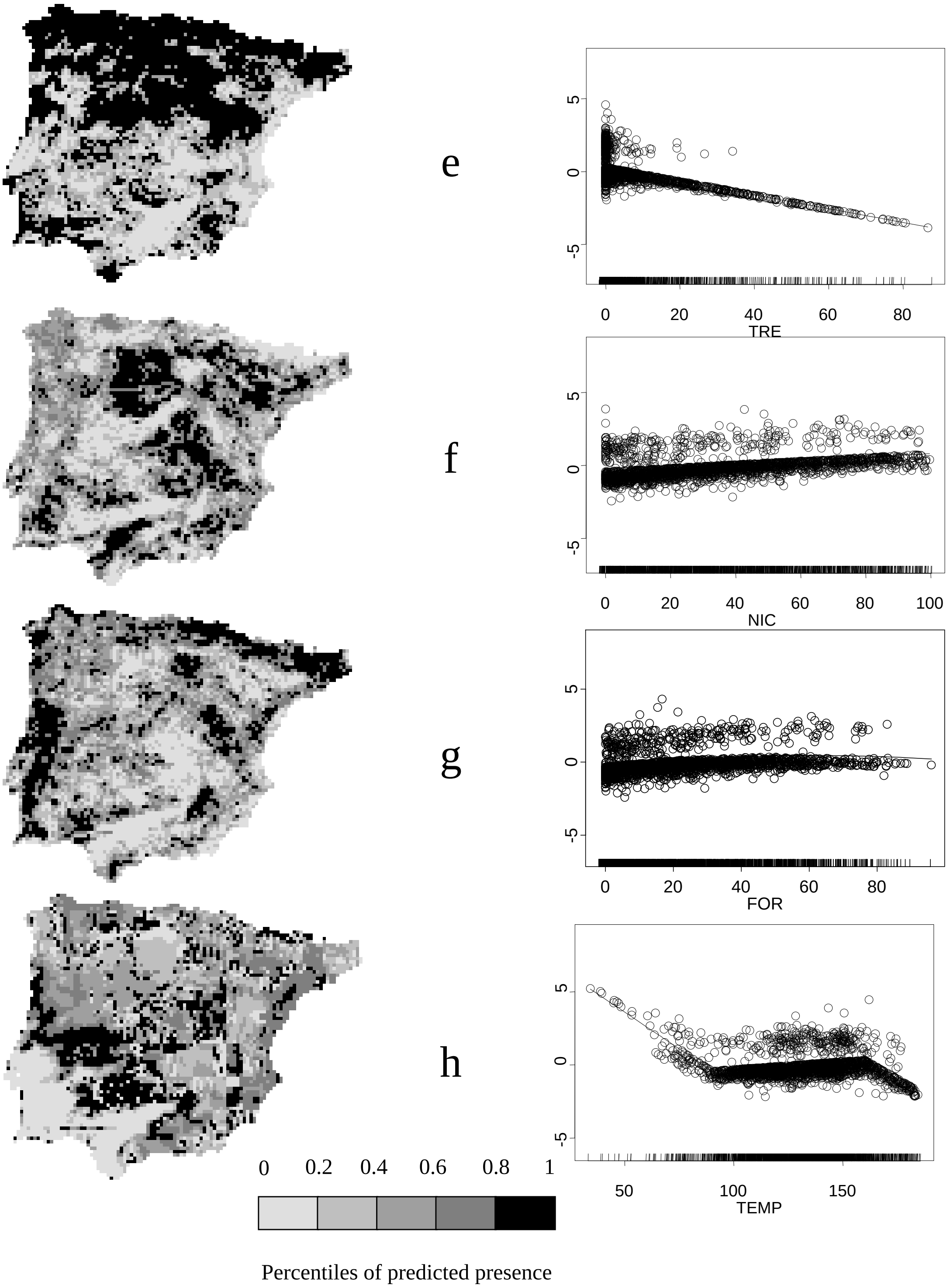


Figure 2 (cont.). Partial residual plot for the individual predictors in the occurence model and their corresponding map.

The autocovariable was also significant (change in deviance = 128.8, change in df = -1, *p*<0.0001) and improved the discrimination ability of the model (Table 3). Final models with the addition of the spatial coordinates had a correct classification rate of some 8 to 9 in each 10 squares, which means a 48% more than what expected by chance (as estimated by Kappa). According to AUC, 9 in each 10 pairs of squares (one square occupied and the other one unoccupied) are correctly rated. Overall, the occurrence model could explain about a 40% (r=0.63, t=44.6, p<0.0001) of the variability of the data according to the Pearson correlation between prediction and actual outcomes (Mittlböck & Schemper 1996), which is a fair amount considering the low values of explained variance (or deviance) obtained typically in logistic regressions (Cox & Wermuth 1992; Ash & Shwartz 1999). Accordingly, a calibration plot shows a high agreement between observations and predictions (Fig. 3a). It is interesting to note that predicted probabilities of occurrence correlated also significantly with estimated abundance (r_s=0.51, z=27.9, p< 0.0001).

Table 3. Estimates of discrimination ability for the red kite occurrence models in 10x10 km UTM squares. The *environmental* model is described in table 2, the *autologistic* model is the same but entering an autocovariate (the mean of predicted probabilities in 9 adjacent 10x10 km UTM squares) simultaneously with the rest of predictors, and the *final* model included the spatial coordinates to fit the unexplained variation in the autologistic model. Standard errors are given between parentheses (approximate SE for Kappa following Titus et al. (1984) and asymptotic SE for AUC according to Vida (1993)).

Model type	Correct classification rate	Kappa	AUC
Environmental	0.84	0.35(0.07)	0.84(0.02)
Autologistic	0.86	0.42(0.07)	0.88(0.02)
Final (plus spatial coordinates)	0.87	0.48(0.07)	0.92(0.01)

Table 4. Deviance table of the environmental model for abundance. Change in degrees of freedom and in deviance associated with each variable is estimated by comparison of the reduced model without a particular variable against the saturated model. *P*-values corrected for underdispersion. Names of variables as in table 1.

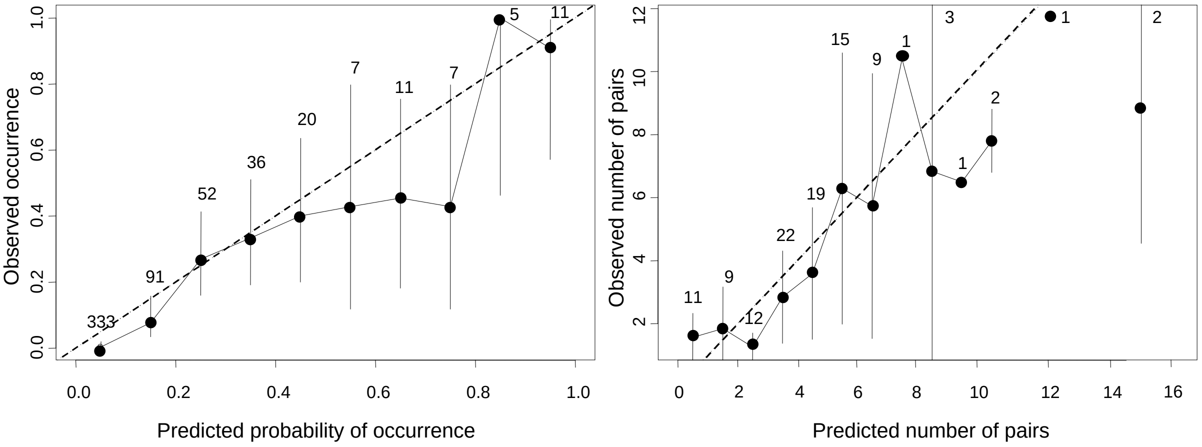
Term	Coefficient	SE	Residual df	Change in Df	Residual deviance	Change in deviance	*F*	*P*-value
Null			278		12.07			
Saturated			272	-6	9.54	-2.53	9.01	<0.0001
Intercept	-4.366	2.108						
SLO*	-0.302	0.319		-1		-0.90	19.33	<0.0001
ALT	0.003	0.005		-2		-0.46	4.91	0.008
ALT^2	$-1.5*10^{-6}$	$3.1*10^{-6}$						
PAS*	0.017	0.027		-1		-0.39	8.32	0.004
IRR	-0.034	0.075		-1		-0.28	6.03	0.015
TRE	-0.053	0.125		-1		-0.24	5.20	0.023

* SLO and PAS modeled as piecewise linear functions (see Figs. 5a and 5c).

The final model predicted a high probability of occurrence in the four main breeding areas of the species in the Iberian peninsula (Fig. 4): southern slopes of the Pyrenees, western side of the Northern Plateau (between Salamanca and Zamora provinces), both sides of the Central Mountains, and Extremadura (see also areas 2, 3, 4, 5 and 6 in Fig. 1). However, the model predicted the occurrence of red kites in an area larger than the current range of the species, where red kites are absent or present only sparsely (e.g. Cantabric and Iberian mountains, and Catalonia). On the other hand, the model predicts a low probability of occurrence in the Doñana marshlands (population 8, Fig. 1), where a small dense population occurs in an atypical area (in Doñana red kites breed in the narrow edge of marshland with pine forest, at sea level).

Abundance model

The environmental model was highly significant (*p*<0.0001) and included 5 of the original set of 11 variables (Table 4), among which topographic variables accounted for most of the change in deviance (about 54%). SLO again suggests a lower predicted abundance for more rugged areas (Fig. 5a), while ALT, that entered as a quadratic polynomial (Fig. 5b), suggests a higher abundance for intermedious altitudes (maximum at 900-1000 m). The rest of the variables in the model belong to the land-use/land-cover type: IRR and TRE, with a negative sign, and PAS, with a positive sign (Figs. 5c-5e).



a b

Figure 3. (a) Calibration plot for the red kite occurrence model (following Pearce and Ferrier, 2000). The predicted probability of occurrence (in ten equi-interval classes) is plotted against the observed proportion of occupied squares in the test set. The number of evaluation squares and the 95% confidence interval for the observed occurrence is shown for each class. (b) Calibration plot for the abundance model. The predicted number of breeding pairs is plotted against the observed number in the test set (the model did not predict any square having 11 to 12 and 13 to 15 pairs, so the line joining the points is broken). The number of evaluation squares and the 95% confidence interval for the mean abundance is shown. In both graphs the thin discontinuous line shows a perfect relationship between observations and predictions.

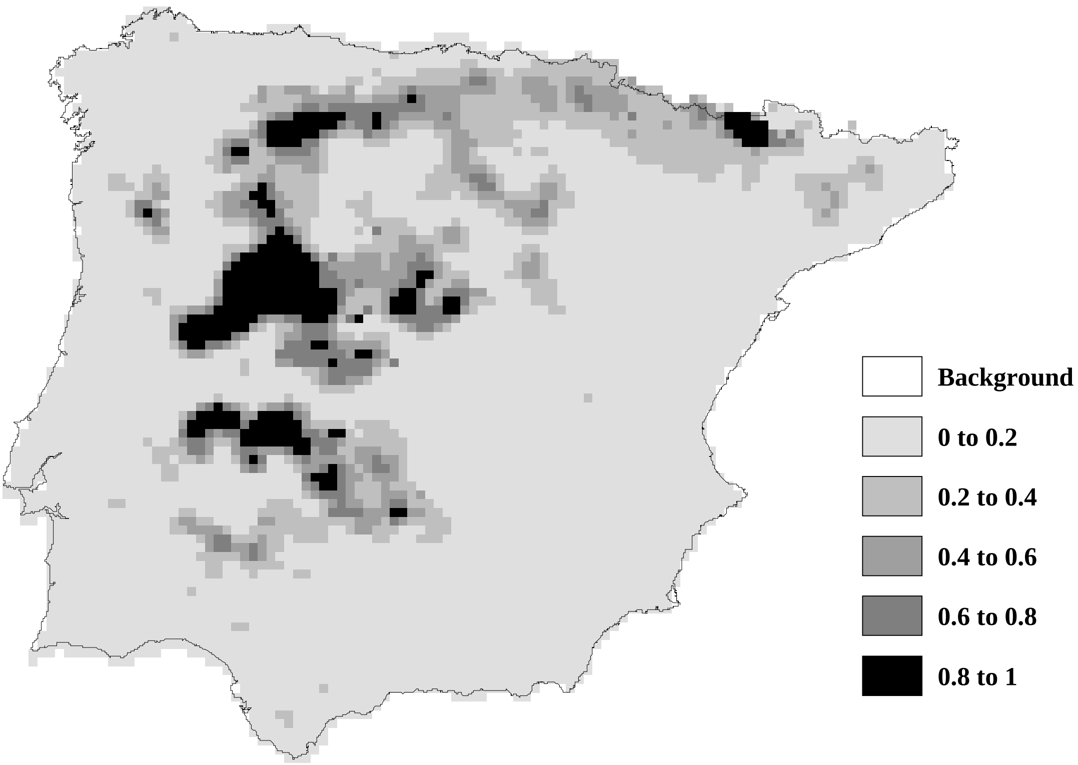


Figure 4. Final predictions of red kite occurrence (probability of presence) in 10x10 km UTM squares in the Iberian peninsula.

The autocovariable was also significant (change in deviance = 0.48, change in df = 1, F=10.48, p=0.001), and improved the predictive ability of the model from r_S=0.21 (z=2.2, p= 0.003) to r_S=0.29 (z=2.9, p= 0.003). The inclusion of the geographical coordinates further enhanced the accuracy of the model (r_S=0.41, z=4.3, p< 0.0001). Overall, the abundance model could explain only a small amount of the variability of the data (r2=0.14, p=0.0001, Mittlböck & Schemper 1996). The average model predictions agreed closely with observations in squares with low abundance, but overestimated the number of breeding pairs for squares with predicted numbers above 9 pairs per 100 km ^{2} (Fig. 3b).

Final predicted abundances were highest for Western side of the Northern plateau, Southern Pyrenees, Central mountains and some areas in Extremadura, where the maximum densities of red kite actually occurr. Predicted abundance was low in areas of the Cantabric Mountains and the Southern Plateau were low abundances have been observed. However, predicted abundance was high in other areas where no high density of red kites actually occur, such as some parts of the Iberian Mountains, Catalonia and a single square in Andalusia (Fig. 6).

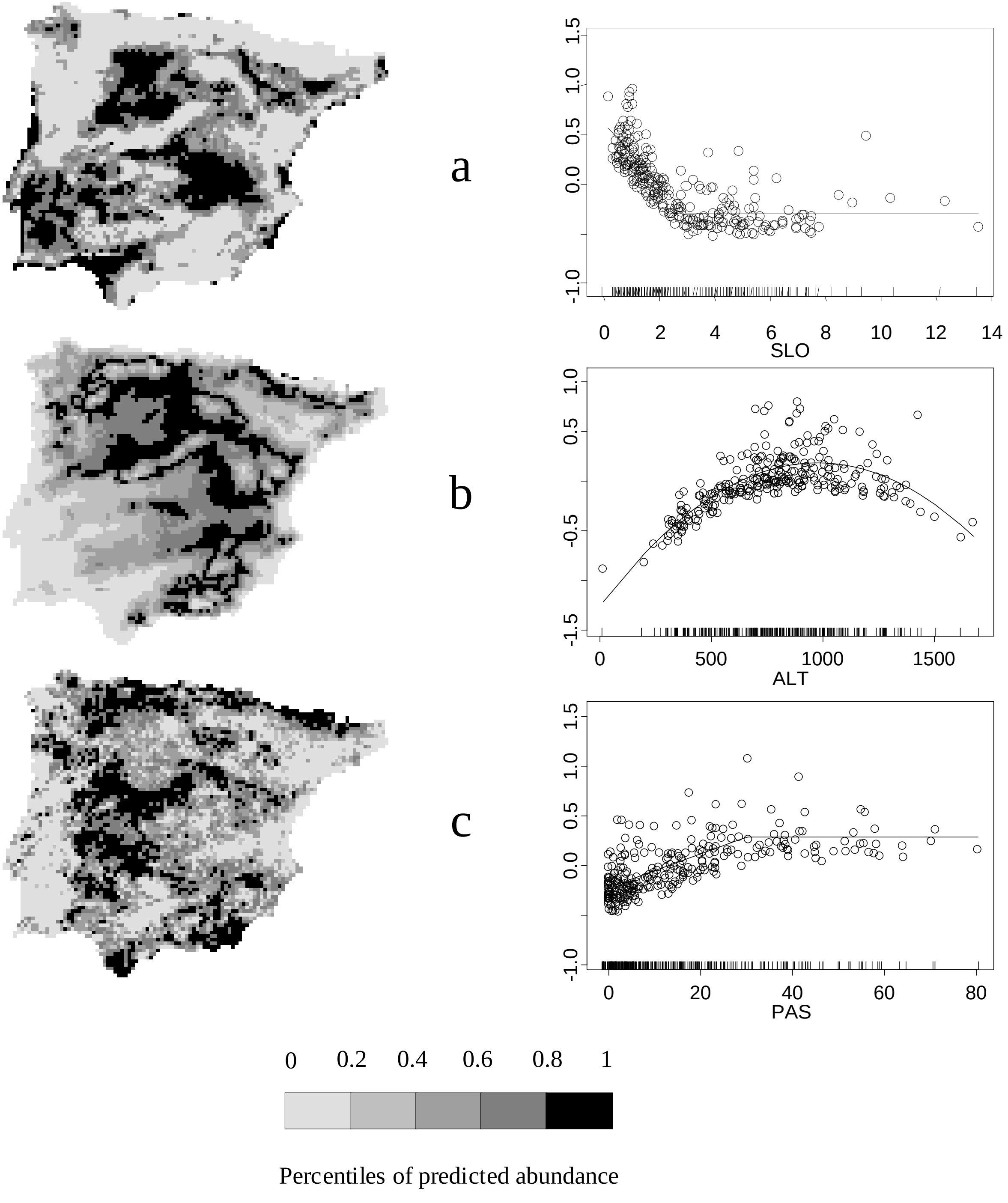


Figure 5. Partial residual plot for the individual predictors in the abundance model and their corresponding map. The partial residual plot is a plot of $r_i+b_kX_{ik}$ versus X_{ik}, where r_i is the deviance residual for the i-th observation, X_{ik} is the value for the k-th predictor and the i-th observation, and b_k is the regression coefficient for the k-th predictor (Hastie and Tibshirani 1990). Lines show the relationship between each predictor and the response variable (abundance of kites, vertical axes), keeping constant the rest of predictors. Circles correspond to partial residuals for each observation.. To have a spatial representation of the effect of each variable, we show maps of predicted values for each term (in the predictor scale) categorized in five 20-quantile levels. Darker squares indicate a higher predicted abundance. IRR, percentage of irrigated cultures; rest of variables as in Figure 2.

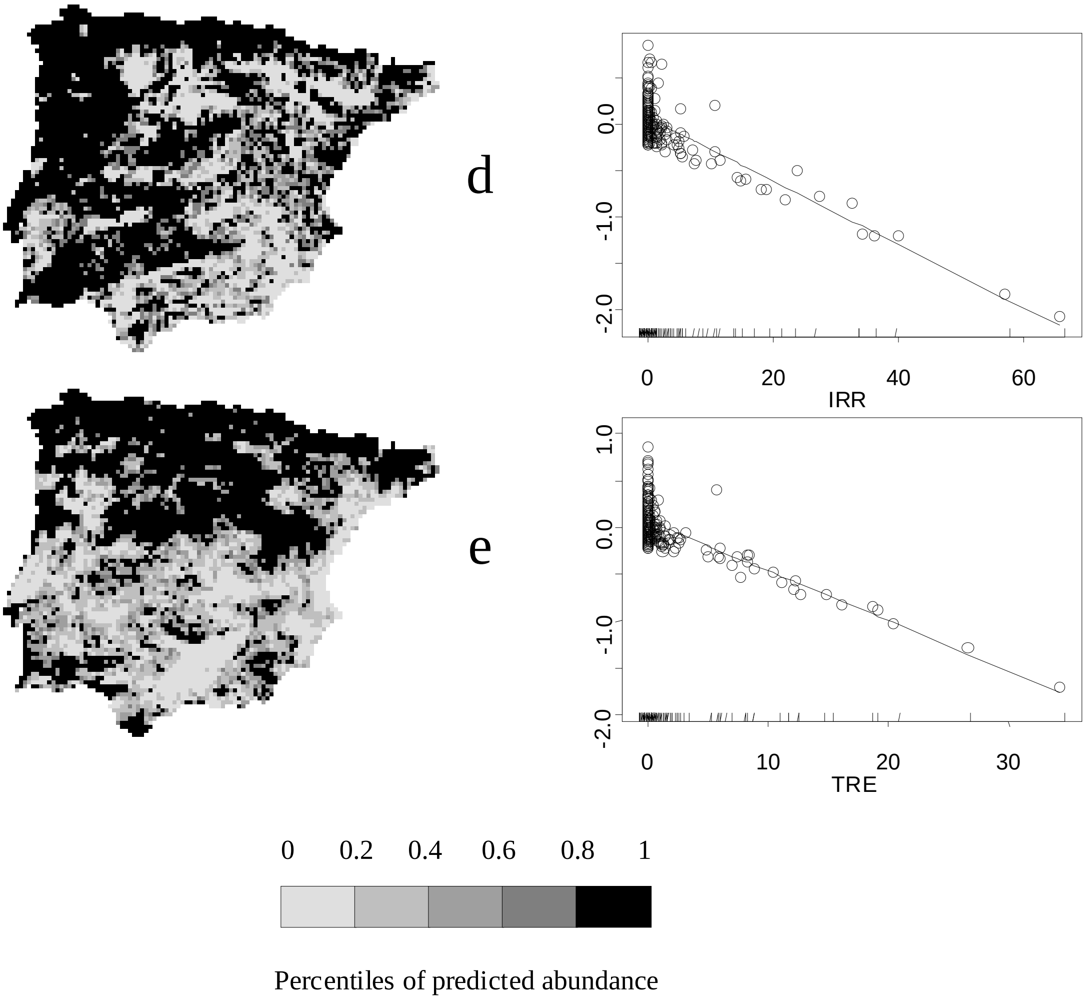


Figure 5 (Cont.). Partial residual plot for the individual predictors in the abundance model and their corresponding map.

DISCUSSION

Factors explaining red kite distribution

Although considered an eclectic species our models show that the red kite distribution can be easily predicted from climate, topography and vegetation cover. The irregular and fragmented distribution currently observed in Spain can be explained largely by these factors although it may have been also influenced by the intensity of present or past human persecution upon the species (Viñuela, Martí & Ruiz 1999). The variables PPI, ALT and TEMP represent 45% of the deviance explained by our environmental model. We consider these three variables as representing the response of red kite to climate (although ALT was derived from the digital elevation model, as SLO, we will consider it a surrogate for climatic conditions in the discussion).

PPI is an index of plant productivity derived from NOAA AVHRR imagery that, at this spatial scale, represents the response of vegetation growth to rainfall and temperature. The bell-shape response of red kite ocurrence to altitude probably also reflects a selection of particular climatic conditions in the Iberian peninsula. The shape of the declining response to mean anual temperature shows an avoidance of the more Mediterranean and semiarid locations. We do not know the ultimate cause of the response of red kites to PPI. The highest values of the index are obtained in rainy areas of Atlantic climate in the north of the Iberian peninsula and the lowest values in the semi-arid Mediterranean southeast. PPI values optimum for the red kite (intermediate-high values) occur in areas surrounding the mountain ranges and increase in areal extent following a southeast to northwest gradient (Fig. 2a). The distribution of optimum PPI values in the peninsula follows quite closely the known red kite distribution with the exception of some small areas in the southeastern half that currently do not hold breeding populations (compare Fig. 1b and 2a). The predictive ability of PPI could be due to an avoidance by red kites of rainy climates and at the same time a preference for areas of relatively high biological productivity. In a similar species, the black kite *Milvus migrans*, it has been observed that rain in spring has a direct negative effect on hatching success (Viñuela & Sunyer 1992), and on nestling's growth rate (Hiraldo, Veiga & Mañez 1990). The remnant red kite population in Wales (U.K.), living in a rainy climate, has one of the lowest breeding rates known for the species, due to low hatching success and high nestling mortality, apparently associated to poor feeding rates (Lovegrove 1990; Newton, Davis & Moss 1994). In contrast, the reintroduced population in east England, in one of the driest areas in the country, is having a relatively high breeding success (Carter 2001, pers. comm.). The PPI index probably also reflects average biological productivity of the area. The red kite is basically an opportunistic searcher, able to hunt only small size, handicapped or easily caught live prey, and relies largely on small carrions (see Cramp & Simmons 1980; García, Viñuela & Sunyer 1998; Carter 2001). Areas with low PPI values must be areas with relatively low average biological productivity, where the kind of prey or carrion searched by red kites may be more scarce. This could be especially true during the typical hot summer drought periods of Mediterranean latitudes. Furthermore, this unfavourable summer period covers a critical stage, such as the period of transition to independence of fledglings (Bustamante 1993). The preference of relatively high ground (optimum around 850 m) where summer drought is shorter and less intense (Font Tullot 1983) and the negative relationship between red kite occurrence and mean annual temperature gives aditional support to the idea that hot summers may be a limiting factor on the distribution of the species.

To test the idea that biological productivity may be setting a lower limit to the distribution of the red kite and that rainfall has a negative effect once productivity is controlled for, we built an alternative environmental model of occurrence in which PPI was modeled as a piecewise linear function with a constant effect after the maximum of 1896 units (that is, we assume that productivity has a positive linear effect on red kite distribution below this value but a constant effect above) and RAIN was introduced as a linear term. This alternative model indicated that there was a significant negative relationship between red kite occurrence and rainfall once the effect of PPI was controlled for. This model had a predictive ability similar to the environmental model (Kappa= 0.45[SE=0.08], AUC=0.83[0.03]) (compare with Table 3), but being less parsimonious it was not selected by our statistical analysis procedure.

Topography was the next most important factor affecting red kite distribution. The variable SLO was responsable for a 15% of the reduction in deviance of the environmental model. According to this variable, red kites show a clear preference for rather flat areas (at our coarse resolution: 10x10 km) or an avoidance of the more rugged areas, what corresponds to a selection of mid-mountain locations as indicated by the relationship with altitude. This effect of topography in red kite distribution had been previously suggested by several authors (Meyburg 1973; Elósegui 1985). The absence of the species from the more rugged terrain in mountain areas could look surprising at first sight, because these are usually the best areas for raptors in Spain, since they provide adequate breeding sites and usually are exposed to lower illegal predator control (González, Bustamante & Hiraldo 1990; Sánchez-Zapata & Calvo 1999). The reason could be the scarcity of the extensive open lands prefered for hunting or an avoidance of species of birds of prey of larger size such as imperial eagles *Aquila adalberti*, golden eagles *Aquila chrysaetos* or eagle owls *Bubo bubo* that can predate on red kites (Cramp & Simmons 1980; Ferrer 1993; Serrano 1998; Serrano 2000), and are more abundant in these areas. The selection of mid-mountain areas could also be related to the foraging technique of the species. Red kites are superb gliders with one of the lowest wing loading among raptors, and show a marked use of slope air-currents (Lovegrove 1990). Hilly terrain typical of mid-mountain areas can be specially favourable for this kind of flight, providing cover from strong winds, and lifting on days with less wind, and thus probably allowing an optimal energetic balance for the long searching flights typical of its foraging method. This relationship between relief and red kite distribution is also known for the Welsh population, where this is probably one of the main factors affecting selection of nesting sites (Lovegrove, 1996; Carter, 2001; Doody, pers. comm.).

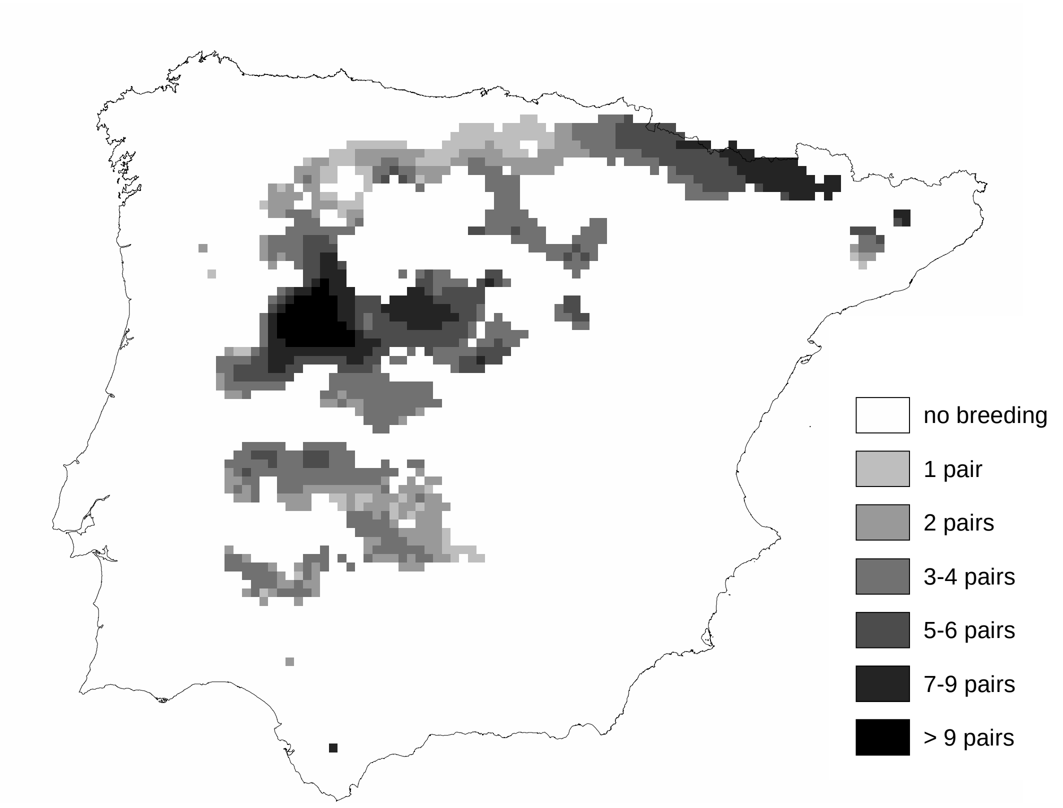


Figure 6. Final predictions of red kite abundance (in pairs/100km^2) in 10x10 km UTM squares in the Iberian peninsula.We represent only the squares for which presence of breeding red kite was previously predicted using a threshold of probability P>0.30, which is the average between the predicted probabilities for squares with recorded presence of red kite and the probabilities for squares with absences, (see Fielding and Haworth, 1995; Guisan et al. 1998).

Interestingly, this pattern of distribution affected by climate and topography probably could also be applied to the red kite population in France, where they are absent from the major part of the Atlantic west of the country, are very scarce in Mediterranean areas in the southeast, and reach highest densities in mid-mountain areas and mountain valleys of Pyrenees, Massif Central, the Vosgues and Alsacie (Voisin 1994).

The variables representing land-use/land-cover constitute the third group of predictors of red kite distribution. They represent aproximately 20% of the deviance explained by the model, but a single variable, the surface occupied by pasturelands, is the most important variable explaining by itself 15% of the deviance.The other three variables: extent of forest, non-irrigated cultures and tree cultures represent a minimal influence (approximately 1 % each) in the model. The importance of pasturelands confirms at a larger scale the importance of this kind of habitat reported locally in Germany (Hille 1995). In fact, recent declines in some German populations have been claimed to be caused by a reduction in surface or change of management of pasturelands (Stubbe, Mammen & Gedeon 1995). Pasturelands may constitute the optimal foraging habitat for red kites, because these are extensive open areas, often with relatively low vegetation cover due to grazing or mowing, and where they may find plenty of easy prey such as Microtines and invertebrates (Hille 1995). In Spain, large concentrations of red kites during breeding season have been observed in recently mowed pasturelands of Pyrenees, and this is a habitat commonly used for food searching by red kites in other areas of Spain too (Viñuela, Martí & Ruiz 1999). This association with pasturelands could aditionally explain selection of mid-mountain areas, because in most of Spain the presence of mowing fields is restricted to mountain areas (e.g. typically between 900 and 1300 m. in the Pyrenees Lasanta 1989).

Although playing a minor role in distribution, probability of occurrence of red kites was maximal at intermediate percentages of forest cover and was positively affected by the percentage of surface covered by non-irrigated cultures, supporting the idea that red kites select areas with some forest providing breeding sites, but avoiding densely forested areas. Cereal fields are also a habitat often used for foraging in Spain, especially in winter and during harvesting (García et al. 1998; pers.obs.). Furthermore, voles *Microtus arvalis* and *Arvicola terrestris*, the main preys of red kite (Cramp & Simmons 1980; García, Viñuela & Sunyer 1998), have invaded agricultural habitats of Northern Spain during last 30 years, and now there are plagues as those found at more northern latitudes (Bonal & Viñuela 1998). Preference for open areas with herbaceous vegetation (pastures, cereal fields) could also explain the negative effect of cover of tree cultures on probability of occurence.

Somehow surprisingly, the variable DEH, indicating surface covered by *dehesas* (extensive pasturelands devoted to cattle, sheep or pig raising, with scattered oaks *Quercus* spp. or ashes *Fraxinus* spp.), did not enter the distribution or abundance models. It has been argued that these open *dehesas* constitute the most important breeding habitat for red kites in Spain (Viñuela, Martí & Ruiz 1999), having the optimal landscape structure: extensive open lands for hunting and large scattered trees for breeding. However, *dehesas* does not seem to be a good predictor by themselves, as there are extensive areas of *dehesas* in Extremadura and Andalusia without breeding red kites, and those where the species breeds are already identified by the combination of climatic and topographic variables. Also, the class agro-forestry areas of the CORINE land-use/land-cover map that we used to assess the extent of *dehesas*, may be quite heterogeneous in regards of tree and shrub cover, since that class includes a range of different landscapes, from *dehesas* with too closed canopies or too much shrub cover to others highly managed in which trees are small or subject to severe pruning, and thus not suitable for breeding of large raptors (Viñuela, Martí & Ruiz 1999).

Factors explaining red kite abundance

Red kite abundance resulted more dificult to model than distribution. Two of the climatic factors with a large effect in the distribution model, PPI and TEMP, were not significant in the abundance model. Only altitude indicated a greater red kite abundance in mid-mountain areas and was responsable for aproximately 18% of the reduction in deviance of the model. Topography (mean slope) was responsable for another 35% reduction and land-use/land-cover variables for another 36%. The abundance model indicated in general a pattern that agrees with the distribution model: greater abundances in mid-mountain areas with relatively plain relief and more than 30% pasture lands, and a rejection of the more intensively managed agricultural landscapes (irrigated cultures and tree crops). Contrary to the occurrence model, in the abundance model land-use factors had more weight than topography and climate (if we consider altitude as a surrogate for climatic conditions).

The calibration plot of the abundance model (Fig. 3b) indicated a very good adjustment of the model to test data for low densities but a clear overestimation for predicted values > 9 breeding pairs per 100 km ^{2}. This result is congruent with an upper density limit in most habitats caused by red kite territoriality; but could also be the result of the species decline by illegal predator control that left habitats insaturated. This second explanation seems more realistic if we consider that there exist a few areas with very high red kite breeding densities (20 pairs per 100 km ^{2}) above those predicted by our model, and the fact that the calibration plot for the distribution model (Fig 3a) also indicates a slight overestimation (8 out of 10 values are below the equal probability line).

Observed vs. predicted distribution and abundance

Overall, the occurrence model explained a fair amount of variance and its predictive power was high, according to the standards suggested by several authors (Monserud & Leemans 1992; Fielding & Bell 1997; Pearce & Ferrier 2000) and comparing our results with those reported in previous habitat models (Austin *et al.* 1996; Manel, Dias & Ormerod 1999; Tobalske & Tobalske 1999; Cumming 2000; Bonn & Schröder 2001; Osborne, Alonso & Bryant 2001; Rico Alcázar *et al.* 2001). Moreover, the correlation between predicted probabilities and estimated abundance (higher probabilities of presence for squares with more kites) gives further confidence in the model. However, the abundance model had a relatively low predictive power.

The models predicted occurrence of red kites in areas where the species is very scarce or does not currently breed. The most striking case are the southern slopes of the Cantabric mountains (provinces of León and Palencia), where the habitat seems to be good for the species, but where only isolated pairs or small populations in restricted areas of the mountains have been found. The high probability of presence predicted in this area (Fig. 4) contrast with the low values predicted by the abundance model (Fig. 6) . Perhaps this discrepancy could be explained by factors not considered in the models, and related with human activities such as an intense use of rodenticides (to which red kite is particularly vulnerable Carter 2001; Thiollay 2001), and the recent increase of irrigated cultures in that zone. The fact that land-use variables have more weight in the abundance model compared to climatic variables in the distribution model support this view.

Our models also predict the presence of red kites in some areas of southern Spain in the western border of the Southern Plateau where only small relict populations or even isolated pairs remain. The reasons behind this discrepancy are likely human factors, mainly illegal predator control (Villafuerte, Viñuela & Blanco 1998). Game hunting has a high economic importance in this part of Spain, and illegal activities to control predators, such as poisoning, are still culturally rooted in the rural societies of these areas. Furthermore, population crash in the two main small game species in Spain (rabbits *Oryctolagus cunniculus* and red-legged partridges *Alectoris rufa*), along with increasing use of intensive game management (e.g. massive releases of partridges), have induced an strong illegal persecution of predators during last 10 years (Villafuerte, Viñuela & Blanco 1998; Viñuela & Villafuerte in press). In Extremadura, where the problem of illegal predator control seems to be lower (Villafuerte, Viñuela & Blanco 1998; Viñuela, Martí & Ruiz 1999; Mañosa 2002), there is still a healthy population of red kites.

A remarkable case is the population in Doñana National Park (population 8 in Fig. 1b) situated in an area where our model predicts a low probability of occurence. This dense population is situated at the highly productive narrow edge of a large marshland in an atypical breeding habitat from the point of view of our models: a flat area of scrubland with scattered trees at sea level, far from the mountains, that has low average rainfall and high mean annual temperature. Red kites may exist there because the exceptional productivity of the marshes apparently not well reflected by our variable PPI . The predicted probabilities of occurrence are very low for this area, which agrees well with low breeding success of red kites and the impression that Doñana population –that has been declining for the last decade– is supported by immigration from other populations (Bustamante, Donázar & Hiraldo 1997; Viñuela, Martí & Ruiz 1999, and personal observation).

The red kite had a much larger distribution in the Iberian peninsula in the past than the one observed during 1994 and 1996 (Cramp & Simmons 1980; Purroy 1997). Our occurrence model predicts an area much smaller than the distribution provided by Cramp & Simmons (1980). Comparing both, the red kite seems to have disappeared from the most arid areas in the southeastern border where our model indicates the habitat was suboptimal for the especies. The species decline seems to continue and even populations in optimal habitat of northwestern Spain are suffering a marked decrease (estimated reduction of 50 % in Northern Plateau between 1994 and 2001 Viñuela & Contreras 2001).

Conclusions derived from models

The occurrence model built for the red kite was discriminative according to the validation with independent data. It predicts occurrence in areas that we can consider as the optimal for breeding according to climate, topography and vegetation cover. The maps elaborated for each of the predictors individually (Fig. 2 and 5) suggest which are the limiting factors for the species in different parts of the Iberian peninsula. Mountain locations in eastern and southern Spain, where the species is absent, tend to have small areas with optimum values of PPI and these tend to be obtained at higher altitudes and in more rugged landscapes than what red kite apparently prefer. So there is not a spatial coincidence of the main limiting factors in these locations.

Another point indicated by our models is that some areas of optimum habitat were not thoroughly covered by the 1994-1996 census. We suggest that these areas should be prospected more thoroughly in the future, since the red kite may still breed but have remained unnoticed. A real absence of the species may indicate some conservation problem that needs to be identified. Even areas where species is known to be absent by recent detailed atlas work (e.g. Catalonia) could be colonized by the species in the future, and should receive adequate attention.

On the other hand, they can have conservation problems that our models are not able to detect. We think that the spatial predictions from our models can help to optimize the allocation of the always limited resources to estimate the species population size and trend in the future.

Our model also remarks that the red kite population in Doñana National Park occupies a very atypical habitat. Although, most of the studies on the ecology of the species in Spain have taken place in this population (Blanco, Hiraldo & Heredia 1990; Veiga & Hiraldo 1990; Heredia, Alonso & Hiraldo 1991; Hiraldo, Blanco & Bustamante 1991; Blanco, González & Hiraldo 1992; Viñuela & Bustamante 1992; Bustamante 1993; Hiraldo, Heredia & Alonso 1993; Bustamante, Donázar & Hiraldo 1997; Van Kleef & Bustamante 1999), but their results might not be extrapolable to other populations. Considering our models, we suggest that future research effort should be directed to more typical habitats where conclusions can be more widely applicable for the management of the species.

Summarizing, it is very possible that the general pattern of occurrence of red kites in the Iberian peninsula is mainly determined by natural factors such as climate, topography and vegetation cover, while their current population abundance is modulated by human-related factors (e.g. González, Bustamante & Hiraldo 1990; Donázar, Hiraldo & Bustamante 1993). We have not included anthropogenic factors in the models, that are very difficult to quantify, and this could explain the relatively low predictive power of the abundance model. Taking into account just natural factors such as climate, topography or habitat, red kites should be more extended in Spain than they currently are.

ACKNOWLEDGEMENTS

The national census of Red kites was funded by the Royal Society for the Protection of Birds, and coordinated by SEO/Birdlife. More than 500 people (listed in the appendix), participated in the census. Red kite census in Andalusia was funded by the Consejería de Medio Ambiente (Junta de Andalucía) and coordinated by F. Hiraldo. LATUV (Laboratorio de Teledetección de la Universidad de Valladolid) kindly provided raw data for our index of interannual plant productivity. Part of the data analysis and writing of this paper was funded by project #1DF-97-0648 from the Ministerio de Ciencia y Tecnología and FEDER program from the European Union. JS acknowledges a predoctoral fellowship (Ministerio de Educación y Ciencia) during part of the writing of the paper.

NOTES

A version of this manuscript, with J.Viñuela, R.Díaz-Delgado y J.Bustamante, is being reviewed in *Biological Conservation*

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APÉNDICE I
APPENDIX I

LISTA DE COLABORADORES DEL PROYECTO "SITUACION DEL MILANO REAL EN ESPAÑA" (1992-1994)
LIST OF FIELD VOLUNTEERS FOR THE PROJECT "SITUACION DEL MILANO REAL EN ESPAÑA" (1992-1994)

COORDINADORES NACIONALES: / NATIONAL COORDINATORS:

Invernada: Javier Viñuela y Alfredo Ortega
Reproducccción: Javier Viñuela

ALAVA. Ramón Arambarri, Arturo F. Rodríguez (GADEN) (coords.). Yolanda Arrondo, Gorka Belamendía, Aurelio Canabal, Mario Corral, Marian Fernández, José M. Fernández García, Luis Javier Fernández García, José Antonio Gainzarain, José M. Iglesias, Estitxu Irazola, Luis Lobo, Carlos López Losada, J.R. López Retamero, Asier Martínez, Iñaki Martínez, José Melena, José A. Nuevo Morena, Txema Pérez Ugarriza, Arturo F. Rodríguez. **ASTURIAS**. Luis Mario Arce, Manuel Enrique Carballal, Coordinadora Ornitoloxica d'Asturies. **AVILA**. José Mª García Jiménez, Gabriel Sierra, Javier Viñuela. (coords.). José Miguel Abarca Antón, Antonio J. Aldea, Segundo Arcones, Carlos Bermejo Arribas, Julio Caballero, Julio Caminero Tapiador, Juan Ramón Cuervo Martín, Aurelio Delgado Hidalgo, Jesús Encinar Muñoz, Marta Fernández Pérez, Pedro L. García, Ana García García, José M García Jiménez, Alicia García Muñoz, Manuel García Tornero, Jesús Gil Martín, Ana Grandal Martín, Isabel Hernández Vallejo, Mariano Hernández Vallejo, Roberto Ivars, Carlos Jarque Bañuelos, Julio Jiménez Encinar, Juan Carlos Marfull Robledo, Carlos Martín, Dionisio Martín, J. Miguel Martín, Ignacio Martín García-Sancho, Luis Martín García-Sancho, Enrique Martín Serrano, Fernando Muñoz Carrera, Manuel F. Pérez Escrivá, Aurelio Ramírez Jiménez, Rosa Rodríguez Manzano, José Luis Robledo Ranea, José Rodríguez Matías, César San Segundo Ontín, David Sánchez Sáez, Francisco Sánchez Sierra, Juan Manuel Sastre González, Julián Zancajo. **BADAJOZ**. Francisco Gragera Díaz. (coord.). Julián Andrés Ledesma, Francisco Barrena, J. Antonio Candelario, José Enrique Capilla, Juan Carlos Delgado Expósito, Carmen Galán Novella, Alfredo Eusebio Garica, María Ledesma Vázquez, Cati León, José Antonio Palomo, Enrique Pérez, José Carlos Pons García, José Elías Rodríguez, Jesús Rojas González, Marcos Romero González, Luis Salguero Báez, Angel Sánchez García, José María Traverso Martínez. **BURGOS.** Roberto J. Milara, Javier Viñuela. (coords.). Enrique Alvarez, Eduardo Angulo, Rubén Arrabal, Gorka Artiguez Gallaga, Luis Miguel Arranz, Jorge Bañuelos, Florentino Barbadillo, José Ignacio Contreras, Pedro José de la Cruz, Pilar Durante, Carlos García, Carlos García Güemes, Eduardo Izquierdo, Roberto López Saiz, Alberto Martínez, Ismael Mediavilla, Fernando Moreno, Miguel Angel Pinto Cebrián, Angel Quero Miguel, Rubén Río, José Román, Vicente Sanz Fernández de Gobero, Ignacio Sanz Moneo. **CACERES.** Pilar López Avila, Sebastián Hidalgo, Javier Viñuela. (coords.). Daniel Abel Schaad, Antonio Acha, Elena Angulo, Ernesto Alonso Juárez, José Antonio Bardají Zúñiga, Juana Barriga Manzano, Socorro Cancho Corrales, Mónica del Castillo Burgos, Gregorio Castillo Fernández, Antonio Civantos, María José Domínguez, Bryan Etheridge, Richard Evans, Isidoro Fagundo Torres, Manuel Fernández, Ian Fisher, Manuel Flores Cid de Rivera, Santos Fuertes, Carmen Galán Novella, Rosana García Macías, Alfredo García Sánchez, Nieves González Jarri, Jaime Iglesias Duarte, Fernando Labrador Romero, Carmen Linares Tello, Pilar López, Penélope Losa Gómez, Juan José Luengo Rodríguez, Paloma Martín García, José Martín Pablo, Alberto Morón Pastor, Justo M. Muñoz Mohedano, Consuelo Muñoz Molina, Adolfo S. Maestre García, Patricio Mateos Quesada, Soledad Mateos Salcedo, Antonio Muriel Bernal, Magín Murillo Fernández, Alberto Navalón, Ana Núñez Cansado, Francisco José Ordiales, Asunción Pacheco, Serafín Polo, Alfonso Polvorinos Ovejero, Mª José Rincón Matesanz, Francisco Serrano, Mercedes Silveira Torremocha, Innes Sim, Luis Suárez Arangüena, Maite Torres Fernández, Carmen Usin, Salvador Vaquero, Francisco Serrano. **CADIZ.** Jose Luis Paz de la Rocha. **CIUDAD REAL.** Juan Pablo Castaño (coord.).José Carlos García, Tom Gullick, José Guzmán, José Luis Hernández, José Manuel Hernández, José Jiménez, Manuel López Sánchez, Juan Ramón Morcillo, Javier Muro, Manuel Muro, Rafael Palomo, Leonardo Rodríguez, Manuel Salgado. **COMUNIDAD VALENCIANA.** Mario Jiménez Ripoll. **CORDOBA.** Juan Antonio Antón, Federico Cabello de Alba Jurado, Antonio Gómez Miranda, Antonio Leiva Blanco, Francisco Sánchez Tortosa. **CUENCA.** Marcos Costa Belinchón. (coord.). Francisco Costa Belinchón, Eduardo Hervás Domínguez, David Manzanares Sáez, Juan Pedro Morales Gallego, Grupo Elyomis, Grupo de Estudio de las Zonas Esteparias Conquenses. **GRANADA.** José Mª Gil Sánchez. (coord.). Natalia Ildefonso Huertas, Rosa María Ildefonso Huertas, Francisco Manuel Molino Garrido, Gerardo Valenzuela Serrano. **GUIPUZCOA.** Héctor González Arcelos. **HUELVA.** Andrea Gardiazábal. (coord.). F. Alcántara, Rafael Carmona, José Mª Correa, Rafael Galán, Fernando Hiraldo, Manuel Máñez, Mariano Marchena, Alberto Moya, Ignacio Olano, Mercedes Sánchez, José Manuel Sayago, Luis Urbina, Javier Vilches, Escuela-taller Guadiana. **HUESCA.** Alberto Bueno Mir. (coord.). Carlos Acín Canfranc, Ana Alastrué, Juan Carlos Albero, J.J. Almazán, R. Aquilué, Ignacio Arizón, Antonio Arnal Martí, Guillermo Ascaso, Juan Carlos Ascaso, M.

A. Aspiroz, Joaquín Barrabes, Matías Belda, Francisco Bescós Claver, J. Bastarós, M. Bellosta, V. A. Boucher, José Mª Canudo, Mamen Carmena, Fernando Carmena Flores, J.M. Cereza, Guillermo Costas, Oscar Díez Sánchez, Curro Domínguez, F. Domínguez, Joaquín Español, Alfredo Espinosa, Ramón Espuña, CH. Ferrer, J. Ferrer, Francisco Ferrer Lerín, G. Fornies, José Antonio Garcés, Juan Antonio Gil Gallús, Gerardo Goded, David Gómez, Manuel Grasa Francés, Julián Lacosta, José Luis Lacostena, D. Lanaspa, Jesús Lavedán, Isabel López, M. Losfablos, J.J. Moreno, José Damián Moreno Rodríguez, Clara Ortega, Jesús Peña, José Andrés Pintado, Maarten Platteeuw, C. Pradel, I. Pueyo, F. Ramos, Balbino Riobó, José Enrique Ríos Cabrera, J. Sánchez, J.L. Sasot, D. Saura, Alejandro Serrano, J.R. Sesé, Carlos Tarazona, A. Torralba, J. Carlos Usieto, Fernando Vallés, Rafael Vidaller, A.G. Villacampa, Emilio Yñigo. **JAEN.** Joaquín Muñoz Cobo. Francisco Campos, José García, José García Santiago, Alfonso Godino Ruiz, Mª Carmen López, F. Ortega. **LEON.** Mª Teresa Andrés Ponga, Alejandro Onrubia Baticón. (coords.). Nemesio Andrés García, Concepción Andrés Ponga, Cristina Borrego, Olga Borrego Rodríguez, Javier Calzada, Mercedes Fernández Fernández, Javier García Fernández, Benito Fuertes Marcos, Benedicto González, Carlos Gutiérrez Expósito, Concepción Ponga Martínez, Eloy Revilla, José Luis Robles Prieto, Mª Luisa Robles, Jacinto Román, Eva Sagües, Carlos Sánchez, Jesús Villadangos Fuertes, URZ (Blanca, Noemi, Pablo y Rafael). **LERIDA.** Jordi Canut. (coord.). A. Baker, J. Bonfill, T. Carulla, F. Fernández, J. García, D. García-Ferre, R. Gutiérrez, A. Margalida, J. Martí, R. Martínez, A. Martínez-Vilalta, J. Medina, J.M. Parde, J. Puig, M.D. Rodríguez, R. Torres, D. Saavedra, J. Sargatal, M. Sicart, E. Streich. Patrullas del Servei d'Agents Rurals (D.A.R.P.): Pallars Jussà (J. Bolado, L. Cruz, J. Palacín); Pallars Sobira (J. Arilla, M. Arilla, J. Jové) y Urgell (L. Tomás, J. Mª Freixes, J. Reig y J. Puig). **LOGROÑO.** Jesús Mª García García, Carlos Gutiérrez Expósito. (coords.). Juan Carlos Luis Gil, Santiago Peña López. **MADRID.** Iñigo Fajardo, Alfredo Ortega, Javier Viñuela. (coords.). Ana Barón, Miguel Angel Blanco, Miguel Angel Blasco Rodríguez, Alberto Cameo, Ana Cameo, Ramona Carpintero, Pilar Cavia Cuesta, Teresa Córcoles, Manuel Cuesta Nieto, Sandra Ducazcal, Alfredo Espinosa, Iñigo Fajardo, Ignacio Fernández Aransay, Olivia Gaona Palop, Francisco García González, Jesús García González, Pedro A. García Sánchez, Ricardo Gómez Calmaestra, Laura Gómez Moreno, Francisco González, Ana I. González de Castro, Mario González Pérez, Raquel Gordo Méndez, Luis Haro, R. Hernández, Miguel Angel Herrera, Mª José Linares Tello, Isabel López, Javier Marchamalo, M. Martínez Duchel, R. Millán, Julián Moral Sánchez, M. Andrés Moreno, Juan Carlos Palermo, E. Pérez Balsalobre, Yolanda Pérez Chirinos, Marina Pérez Zahonero, Luis Picazo Casariego, M.A. Ramiro, Adolfo Rodríguez Pérez, Enrique Sánchez Airas, Lino Sánchez-Mármol, David Sánchez de Ron Martínez, Eduardo Soto-Largo, Carlos Sunyer, Francisco Yago. **MALAGA.** Jose A. Cortés. (coord.). Carla J. Atkins, Adolfo Aguilar, Miguel A. Domínguez, José L. Medina, Juan Luis Muñoz. Francisco J. Peso, Juan J. Rodríguez, Antonio Román Muñoz. **MALLORCA.** Carlota Viada. (coord.). Juan Salvador Aguilar, Pere L. Dietrich, Javier Gassó, Jordi Muntaner, Toni Muñoz, Matías Rebassa, Miguel A. Reus, Juan José Sánchez, Manuel Suárez, Pep Sunyer, Evelyn Tewes. **MENORCA.** GOB-Menorca (Josep Capó Nin, Evaristo Coll, Santi Catchot, Guillem Orfila, Félix de Pablo, Rafel Triay). **NAVARRA.** Juan I. Deán, Jesús Elosegui. (coord.). 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Javier Zalba, GURELUR (Koldo Aranguren Martiarena, Marcelino Barbería, Iñigo Calonge Isturiz, Miguel Ciriza Isturiz, Jesús Domínguez Iglesias, Manuel Fernández Recio, Raúl Fernández Recio, Oscar Ibáñez Escarda, Fidel Mediavilla Ayala, Iñaki Morrás del Río, Antonio Munilla, Jorge Nuble Carmona, Iosu Oroz Legal, Iñigo Petri Nabarlaz,). **ORENSE.** Antonio Villarino Gómez. (coord.). Isabel Alvarez Balvis, Marcos Manuel Freán Hernández, Celso Nieto Pérez, José Manuel Pérez Pérez. **PALENCIA.** Enrique Gómez Crespo, Fernando Jubete, Javier Pastor. **SALAMANCA.** Pedro Luis Ramos Bueno. (coord.). Antonio Acha, Mª de los Angeles Coca, Raúl Bueno Hernández, Roberto Carbonell Alanís, José Miguel Colorado, Lorenzo Corrales, Myriam Cuadrado López, Pablo C. Díaz, Casimiro Domínguez Martín, Francisco Javier Galvache, Eugenio García García, Andrés C. García Montero, J. Pablo García Montero, Luis Gómez Albanán, Jesús Gómez Gómez, Javier Gómez Labrador, Oscar J. González, Angel González Losa, Mª de los Angeles González Sánchez, José Antonio Hernández, Guillermo Hernández Cordero, Luis Javier Hernández Martín, Vicente López Alcázar, Tomás Merchán Sánchez, Francisco Panadero Sáez, Manuel de Pedro, Eladio Sánchez, Jesús Serradilla Rodríguez, Juan Carlos Vadillo Sanz, José Antonio Velasco Mendo. **SANTANDER.** Juan José Aja. (coord.). Manuel Bahillo, Luis Felices, Ana García García, Javier García-Oliva, José Manuel González González, Angel Herrero Calva, Gonzalo Palomero, Olga Pérez, Carlos Sánchez, Antonio Sanz Carro. **SEGOVIA.** Fernando Barrio, Javier Viñuela. (coords.). Fernando de Antonio, Fernando Aparicio, Mark Avery, Angel Carballés Muñoz, Richard Cowie, Juan A. de Diego Fuentenebro, Angel Gómez-Manzaneque, Mª José Jiménez Armesto, Ross Johnston, Eduardo de Juana, Lola Manteiga, Ramón Martí, Gonzalo Llorente Alvarez, Andrés López Moreno, Javier Oria Martín, Daniel Pinela, Marino Rodríguez de Miguel, Javier Sánchez Vaquero, Jean Sears, Eduardo Sotolargo, Carlos Sunyer, Fernando Vázquez Gallardo, A.E.LANIUS (Mercedes Alonso y Andrés López). **SEVILLA.** Francisco Parreño. (coord.). Verónica Alarcón, Ricardo Arroyo, Francisco Javier Avila Domínguez, Diego Fuentes Baquero, Hipólito Benítez León, Hipólito Benítez Morgado, José Mª Bermudez, Salvador Borrego, Sergio

Braña Montes, Rafael Carmona Vilches, Antonio Díaz Espejo, Manuel Díaz Palma, Francisco Domínguez, Luis Miguel Escalera, Fernando Fernández Parreño, José Manuel Galera, Miguel Galuez, José Manuel García, Juan Luis García Castaño, Manuel Giraldez, Eusebio Gómez, Manuel Gracia, Inmaculada Llach, Francisco Morales, Agustín Parejo, Manuel Carlos Pérez Gómez, Francisco Pérez Montiel, Luis MIguel Platero, Juan Pedro Segura, Manuel de la Riva, José Manuel Rivero Hidalgo, Manuel Raimundo Rodríguez, Manuel Vega, J. Antonio del Valle, Manuel Zayas. **SORIA.** Félix Martínez Olivas, Fernando Chagüaceda. (coords.). Pilar Cavia Cuesta, Inmaculada Cuchillo Ibáñez, Manuel Cuesta Nieto, Ignacio Fernández Aransay, Andrés García Pérez, Pedro A. García Sánchez, Ricardo Gómez Calmaestra, Juan Luis Hernández Hernández, María Herrera, José María Lenguas Gil, Félix Martínez Olivas, Manuel Meijida Fuertes, José Mercader, Javier Muñoz Jiménez, Manuel F. Pérez Escrivá, Federico Roviralta García, Pilar Sánchez Sánchez. **TOLEDO.** Marino López de Carrión, Javier Viñuela. (coords.). José Antonio Benavides, Luis Santiago Cano Alonso, Carlos Carbajal, Luis Otero Espinosa, Fernando Fernández Morcuende, Ignacio del Moral, Mariano Vidal, Félix Zaragoza, Javier Zaragoza. **VALLADOLID.** Alfonso Balmori, Jesús Fernández-Gutiérrez. (coords.). Harry Bayley, Juanjo Becerril Trigueros, Luis Carlos Castellanos, José Mª Collazos, Ignacio Conde, Juan Criado, Javier Espinosa, Rosa de la Fuente Torre, Dolores García González, Carlos Gil Palomo, Tomás Gómez, Santiago González Martínez, Ainda Goyenechea, Vicente Guerra, Juan Carlos Guerra Velasco, Luis Hurtado Vergara, Francisco Javier Jiménez Martín, José Mª Lorenzo García, Xavier Martín, Ana Martínez, Francisco Martínez, Antonio Martínez Ruiz, Mercedes Medina, Francisco Merage, Orlando Parrilla, Julio Pérez Gil, Rafael Ramos, Emma Rodríguez, Blanca Ruiz Otazo, Tomás Sanz Sanz, Jesús Ucero, Pedro Villalón. VIZCAYA. Gorka Artiguez Gallaga. **ZAMORA.** Alfredo Ortega, Javier Viñuela. (coords.). Mark Avery, Gregorio Ballestero, Len Campbell, J.F. Carreño, Carlos de Celis, Jesús Domínguez García, V. Fernández, Jesús García González, Miguel Angel García Matellanes, Hipólito Hernández Martín, Manuel José Hernández Rodríguez, José Alfredo Hernández Rodríguez, Andy Hughes, Antonio Mediavilla Largo, Manuel Miñambres, Pedro Moldón, Ken Norris, Debbie Pain, Jesús Palacios Alberti, Tomás Rivero Rivero, Mariano Rodríguez Alonso, Luis Fernando San José, Ken Smith, José Luis Vicente, C. Zamora, OCELLUM DURII (Miguel Angel García Matellanes, José Alfredo Hernández Rodríguez, Ana Vecilla Rodrigo). **ZARAGOZA.** José Manuel Sánchez Sanz. (coord.). Elisa Andrés, Gerardo Báguena, José Miguel Baselga, Manuel Benzar, Plácido Antonio Brotons, Luis M. Bueno, Adérito Calzón, Isabel Casaña, Juan Carlos Cirera, Félix Compaired, Alejandro Cortes, Juan Luis Fernández, Alvaro Gajón Bazán, Julio Giménez Laaraga, Francisco Hernández Fernández, José Ignacio Iglesias, Oscar Iglesias, Ana Belén Lacueva, M. Nieves Laín, César Lolumo García, Javier Gomollón, Daniel Magdalena, José M. Marco, Pedro Martínez Pérez, Manuel Mercadal, Juan Moreno Twose, Luis Palacio, Enrique Pelayo Zueco, Carlos Pérez Laberda, Alfredo Pérez Pina, Patxi Picón, José Antonio Pinzolas, José Luis Rivas González, Miguel Angel Romeo Lafuente, Javier Ruiz Alba, José Luis Ruiz Cerra, Francisco Javier Sampietro, Federico Sancho Puertas, José Mª Sierra Robres, José Luis Tella, Luis Tirado, Fermín Torres, José de Uña, Francisco Ventura.

CAPÍTULO IX: Una evaluación con modelos estadísticos de la cartografía de especies generada mediante criterio de expertos

RESUMEN

En numerosas circunstancias, aplicadas, de investigación básica, o de conservación, se requiere tener un conocimiento detallado de la distribución de las especies. La cartografía de especies derivada del criterio de expertos es subjetiva, difícil de evaluar y se presenta a una baja resolución. El criterio de expertos puede usarse para refinar la información de los atlas de especies, cuyos datos se consiguen con un trabajo de campo intensivo. En este caso la resolución espacial de los mapas aumenta, pero aún es insuficiente para satisfacer los objetivos que la mayoría de las aplicaciones prácticas suelen demandar (es aún mayor que 100 km^2). En contraste, la cartografía de especies derivada de modelos estadísticos es objetiva, fácil de evaluar y puede obtenerse a muy alta resolución. En este capítulo nos planteamos la comparación de la capacidad predictiva de modelos estadísticos y modelos generados con criterio de experto aplicados al análisis de la distribución de aves reproductoras en Andalucía. Las preguntas que abordamos son: (1) ¿se puede generar una cartografía equivalente a la de un atlas con menor esfuerzo de muestreo mediante modelos estadísticos? y (2) ¿el criterio de experto permite obtener modelos de alta resolución espacial con una capacidad predictiva equivalente a la de un modelo estadístico

CHAPTER IX: Using statistical models to evaluate species cartography derived from expert opinion

ABSTRACT

In a great number of circumstances, related to applied practices, basic research or conservation, it is needed a detailed knowledge of species distribution. The species cartography derived from expert opinion is subjective, difficult to evaluate and it is commonly presented with a low spatial resolution. Expert opinion may be used to refine the information of species atlases, which data is gathered by intensive field surveys. In this case, the spatial resolution of the resulting maps increases, but it is not enough to satisfy the objectives desired by most of applied practices (it is >100 km^2 yet). In contrast, the species cartography that is derived from statistical models is objective, easy to evaluate and it can be obtained at a high spatial resolution. In this chapter we compare the predictive ability of statistical models and models generated with expert opinion, applied to the analysis of nesting birds in Andalucía. The questions we address are: (1) could a cartography equivalent to that derived from atlases be generated with less sampling effort by statistical techniques?, and (2) can the expert opinion obtain models of high spatial resolution with a predictive ability equivalent to that of statistical models?

1. Introducción

Como se ha mencionado en capítulos anteriores, las circunstancias en que se requiere tener un conocimiento de la distribución de las especies son numerosas y responden a motivaciones de investigación científica básica (Mourell & Ezcurra 1996; Manel, Buckton & Ormerod 2000), de aplicaciones conservacionistas (Corsi, Duprè & Boitani 1999), de planificación y evaluación de impactos (Lavers & Haines-Young 1996), o, simplemente, recreativas (Donald & Fuller 1998). Una primera aproximación a tal conocimiento puede hacerse con los mapas publicados en guías de campo o trabajos monográficos (por ejemplo: Beaman & Madge 1998; Wilson & Ruff 1999). Esta solución no suele ser satisfactoria para la mayoría de las necesidades debido a que los mapas se presentan a muy baja resolución, se dibujan con una cobertura de la información heterogénea y, por último, su calidad es difícil de evaluar. Los atlas de distribución de especies pueden ser más útiles, ya que se construyen con una metodología sistemática (principalmente respecto a su ventana temporal y, en menor medida, en cuanto a los muestreos que se emplean), aunque su resolución es todavía grosera (por encima de los 100 km2 habitualmente, ver Hagemaijer & Blair 1997; Purroy 1997; Doadrio 2001). Sin embargo, en los atlas es difícil distinguir entre cuadrículas con distinta abundancia de las especies y entre cuadrículas prospectadas con diferente esfuerzo de muestreo (Donald & Fuller 1998). Esto es así porque la presencia de uno sólo o de numerosos individuos de una especie identifican de igual manera a una cuadrícula de 100 km^2 como área de reproducción, y porque la distinta intensidad de muestreo no se suele representar en la cartografía final.

Quizá el peor efecto del poco detalle de los mapas de manchas y los atlas es que tanto las áreas coloreadas como las cuadrículas marcadas dan la falsa impresión de que una especie en cuestión se puede encontrar en toda la superficie que destacan. ¿Cómo puede mejorarse entonces la resolución espacial de los mapas y atlas para aumentar su utilidad?. Si asumimos que las especies seleccionan los hábitats que ocupan (Cody 1985; Morrison, Marcot & Mannan 1998), se puede recurrir al criterio de expertos que determinen los hábitats adecuados para cada especie dentro de las manchas o de las cuadrículas en que se registraron (Scott *et al.* 1993; Díaz, Illera & Hedo 2001), lo que se hace definiendo relaciones cualitativas entre las especies y sus hábitats (conocidas como *wildlife-habitat relationships*). El ejemplo más conocido del uso de modelos de experto para refinar mapas generales de distribución de especies son los proyectos, denominados “Gap”, que se han estado realizando desde hace 10 años principalmente en EE.UU. (Scott *et al.* 1993). En la primera fase de estos proyectos se reúnen todos los registros disponibles de cada especie (avistamientos, censos *ad hoc* y muestras de colecciones) elaborándose una cartografía de su distribución. Después se cartografían los distintos hábitats de la zona de estudio y se sintetiza la información existente sobre la selección de hábitat de cada especie. Finalmente, un comité de expertos acaba definiendo las relaciones entre las especies y los hábitats, que se aplican a las áreas del mapa creado en la primera fase en las que se supone que están las especies (Bojórquez-Tapia *et al.* 1995; Caicco *et al.* 1995; Kiester *et al.* 1996; Powell, Barborak & Rodriguez 2000). La crítica principal que ha recibido el diseño de estos proyectos es que no se comprueba que las relaciones especies-hábitats que se definen són válidas (es decir, los modelos cualitativos que son tales relaciones no se evalúan con un conjunto independiente de datos, ver Short & Hestbeck 1995). Además, no se conocen suficientemente los requerimientos de hábitat de la mayoría de las especies como para que el criterio de experto genere predicciones fiables en muchas aplicaciones (p.e. en las evaluaciones de impacto ambiental, donde este problema se ha identificado como una de sus deficiencias más graves, Treweek 1996).

Otra opción para la cartografía de especies se puede hacer, como se ha mencionado en capítulos anteriores, a través de modelos cuantitativos de distribución de especies, que se han utilizado en numerosas ocasiones para determinar la extensión potencial de ciertos organismos y para valorar la adecuación del hábitat (Austin *et al.* 1996; Guisan, Theurillat & Kienast 1998; Corsi, Duprè & Boitani 1999; Osborne, Alonso & Bryant 2001). Con estos modelos las relaciones entre las especies y el entorno físico y biótico que las rodea se definen a través de técnicas estadísticas (Guisan & Zimmermann 2000). Los modelos estadísticos permiten generar mapas de distribución interpolando los resultados de un muestreo a las áreas no prospectadas (la extrapolación, sin embargo, presenta mayores problemas, Ertsen *et al.* 1998), lo que supone un ahorro de los recursos humanos o económicos que pueden destinarse a otras tareas. Además, cuentan con las ventajas respecto los modelos elaborados mediante criterio de experto, de que, una vez establecido un protocolo de construcción, son herramientas objetivas, transmisibles y fácilmente evaluables.

Las escasas comparaciones que se han realizado sugieren que los modelos estadísticos generan mapas más predictivos que los generados mediante criterio de experto (Pearce *et al.* 2001), al menos para las especies que son muestreadas con mediana intensidad (los modelos estadísticos no parecen funcionar bien con especies muy raras). No obstante, la opinión de experto y las técnicas estadísticas pueden considerarse criterios complementarios (en vez de alternativos) en las aplicaciónes prácticas que precisan generar cartografía de especies. Así, Díaz *et al*. (2001) elaboraron una metodología de evaluación estratégica ambiental con la que valoran los efectos de planes de desarrollo sobre la avifauna a través de las afecciones que tales planes ejercían sobre la distribución y abundancia de las especies. Las relaciones entre las especies y los hábitas afectados por los planes se determinaron también mediante criterio de expertos (Tucker & Evans 1997). Nosotros compartimos la opinión expresada por Díaz *et al.* (2001) de que la validación de esas relaciones especies-hábitat, mediante modelos estadísticos basados en datos de campo, es el método más convincente y efectivo para evaluar las predicciones de impacto generadas por metodologías como la suya.

Dadas estas opciones de cartografía de especies, en este capítulo nos planteamos la comparación de la capacidad predictiva de modelos estadísticos y modelos generados con criterio de experto, aplicados al análisis de la distribución de aves reproductoras en Andalucía. Los modelos estadísticos son del tipo que se ha venido desarrollando en los capítulos previos de esta tesis doctoral. Los modelos de experto son las mejores aproximaciones posibles a la utilización de criterios de experto, con la información disponible actualmente, en los estudios del medio físico propios de las evaluaciones ambientales o los planes de ordenación territorial. Tratando de reflejar las dos situaciones más típicas en que ambos tipos de modelos podrían ser usados, se escogen dos tipos de sujeto de estudio que implican dos escalas muy diferentes de análisis. Primero, se comparan modelos para paseriformes y especies afines, cuyos mapas tienen una extensión local (1400 km^2) y una gran resolución (<1ha) y, segundo, la comparación se realiza para cuatro especies de rapaces, cuyos mapas tienen una extensión regional (la Comunidad Autónoma de Andalucía) y una baja resolución (100 km^2). Las preguntas que abordamos son: (1) ¿se puede generar una cartografía equivalente a la de un atlas con menor esfuerzo de muestreo? y (2) ¿el criterio de experto permite obtener modelos de alta resolución espacial con una capacidad predictiva equivalente a la de un modelo estadístico?

2. Áreas de estudio y métodos

2.1. Paseriformes y afines

Para el estudio de paseriformes y afines se analizaron los resultados de 1137 estaciones de escucha de 15 minutos de duración y sin límite de banda, que se realizaron en las primaveras de 1999 y 2000 en los dos cuadrados de 70x70 km en Andalucía occidental mencionados en anteriores capítulos (centros: 6° 21’ W 37° 39’ N, y 5° 28’ W 36° 44’ N, ver figura 1 del capítulo IV). Del conjunto de especies detectadas se seleccionaron 10 representativas de distintos tipos de hábitats y de distinta frecuencia en las muestras (excluyéndose en particular las especies muy raras o las propias de hábitats poco extensos). Estas fueron: *Alectoris rufa* (frecuencia 19%), *Carduelis cannabina* (28%), *Certhia brachydactyla* (27%), *Erithacus rubecula* (14%), *Galerida theklae* (12%), *Melanocorypha calandra* (7%), *Parus caeruleus* (29%), *Sitta europaea* (15%), *Sylvia melanocephala* (44%) y *Troglodytes troglodytes* (15%).

2.2. Rapaces

En la comparación de los modelos realizados para rapaces se dividió la Comunidad Autónoma de Andalucía en cuadrículas UTM 10x10 km, de las que se seleccionaron aquellas correspondientes a las áreas de montaña (n=383, que cubren sólo 37.700 km^2 porque algunas son costeras o están en el borde de los husos 29-30 o 30-31). De este conjunto se escogieron 88 para realizar censos de rapaces por carretera, tal como se explica en el capítulo VII (ver figura 1 de ese capítulo). Las especies que se consideran en este apartado son *Buteo buteo* (que aparece en el 45% de las cuadrículas censadas por carretera), *Circaetus gallicus* (43%), *Hieraaetus pennatus* (42%) y *Milvus migrans* (39%). Todas ellas tienen en común el ser rapaces forestales de mediana abundancia para las que los censos de carretera ofrecen resultados satisfactorios.

3. Generación de los modelos

3.1. Modelos estadísticos

3.1.1. Paseriformes y afines

Las variables predictoras usadas en los modelos estadísticos se extrajeron y modificaron a partir del mapa digital de usos y coberturas de Andalucía (Moreira & Fernández-Palacios 1995), de un modelo digital de elevaciones y del análisis de imágenes de satélite (todas con resolución espacial inferior o igual a 50 metros). El conjunto de variables predictoras potenciales comprende variables descriptoras de la vegetación (p.e., porcentaje de bosque de frondosas), del paisaje (p.e., longitud de borde entre áreas de bosques y matorral) y de la topografía (p.e., altitud). Este conjunto es muy numeroso (n=65) e incluye variables muy correlacionadas entre sí, por lo que se realizó un análisis de componentes principales (ACP) con el que se identificaron las 13 variables que, estandarizadas, obtuvieron mayores pesos en los primeros componentes del ACP (tabla 1) (algunas pruebas previas indicaron que 13 variables era el número máximo manejable para los análisis estadísticos que siguen). Estos predictores se promediaron en círculos de 350 y 1250 metros de diámetro, centrados en los puntos de muestreo, cuya superficie equivale, respectivamente, a las áreas de campeo de la mayoría de las aves de pequeño tamaño y a la escala que generó los modelos más predictivos en análisis anteriores (ver capítulo V).

Se utilizaron modelos aditivos generalizados (GAM, Hastie & Tibshirani 1990) para modelar la presencia/ausencia de las especies escogidas, empleándose errores binomiales y enlace logit. Los modelos se hicieron por separado para cada diámetro en el que se promediaron las variables predictoras potenciales. Éstas se escogieron mediante un procedimiento automático por

Variable predictora	Descripción	350 mts	1250mts
% Forestal [a]	Proporción de píxeles que pertenecen a cualquier categoría forestal (incluye áreas forestales dispersas como dehesas pero no olivares)	?	
% Forestal planifolio [a]	Proporción de píxeles que pertenecen a cualquier categoría forestal de árboles planifolios	?	
% Matorrales riparios [a]	Proporción de píxeles que pertenecen a cualquier categoría riparia con vegetación subarbórea (p.e., *Rubus*, *Phragmites*)	?	?
% Agrícola [a]	Proporción de píxeles que pertenecen a cualquier categoría agrícola (olivares y otros cultivos tanto en secano como en regadío)	?	?
% Cultivos leñosos [a]	Proporción de píxeles que pertenecen a categorías de cultivo leñoso (principalmente olivares)	?	?
% Urbano [a]	Proporción de píxeles en áreas urbanas o industriales	?	
Arbolado denso [a]	Presencia/ausencia de cobertura arbolada densa (p.e., incluída en un área heterogénea de matorral)		?
Matorral denso [a]	Presencia/ausencia de cobertura densa de matorral (p.e., incluída en un área dominada por masas forestales)		?
Pastizal [a]	Presencia/ausencia de pastizal (p.e., incluída en un área dominada por masas forestales)		?
Longitud de borde [a]	Longitud de bordes entre la categoría forestal y el resto de categorías	?	
Heterogeneidad espacial [b]	Dimensión fractal de un Índice Normalizado de Vegetación (NDVI) obtenido de imagen de satélite como un índice de heterogeneidad en cultivos	?	?
Distancia a cultivo [a]	Distancia al área de cultivo más próxima mayor de 10 ha	?	?
Distancia a matorral [a]	Distancia al área de matorral más próxima mayor de 10 ha	?	?
Distancia a coníferas [a]	Distancia al área forestal de coníferas (incluye eucaliptos) más próxima mayor de 2 ha	?	?
Distancia a cultivo leñoso [a]	Distancia al área de cultivo leñoso más próxima mayor de 10 ha		?
Distancia a vegetación riparia [b, c]	Distancia al área de vegetación riparia más próxima mayor de 2 ha		?
Distancia a cultivo herbáceo [a]	Distancia al área de cultivo herbáceo más próxima mayor de 2 ha	?	
Pendiente [c]	Pendiente media (en grados)	?	?

Tabla 1. Conjuntos de variables probadas como predictores en los modelos estadísticos de distribución de aves de pequeño tamaño a cada resolución espacial. Fuentes:**a**, mapa de usos y coberturas de Andalucía (1995) (SinambA: Consejería de Medio Ambiente, Junta de Andalucía); **b**, Imagen del sensor LISS III del satélite IRS (fechas: 19/07/99 y 16/07/99 para ambas áreas de estudio). La dimensión fractal se calculó con IDRISI 32 sobre una imagen de NDVI; **c**, Modelo digital de elevaciones de Andalucía a 50 metros de resolución. Los puntos indican, para cada variable, si ésta fue utilizada en los modelos con 350 y 1250 mts de resolución.

pasos (con la función step.gam de S-PLUS 2000, MathSoft 1999) que usa una aproximación del Criterio de Información de Akaike (Akaike´s Information Criterion, Sakamoto, Ishiguro & Kitagawa 1986) como criterio para introducir o eliminar variables. Puesto que la forma de la relación entre la variable respuesta y los predictores puede ser no lineal, estos últimos se probaron a introducir en los modelos como splines de suavizado (*smoothing splines*) con 3 grados de libertad (Harrell 2001). Sin embargo, los modelos resultantes no son paramétricos y resultan difíciles de implementar en un SIG (Guisan & Zimmermann 2000), por lo que se aproximaron a modelos lineares para representar espacialmente sus predicciones (una técnica similar se empleó en el capítulo III).

3.1.2. Rapaces

Las fuentes de información utilizadas para obtener predictores ambientales fueron las mismas que para el trabajo de paseriformes y afines: el mapa de usos y coberturas del SinambA, el modelo digital de elevaciones e imágenes de satélite (ver tabla 1 del capítulo VII). Se calculó también el índice experimental calibrado de vegetación global (*Experimental Calibrated Global Vegetation Index*) derivado del sensor AVHRR del satélite NOAA (NOAA 1992). Para cada cuadrícula 10x10 se obtuvo un valor promedio de los predictores.

La presencia/ausencia de cada especie en las cuadrículas censadas por carretera se analizó con modelos GLM y GAM por pasos, que incluían errores binomiales y enlace logit, según se detalla en el capítulo VII. En este caso las relaciones no lineales se prefirieron incorporar con polinomios ortogonales, que tienen la ventaja de generar modelos paramétricos fáciles de pasar a un entorno de SIG. Además, se generaron predicciones para el resto de cuadrículas serranas andaluzas que no fueron censadas por carretera (n=295).

3.2. Modelos de experto

3.2.1. Paseriformes y afines

La elaboración de los modelos de opinión de experto se obtuvo mediante la colaboración de 3 ornitólogos profundos conocedores de la avifauna local. Se les pidió que estimaran la probabilidad de aparición de cada especie en el entorno del área de estudio. Para ello se emplearon dos esquemas de clasificación de hábitats: uno *complejo*, que incluía todas las 112 categorías del mapa digital de usos y coberturas del suelo de Andalucía (SinambA) y otro esquema, *simple*, que era una reclasificación de las categorías anteriores en sólo 8 (cultivos herbáceos y pastizales, cultivos leñosos, áreas forestales planifolias, áreas forestales acutifolias, matorrales, vegetación riparia o lacustre y áreas urbanas e infraestructuras). Los expertos estimaron la probabilidad de presencia en cada categoría de hábitat según cuatro clases (0, la especie nunca está presente en el hábitat considerado; 1, presencia ocasional; 2, presencia común; 3, la especie siempre está en ese hábitat). La estima de probabilidades según el esquema complejo es más lenta de realizar que la estima según el esquema simple y necesita un mayor conocimiento previo de la avifauna local. Estos dos esquemas tratan de reproducir dos posibilidades extremas que existen ante una clasificación de la idoneidad de los hábitats para la fauna según un criterio de experto, que es el procedimiento más común que se emplea en las evaluaciones de impacto ambiental o en los estudios de ordenación territorial. Se obtuvo además un promedio de la probabilidad predicha por los tres expertos para cada hábitat (lo que llamaremos en adelante el *experto promedio*), con la intención de comprobar si una forma tan sencilla de sintetizar la información es útil. Finalmente, estos valores se reclasificaron a un intervalo [0,1] de probabilidad (0=0, 1=0.1, 2=0.6, 3=1), y la información se pasó a un entorno SIG donde se generaron, para cada especie, 8 mapas de probabilidad de presencia con una resolución de 50 mts (2 clasificaciones del hábitat x [3 expertos + experto promedio]). La probabilidad predicha por cada modelo de experto en cada punto de muestreo se estimó como el promedio de la probabilidad de presencia en círculos de 350 y 1250 metros de diámetro centrados en los puntos de muestreo.

3.2.2. Rapaces

La dificultad de valorar mediante el criterio de expertos la adecuación del hábitat en unidades de área extensas (las cuadrículas de 100 km^2 que se usan en este trabajo), hizo que abandonáramos la estrategia seguida en el estudio de los paseriformes y afines. En este caso, el criterio de experto se tomó de los datos del nuevo atlas de aves reproductoras de España (en elaboración) para Andalucía (SEO/BirdLife 2002). En éste, numerosos colaboradores (generalmente expertos locales) han recorrido las distintas cuadrículas UTM 10x10 de España durante 1998-2001 dedicando un esfuerzo heterogéneo a la búsqueda de indicios de cría de las especies que las habitan. Las observaciones de aves se categorizan en tres clases principales de evidencia de reproducción creciente (reproducción posible, probable y segura, Purroy 1997), que fueron transformadas en probabilidades de presencia entre 0 y 1 (tabla 2). Los atlas no se generan con modelos de criterio de experto pero su interpretación típica los asemeja a tales modelos de experto (la distribución de las especies se suele considerar continua).

3.3. Evaluación de los modelos

3.3.1. Paseriformes y afines

La evaluación de los modelos estadísticos se llevó a cabo según un procedimiento de remuestreo de datos por validación cruzada en conjuntos (*k-fold crossvalidation*) . Las observaciones se dividieron aleatoriamente en 5 conjuntos de forma que con el 80% de las observaciones (4 de estos conjuntos) se construía un modelo que generaba predicciones para el restante 20% (el conjunto que queda), donde se evaluaba su capacidad predictiva (Verbyla & Litvaitis 1989). Ésta se calculó como el área bajo la curva (AUC de Area Under the Curve, Hanley & McNeil 1982; Swets 1988) de un gráfico de operador-receptor (gráfico ROC de Receiver Characteristic Operating plot, Cumming 2000), que es la medida de discriminación más adecuada para los modelos de distribución (ver capítulo I, Manel, Williams & Ormerod 2001). También se calculó el

Categoría	Descripción
Sin reproducción (0)	Ausencia de la especie en época reproductora
Reproducción posible	
V (0.1)	Especie vista en época adecuada y hábitat de cría adecuado
Reproducción probable	
MC (0.2)	Macho con cantos territoriales
T (0.3)	Ave o pareja con territorio establecido
C (0.4)	Cortejo, parada nupcial, disuasión ante depredadores, ...
CN (0.5)	Construcción de nido, entrada en agujeros, ...
Reproducción segura	
CD (0.6)	Distracción o fingimiento de heridas por parte de los adultos
UN (0.7)	Nido usado en el año o cáscaras de huevo asignables a la especie
J (0.8)	Jóvenes recién salidos del nido
AC (0.9)	Adultos con cebo o saco fecal en el pico
N (1)	Nido ocupado

Tabla 2. Categorías de reproducción que se asignan a cada especie de rapaz en las cuadrículas 10x10 muestreadas en el nuevo atlas de las aves reproductoras de España. Entre paréntesis se indica la probabilidad de aparición de la especie que se ha considerado en cada caso.

porcentaje de clasificación correcta (PCC), medido como la proporción de presencias y de ausencias acertadas con un punto de corte igual a 0.5 (e.d., consideramos que el modelo predecía la presencia de una especie si el valor de probabilidad que estimaba para un punto era mayor o igual que 0.5). El PCC está afectado por la prevalencia y se ha considerado una medida engañosa de capacidad predictiva (Fielding & Bell 1997, y capítulos anteriores de esta tesis doctoral); no obstante, decidimos calcularlo por su mayor familiaridad y a modo comparativo con el AUC. El proceso de remuestreo se realizó 20 veces para obtener 100 estimas de capacidad predictiva (5 por cada una de las 20 veces que se dividieron los datos).

Los modelos de experto se evaluaron mediante la estimación de la capacidad predictiva en los mismos 100 conjuntos de observaciones que se usaron en los modelos estadísticos. Los valores de probabilidad de presencia de cada especie para cada conjunto de los puntos de muestreo (que comprende un 20% de las observaciones) se compararon con la presencia/ausencia detectada en los censos, obteniéndose las estimas de AUC y PCC que después se promediaron.

Por último, se analizó mediante ANOVA el efecto sobre las estimas de capacidad predictiva de los tipos de modelo según su origen (nueve por cada especie: uno estadístico y cuatro de expertos), del esquema de clasificación adoptado (dos por especie: esquemas sencillo y complejo), de la resolución espacial (350 vs 1250 mts) y de la variabilidad entre especies.

3.3.2. Rapaces

En este apartado comparamos primero la capacidad predictiva del atlas, considerado como un modelo de experto, con la de los modelos estadísticos. Segundo, nos planteamos hasta qué punto las predicciones de los modelos estadísticos coinciden con los resultados de los atlas de distribución, pues, de existir un alto grado de solapamiento, los modelos estadísticos podrían emplearse para extrapolar la información recogida a áreas sin prospectar en los atlas. En el primer caso la información del atlas se utilizó como si se tratara de un modelo de experto. En el segundo caso esa información se consideró como la distribución *real* de las especies. Por tanto, se hicieron dos evaluaciones diferentes según si los datos de referencia con los que comparar las predicciones de los modelos eran los de los censos por carretera (n=88 cuadrículas) o los de los resultados del atlas (n=383 cuadrículas, el atlas se utilizó como verdad terreno).

Los modelos estadísticos que se compararon fueron los que incorporaban variables de vegetación, topografía y coordenadas espaciales (modelos TUC del capítulo VII). En el primer tipo de evaluación (n=88) se generaron predicciones *jackknife* para cada cuadrícula (e.d., se construía un modelo estadístico con 87 cuadrículas y se predecía para la restante, ver detalles en capítulo VII), que se comparaban con los resultados de los censos por carretera (Verbyla & Litvaitis 1989). Se prefirió usar *jackknife* frente a otras técnicas de remuestreo de datos porque esta es la más apropiada cuando se tiene un tamaño muestral reducido. Los datos del atlas correspondientes a las 88 cuadrículas censadas por carretera se compararon con los resultados de los censos de dos formas: considerando los datos básicos (cualquier indicio de reproducción se tomó como presencia de la especie), y transformando las clases nominales en probabilidades de presencia (tabla 2). En el segundo tipo de evaluación (n=383) se evaluó la capacidad del modelo estadístico para predecir la presencia/ausencia de las especies según el atlas. La presencia de las especies en las cuadrículas del atlas se consideró con tres criterios: presencia en todas las cuadrículas con indicios de reproducción, en sólo aquellas con al menos indicios probables de reproducción y, por último, en sólo las que se había detectado una reproducción segura. Los estadísticos utilizados en las evaluaciones fueron el AUC y el PCC (con 0.5 como punto de corte). Varias cuadrículas tenían menos de 100 km^2 de superficie al estar ocupadas en parte por el mar o bien por disponerse en el borde de un cambio de huso. Por esta razón se dieron pesos proporcionales a la superficie terrestre que ocupaba cada cuadrícula tanto a las predicciones de los modelos estadísticos como a las observaciones del atlas. Los errores estándar se estimaron mediante *bootstraping*, recalculando los estadísticos en 250 muestras de tamaño igual al conjunto original (e.d., n=88 o n=383) cuyas observaciones se escogieron al azar con repetición.

4. Resultados

4.1. Paseriformes y afines

El desequilibrio de nuestro diseño del estudio (existe un solo modelo estadístico por cada especie frente a dos por cada experto) nos obliga a analizar el efecto del tipo de modelo de una manera poco directa. Primero damos los resultados de los análisis en los que nos interesa comparar los distintos modelos de criterio de experto y los estadísticos, y después mostramos los análisis que se refieren sólo a los modelos de experto.

En primer lugar, la capacidad predictiva de los distintos modelos de experto y de los modelos estadísticos, medida como AUC o el porcentaje de clasificación correcta (PCC), difirió entre especies (tablas 3 y 4). Así, el ANOVA de dos vías mostró una interacción significativa entre el tipo de modelo y la especie (AUC: F=18.0, P<0.0001; PCC: F=28.5, P<0.0001). Esta interacción sugiere la posibilidad de que algún tipo de modelo (según si deriva de un esquema simple, un esquema complejo, o de un modelo estadístico) o alguno de los expertos sean más predictivos que el resto para algunas especies. Esta segunda posibilidad se consideró al repetir el ANOVA con los modelos de cada experto por separado, encontrándose la misma interacción (P<0.0001 en todos los casos). Finalmente, se controló la variabilidad introducida por las distintas especies para

Fuente de variación	gdl	Suma de cuadrados	Cuadrados medios	F	P
tipo de modelo (expertos y estadístico)	8	1.98	0.25	182.8	<0.0001
especie	9	2.49	0.28	204.1	<0.0001
modelo x especie	72	1.76	0.02	18.0	<0.0001
residuos	90	0.12	0.001		

Tabla 3. ANOVA del AUC para los modelos de especies paseriformes y afines. Nótese que en este análisis se consideraron nueve modelos para cada especie: uno estadístico y dos por cada uno de los tres expertos y el promedio de expertos (según un esquema de clasificación simple y otro complejo).

Fuente de variación	gdl	Suma de cuadrados	Cuadrados medios	F	P
tipo de modelo (expertos y estadístico)	8	1.01	0.13	97.0	<0.0001
Especie	9	3.73	0.41	317.5	<0.0001
modelo x especie	72	2.68	0.04	28.5	<0.0001
residuos	90	0.12	0.001		

Tabla 4. ANOVA del porcentaje de clasificación correcta para los modelos de especies paseriformes y afines. Nótese que en este análisis se consideraron nueve modelos para cada especie: uno estadístico y dos por cada uno de los tres expertos y el promedio de expertos (según un esquema de clasificación simple y otro complejo).

separar su efecto del producido por el tipo de modelo: en este caso se encontró un efecto significativo del tipo de modelo (tablas 5 y 6). Además, la capacidad predictiva alcanzada para cada especie no fue diferente en los modelos realizados a distinto radio (figuras 1 y 2).

Segundo, nos planteamos si la capacidad predictiva difería entre los modelos de expertos realizados según un esquema simple y los que siguieron un esquema complejo. No encontramos diferencias en las estimas de AUC (tabla 7) pero sí en las de PCC (tabla 8), siendo algo mayor la capacidad predictiva que alcanzan los modelos realizados según un esquema complejo (media=0.74, sd=0.18 vs media=0.69, sd=0.24). Después comprobamos que los modelos derivados del criterio de los distintos expertos no difieren en cuanto al AUC que obtienen (tabla 9, figura 1), pero sí tienden a diferir en cuanto al PCC (tabla 10, figura 2). En concordancia, los modelos del experto promedio sólo difirieron del resto en el PCC (AUC, diferencia en las medias de 0.02, test de la t apareado: t=0.83, gdl=9, P=0.43; PCC, diferencia de 0.09, t=2.81, gdl=9, P=0.02). Los modelos estadísticos alcanzaron valores de AUC significativamente mayores que el promedio de los modelos de experto (diferencia de 0.33, t=8.79, gdl=9, P<0.0001).

Variable	gdl	Suma de cuadrados	Cuadrados medios	F	P
Error: especie					
Residuos	9	2.49	0.28	-	-
Error: entre variables					
tipo de modelo (expertos y estadístico)	8	1.98	0.25	20.24	<0.0001
radio	1	0.004	0.004	0.34	0.56
modelo x radio	8	0.006	0.001	0.06	0.99
Residuos	153	1.87	0.01	-	-

Tabla 5. ANOVA del AUC para los modelos de paseriformes y afines en que se ha controlado la variabilidad introducida por las distintas especies. Nótese que en este análisis se consideraron nueve modelos para cada especie: uno estadístico y dos por cada uno de los tres expertos y el promedio de expertos (según un esquema de clasificación simple y otro complejo).

Variable	gdl	Suma de cuadrados	Cuadrados medios	F	P
Error: especie					
Residuos	9	3.73	0.41	-	-
Error: entre variables					
tipo de modelo (expertos y estadístico)	8	1.01	0.12	7.07	<0.0001
radio	1	0.04	0.04	2.44	0.12
modelo x radio	8	0.01	0.00	0.10	0.99
Residuos	153	2.74	0.02	-	-

Tabla 6. ANOVA del porcentaje de clasificación correcta para los modelos de paseriformes y afines en que se ha controlado la variabilidad introducida por las distintas especies. Nótese que en este análisis se consideraron nueve modelos para cada especie: uno estadístico y dos por cada uno de los tres expertos y el promedio de expertos (según un esquema de clasificación simple y otro complejo).

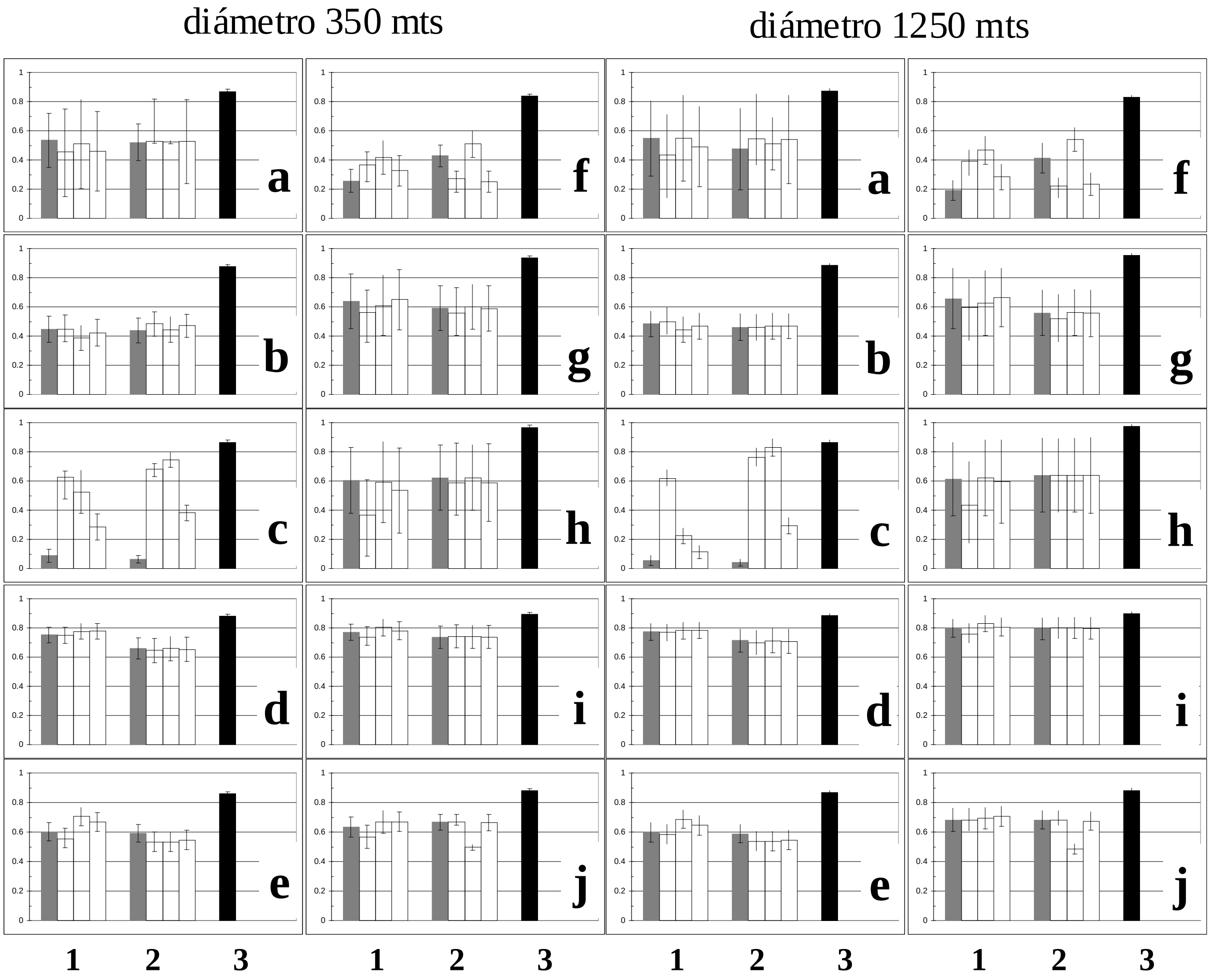

Figura 1. AUC de los modelos de experto generados mediante un esquema simple (1) y otro complejo (2, con el experto promedio en blanco), y de los modelos estadísticos (3) a dos resoluciones espaciales. a, *Alectoris rufa*; b, *Certhia brachydactyla*; c, *Galerida theklae*; d, *Parus caeruleus*; e, *Sylvia melanocephala*; f, *Carduelis cannabina*; g, *Erithacus rubecula*; h, *Melanocorypha calandra*; i, *Sitta europaea*; j, *Troglodytes troglodytes*. Los datos son valores promedio (n=20) de los valores medios (n=5) obtenidos en cada remuestreo. Las barras de error son 2*SE.

En contraste, los modelos estadísticos tendieron a alcanzar valores de PCC mayores que los modelos de experto, pero las diferencias sólo fueron significativas en algunos casos (experto 1: diferencia de 0.13, t=2.37, gdl=9, P=0.04; experto 2: diferencia de 0.18; t=2.35, gdl=9, P=0.04; experto 3: diferencia de 0.04, t=1.25, gdl=9, P=0.24; experto promedio: diferencia de 0.02, t=0.59, gdl=9, P=0.57).

Además, y como resulta especialmente notable en las figuras 1 y 2, la estima de la capacidad predictiva de los modelos estadísticos tuvo una variabilidad menor que la de los modelos generados por expertos, tanto en el AUC (diferencia en el tamaño del intervalo de confianza aproximado [2*SE] de 0.051; t=4.11, gdl=9, P=0.003), como en el PCC (experto 1: diferencia de 0.014, t=14.55, gdl=9, P<0.0001; experto 2: diferencia de 0.013; t=8.83, gdl=9, P<0.0001; experto 3: diferencia de 0.011, t=6.84, gdl=9, P=0.0001; experto promedio: diferencia de 0.010, t=6.43, gdl=9, P=0.0001).

Finalmente, las estimas de capacidad predictiva alcanzada por los modelos estadísticos para todas las especies fueron superiores a las que tendría un modelo nulo (figuras 1 y 2). Sin embargo, AUC y PCC difieren algo en cuanto al escenario que nos presentan: todos los modelos pueden

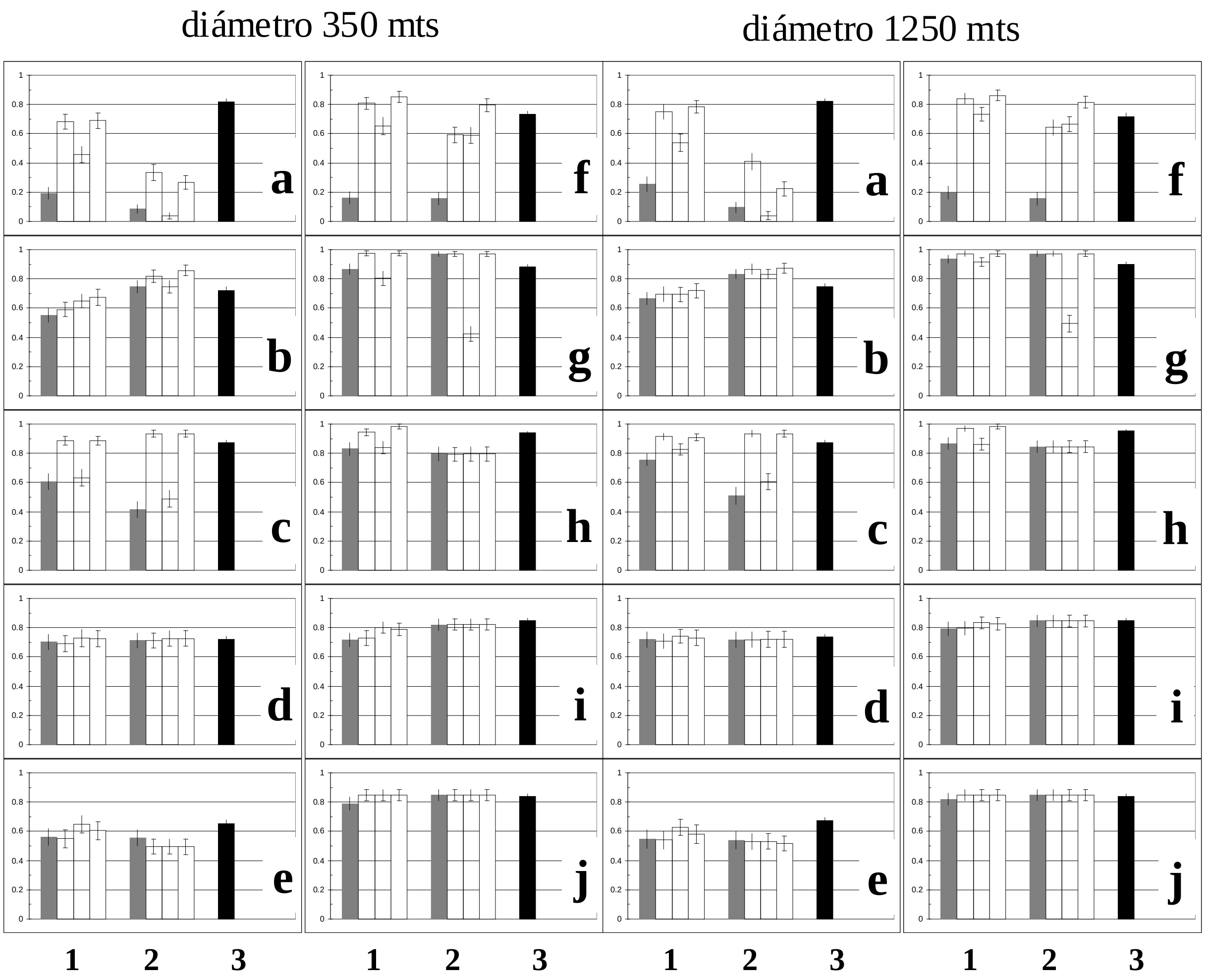

Figura 2. Porcentaje de clasificación correcta (PCC) de los modelos de experto y de los modelos estadísticos. Abreviaturas como en la figura 1.

considerarse buenos según el AUC (>0.8 en todas las especies), pero son más desiguales según el PCC (*Certhia brachydactyla*, *Parus caeruleus* y *Sylvia melanocephala* tienen relativamente bajos PCC entre 0.6 y 0.7). Los modelos de experto se comportaron también de manera heterogénea (figuras 1 y 2). Los modelos para algunas especies alcanzaron valores altos tanto de AUC (0.6-0.7) como de PCC (>0.8) (*Erithacus rubecula*, *Melanocorypha calandra* y *Sitta europaea*), mientras que los de otras fueron poco predictivos (no mejores que un modelo nulo), especialmente según el AUC (*Alectoris rufa*, *Certhia brachydacyla* y *Carduelis cannabina*). En general, las estimas de PCC alcanzadas por los modelos de experto fueron relativamente mayores que sus estimas de AUC y, salvo excepciones (*Alectoris rufa*, *Carduelis cannabina* y *Galerida theklae*), los modelos de los distintos expertos obtuvieron resultados similares.

Los mapas de probabilidad predicha para cada especie por los modelos de experto promedio y por los estadísticos pueden verse en el apéndice I.

4.2. Rapaces

En el primer tipo de evaluación, donde la referencia son los censos por carretera, los modelos estadísticos obtuvieron una alta y similar capacidad predictiva para las cuatro especies consideradas según el AUC

Variable	gdl	Suma de cuadrados	Cuadrados medios	F	P
Error: especie					
Residuos	9	2.71	0.30	-	-
Error: entre variables					
tipo de modelo (simple vs complejo)	1	0.000	0.000	0.01	0.92
radio	1	0.004	0.004	0.35	0.55
modelo x radio	1	0.000	0.000	0.02	0.90
Residuos	147	1.71	0.01	-	-

Tabla 7. Comparación de AUC entre los modelos de experto (dos tipos de modelo por cada especie, uno sigue un esquema de clasificación simple y el otro un esquema complejo) para especies paseriformes y afines.

Variable	Gdl	Suma de cuadrados	Cuadrados medios	F	P
Error: especie					
Residuos	9	3.88	0.43	-	-
Error: entre variables					
tipo de modelo (simple vs complejo)	1	0.11	0.11	5.30	0.023
radio	1	0.05	0.05	2.15	0.14
modelo x radio	1	0.00	0.00	0.09	0.76
Residuos	147	3.19	0.02	-	-

Tabla 8. Comparación del porcentaje de clasificación correcta entre los modelos de experto (dos tipos de modelos por cada especie, uno sigue un esquema de clasificación simple y el otro un esquema complejo), para especies paseriformes y afines.

(media±SD: 0.78±0.04), aunque no tanto según el PCC (media±SD: 0.72±0.06, figura 3). La capacidad predictiva de estos modelos fue mayor que las de los derivados del atlas, tanto de los generados con los datos básicos como de los generados con datos en 10 categorías de probabilidad. Los intervalos de confianza aproximados de las medias tendieron a no solaparse (las diferencias fueron, respectivamente, de 0.22 y 0.17 en AUC, y de 18 y 14% en PCC respecto los datos básicos y en categorías). Los mapas derivados de datos en categorías fueron algo más predictivos que los derivados de los datos básicos, pero los intervalos de confianza de las medias se solapan en gran medida por lo que la diferencia debería interpretarse como no significativa (figura 3).

En el segundo tipo de evaluación, donde la referencia son los resultados del atlas, los modelos estadísticos obtuvieron bajas capacidades predictivas para las cuatro especies consideradas según el AUC (media±SD: 0.59±0.03) y el PCC (media±SD: 0.51±0.08). Sólo las predicciones de los modelos estadísticos para *Milvus migrans* parecen acercarse moderadamente a los datos del atlas (figura 4). El PCC sugiere que la concordancia es mayor con el criterio más restrictivo para asumir la presencia de una especie en una cuadrícula (reproducción segura), pero el AUC no muestra ningún patrón (figura 4). Una comparación similar con los datos del atlas no se hizo para el grupo de especies paseriformes y afines porque existía un desacoplamiento muy importante entre la resolución de los datos de censo (1.2 km^2 para el diámetro de censo mayor) y la resolución de los datos del atlas (100 km^2).

5. Discusión

La ventaja principal de los modelos estadísticos de distribución de especies sobre los elaborados mediante el criterio de expertos es su mayor objetividad. Sin embargo, se puede cuestionar si el esfuerzo de muestreo, sus relativamente complejos métodos matemáticos y, en ocasiones, la difícil interpretabilidad de los modelos están justificados, toda vez que el criterio de un experto podría identificar correctamente los hábitats adecuados para una especie y, por extensión, el área en que se distribuye. Nuestros resultados resuelven esta cuestión de manera muy favorables a los modelos estadísticos. En primer lugar, éstos tuvieron una alta capacidad predictiva en los dos grupos de especies analizados que fue mayor que la de los modelos generados mediante criterio de experto. Las diferencias fueron más notables en el grupo de especies paseriformes y afines, lo que indica que los modelos estadísticos son especialmente ventajosos cuando el tamaño muestral de que se dispone para generarlos es grande o, alternativamente, cuando la resolución espacial de los mapas es detallada. Entre los modelos de experto, los más elaborados tendieron a ser mejores que los sencillos, por lo que se podría justificar la adopción de esquemas complejos en su construcción. No obstante, esta tendencia no fue muy clara (sólo se detectó con el PCC) y, entre los paseriformes y afines, parecía depender de cada especie en particular.

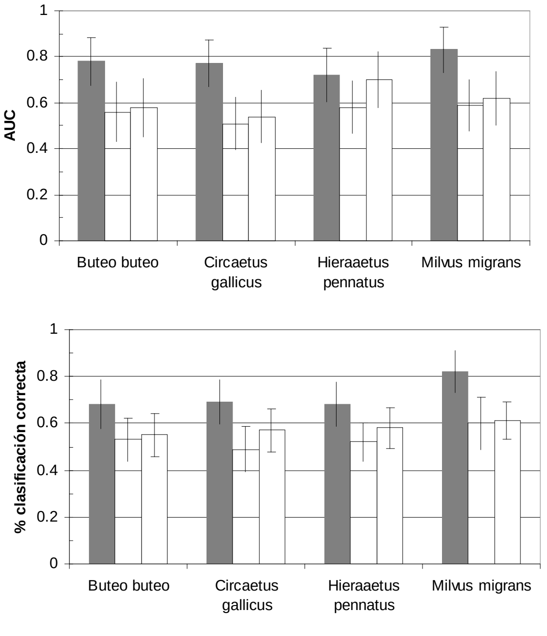

Figura 3. Estimas de capacidad predictiva para las rapaces analizadas de los modelos estadísticos (barra de la izquierda, gris), y de los mapas derivados de los datos del nuevo atlas de aves reproductoras de España (barra del centro, rayada, para los datos básicos de presencia/ausencia y barra de la derecha, blanca, para los datos en 10 categorías de probabilidad). Los datos de referencia son aquí los resultados de censos por carretera en 1996 (n=88 cuadrículas UTM 10x10). Se indican los intervalos de confianza aproximados al 95%.

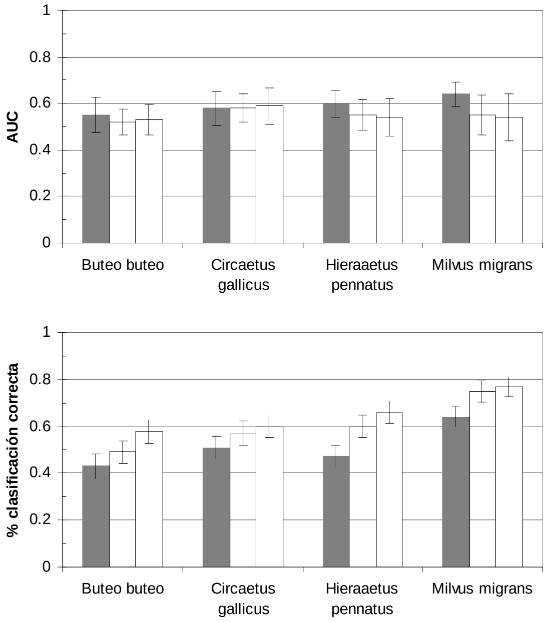

Figura 4. Estimas de la capacidad predictiva de los modelos estadísticos de las rapaces cuando los datos de referencia son los derivados del nuevo atlas de aves reproductoras de España (barra de la izquierda, gris, para cualquier indicio de reproducción; barra del centro, rayada, para las reproducciones al menos probables; y barra de la derecha, blanca, para las reproducciones seguras, n=383). Se indican los intervalos de confianza aproximados al 95%.

En segundo lugar, nuestros resultados sugieren que los modelos de experto son más inconsistentes que los estadísticos, ya que sus estimas de capacidad discriminativa son más variables. Esto quiere decir que la eficacia de

Fuente de variación	gdl	Suma de cuadrados	Cuadrados medios	F	P
tipo de modelo 1 (expertos)	3	0.09	0.03	0.94	0.42
tipo de modelo 2 (simple vs complejo)	1	0.00	0.00	0.00	0.96
radio	1	0.00	0.00	0.14	0.71
modelo 1 x modelo 2	3	0.01	0.00	0.06	0.98
modelo 1 x radio	3	0.00	0.00	0.04	0.99
modelo 2 x radio	1	0.00	0.00	0.01	0.93
modelo 1 x modelo 2 x radio	3	0.00	0.00	0.03	0.99
residuos	144	4.33	0.03		

Tabla 9. ANOVA del AUC entre los distintos modelos de expertos para especies paseriformes y afines. Aquí se consideran los cuatro modelos de experto (tipo 1) y los dos esquemas seguidos (tipo 2).

Fuente de variación	gdl	Suma de cuadrados	Cuadrados medios	F	P
tipo de modelo 1 (expertos)	3	0.68	0.23	5.14	0.002
tipo de modelo 2 (simple vs complejo)	1	0.11	0.11	2.62	0.11
radio	1	0.05	0.05	1.06	0.30
modelo 1 x modelo 2	3	0.06	0.02	0.48	0.69
modelo 1 x radio	3	0.01	0.00	0.06	0.98
modelo 2 x radio	1	0.02	0.02	0.05	0.83
modelo 1 x modelo 2 x radio	3	0.00	0.00	0.01	0.99
residuos	144	6.32	0.04		

Tabla 10. ANOVA del PCC entre los distintos modelos de expertos para especies paseriformes y afines. Aquí se consideran los cuatro modelos de experto (tipo 1) y los dos esquemas seguidos (tipo 2).

s modelos de experto depende del conjunto de áreas en que se evalúen, lo que sólo puede explicarse si estos modelos predicen bien para determinados hábitats y mal para otros. Según esta interpretación, los expertos son capaces de identificar correctamente sólo algunos de los hábitats adecuados para las especies (o bien consideran apropiados algunos que no lo son). Tales errores podrían ser debidos o bien a lagunas en el conocimiento de los expertos o bien, más probablemente, a que las categorías de usos y coberturas del mapa ambiental utilizado como fuente de predictores se diseñaron con un propósito general, por lo que pueden no reflejar los requerimientos de las especies (al menos de forma comprensible). Se podría argumentar que los modelos de experto serían más consistentes, y tendrían mayor capacidad predictiva, si los predictores que usaran describieran mejor los hábitats desde el punto de vista de su interés para la avifauna. Tal argumento es intuitivo, pero olvida que no es abordable crear mapas de variables ambientales medidas teniendo en cuenta las distintas exigencias de las diferentes especies de aves. Los modelos de distribución de especies aplicados a grandes áreas deben recurrir, inevitablemente, a mapas diseñados con un propósito general, que describirán con precisión variable los hábitats de interés en cada caso. Dada esta situación, igualmente desfavorable para modelos estadísticos y de experto, los primeros han demostrado ser la mejor opción en las dos escalas de análisis de este estudio.

Existe cierto contraste, en cuanto a los patrones anteriores se refiere, entre los resultados de las dos medidas de capacidad predictiva que hemos usado. Así, según la más adecuada de ellas, el AUC, los modelos de experto son poco afortunados en todas las especies con la posible excepción de *Troglodytes troglodytes* y *Parus caeruleus*. Por el contrario, el PCC muestra menores diferencias entre los modelos estadísticos y los de experto. Esto se debe probablemente al efecto de la prevalencia en las estimas de PCC. Cuando la prevalencia es cercana al 50% (como en el caso de las rapaces analizadas aquí) no se producen grandes diferencias entre PCC y AUC, pero cuando quedan muy por debajo de ese 50% (como en el caso de los paseriformes), se predicen mejor las ausencias que las presencias de la especie y las estimas de PCC pueden ser engañosamente altas (Manel, Williams & Ormerod 2001). Por ejemplo, los modelos de experto para *Melanocorypha calandra* y *Erithacus rubecula* alcanzan valores altos de PCC, puesto que ambas especies tienen baja prevalencia y sus requerimientos de hábitat pueden describirse en términos de las categorías de usos y coberturas del suelo que se han utilizado aquí (i.e., los definidos por una cartografía temática de propósito general, Moreira & Fernández-Palacios 1995). En conjunto, estas discrepancias nos hacen desconfiar aún más del PCC como medida de capacidad predictiva (Pearce & Ferrier 2000; Manel, Williams & Ormerod 2001).

Dos resultados secundarios de nuestros análisis se refieren a las especies paseriformes y afines. El primero es la ausencia de diferencias sistemáticas en los resultados obtenidos a las dos resoluciones (350 y 1250 mts). Se ha visto anteriormente que los modelos más predictivos incluían variables ambientales medidas a grandes diámetros alrededor del punto de muestreo (capítulo V), lo que se ha relacionado con la importancia que tiene el paisaje como predictor (Saab 1999; Kie *et al.* 2002; Wolff *et al.* 2002). Por tanto, una de las posibles razones por las que los modelos de experto resultan poco satisfactorios es que no incluyen entre sus variables ninguna relacionada con el paisaje. Si esto es así, cabría esperar que los modelos que incluyeran variables medidas en un entorno más amplio (1250 mt) fueran mejores, lo que no ocurre. Aparentemente, promediar las variables en un entorno amplio no equivale a considerar el paisaje. El segundo resultado para mencionar aquí es que la síntesis de la opinión de varios expertos no mejora necesariamente los modelos. En las ocasiones en que se dispone de la colaboración de expertos con criterios diferentes y conocimientos similares (o difíciles de comparar), es necesario sintetizar la información que aportan (Pearce *et al.* 2001). En nuestro trabajo esto se hizo tomando el promedio de las valoraciones que los expertos hicieron para cada hábitat, aunque es posible pensar en otras formas de integrar la información, como buscar un consenso (lo que obliga a que los colaboradores interactúen), o escoger los valores mínimos o máximos en la valoración final. Un criterio sintético podría ser ventajoso al corregir las deficiencias que alguno de los expertos pudiera tener en especies o hábitats que conociera peor. De acuerdo con esto, nuestros resultados sugieren que los modelos realizados con el criterio integrado alcanzan valores de capacidad predictiva elevados (aunque no siempre los mayores) en relación al resto de modelos de experto.

Finalmente, las predicciones estadísticas no coincidieron con las observaciones del atlas para las rapaces, con la posible excepción de *Milvus migrans*. Ante esta disparidad, ¿qué fuente de cartografía deberíamos suponer más fiable? Las cuadrículas del atlas fueron prospectadas de manera no sistemática y con variable esfuerzo por colaboradores con experiencia heterogénea. Por el contrario, los datos con los que se construyeron los modelos proceden de un muestreo estandarizado, en el que se controló el esfuerzo de prospección que se realizó y éste fue siempre superior a un mínimo (Bustamante, Donázar & Hiraldo 1997). Además, se ha comprobado para el Milano real (*Milvus milvus*) que los resultados de los censos por carretera se correlacionan con las abundancias de parejas nidificantes estimadas mediante búsqueda directa de nidos (Viñuela 1997), lo que nos hace confiar en el método cuando se aplica a otras especies. Por tanto, consideramos que la información más próxima a la situación real la aportan, en general, los censos por carretera y los modelos que se derivan de ellos (aunque no hay duda de que los datos para muchas áreas del atlas son de alta calidad). Deben mencionarse, no obstante, dos circunstancias en que la información de los atlas es más fiable que la derivada de los modelos. Se trata de las poblaciones (o parejas en el caso de las rapaces) ligadas a ambientes atípicos, que los modelos estadísticos no detectan pero que pueden ser muy conocidos por los ornitólogos locales (es el caso, por ejemplo, del Milano real en Doñana, ver capítulo VIII). También, basta que exista una pareja aislada de una especie en un hábitat óptimo de pequeña extensión para que la cuadrícula que la contenga se identifique como con presencia de tal especie. Si la mayor parte de esa cuadrícula tiene hábitats subóptimos, un modelo estadístico tenderá a predecir una baja probabilidad de presencia en ella. Aún teniendo en cuenta estas salvedades, creemos que no es prudente usar los mapas derivados de información de atlas para análisis de extensión regional o inferior, como tememos que es común en los estudios del medio físico típicos, p.e., de las evaluaciones de impacto ambiental.

AGRADECIMIENTOS

Paco Chiclana, Javier Salcedo, José Antonio Lama y Jorge Garzón, del grupo ornitológico SEO-Sevilla, prestaron su tiempo para ofrecerme su criterio de expertos en la avifauna local (en esta y en otras muchas ocasiones). El Ministerio de Medio Ambiente cedió amablemente los datos correspondientes a Andalucía del nuevo atlas de aves reproductoras en España, y Juan Carlos del Moral, de SEO/BirdLife (organización encargada de la elaboración del atlas), agilizó los trámites para conseguirlos. Los muestreos del atlas y los censos de rapaces por carretera fueron realizados por numerosos colaboradores, en gran parte no profesionales, sin cuyo trabajo no habría sido posible ni este ni otros tantos estudios (en el apéndice I del capítulo VII se da una lista de colaboradores en los censos de rapaces por carretera).

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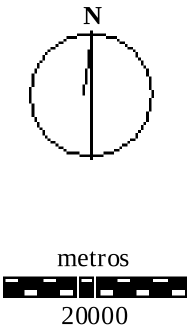


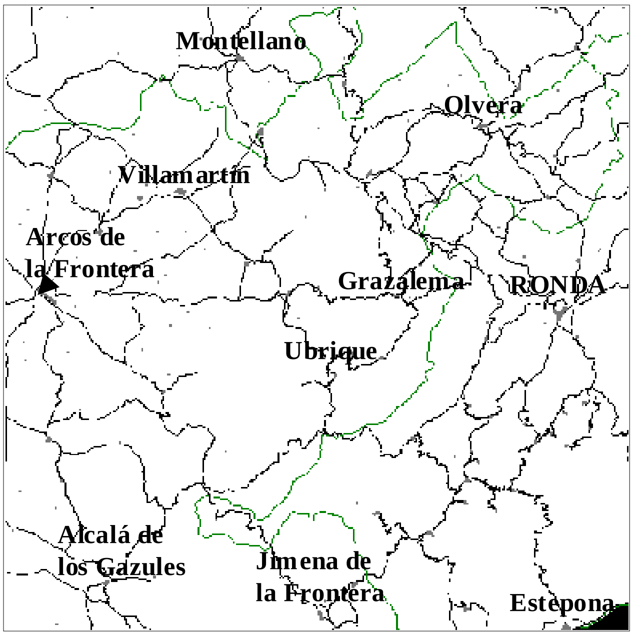


Fig.1. Mapas de referencia para las dos zonas de estudio (Aracena, arriba; Grazalema, abajo). Se señalan, en verde, los límites provinciales, en gris, la red viaria y los núcleos urbanos, y, en negrita, algunos topónimos (que se han centrado en la parte superior del área al que se nombran).

Alectoris rufa
Aracena

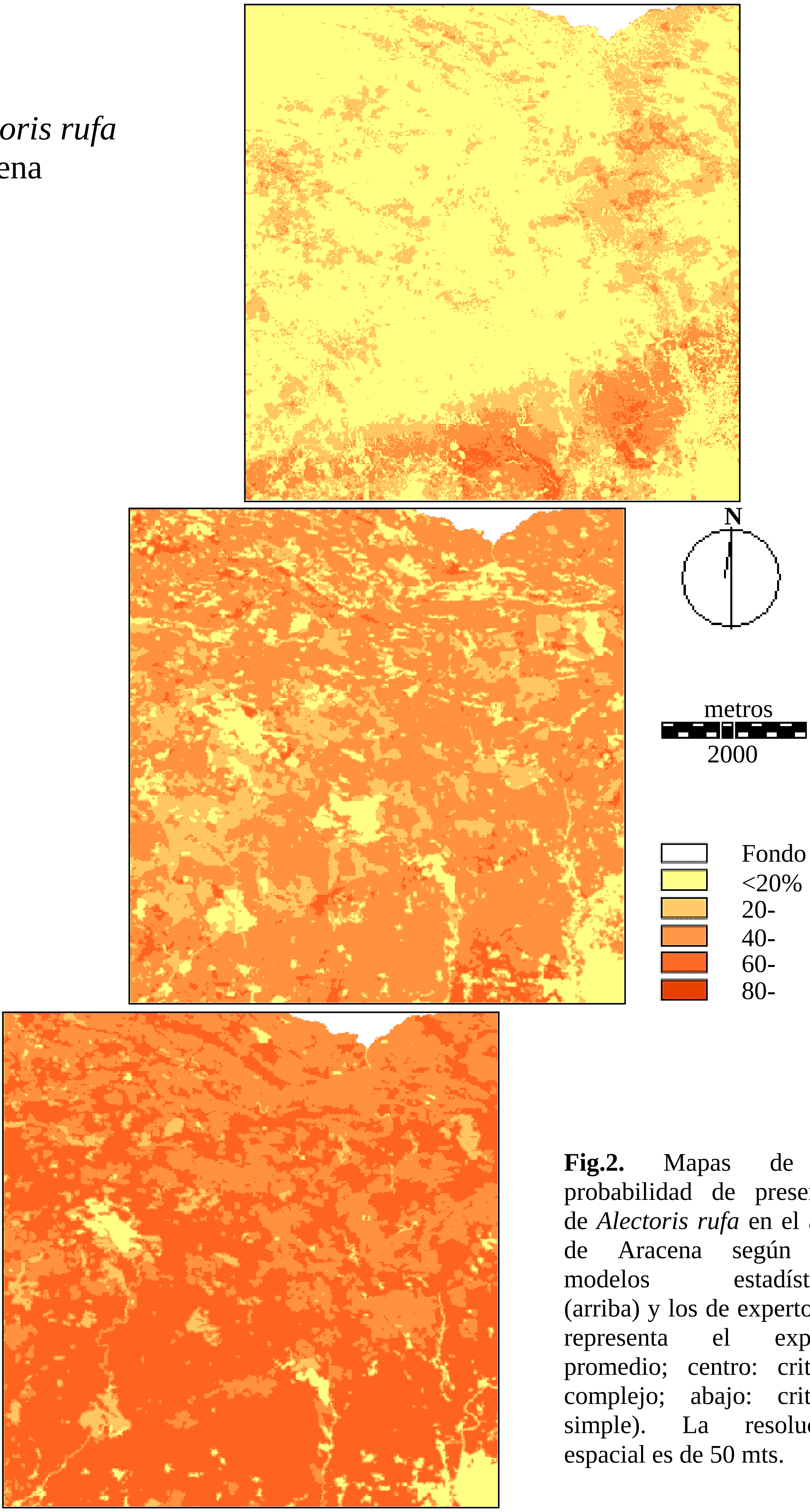


Fig.2. Mapas de la probabilidad de presencia de *Alectoris rufa* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Carduelis cannabina
Aracena

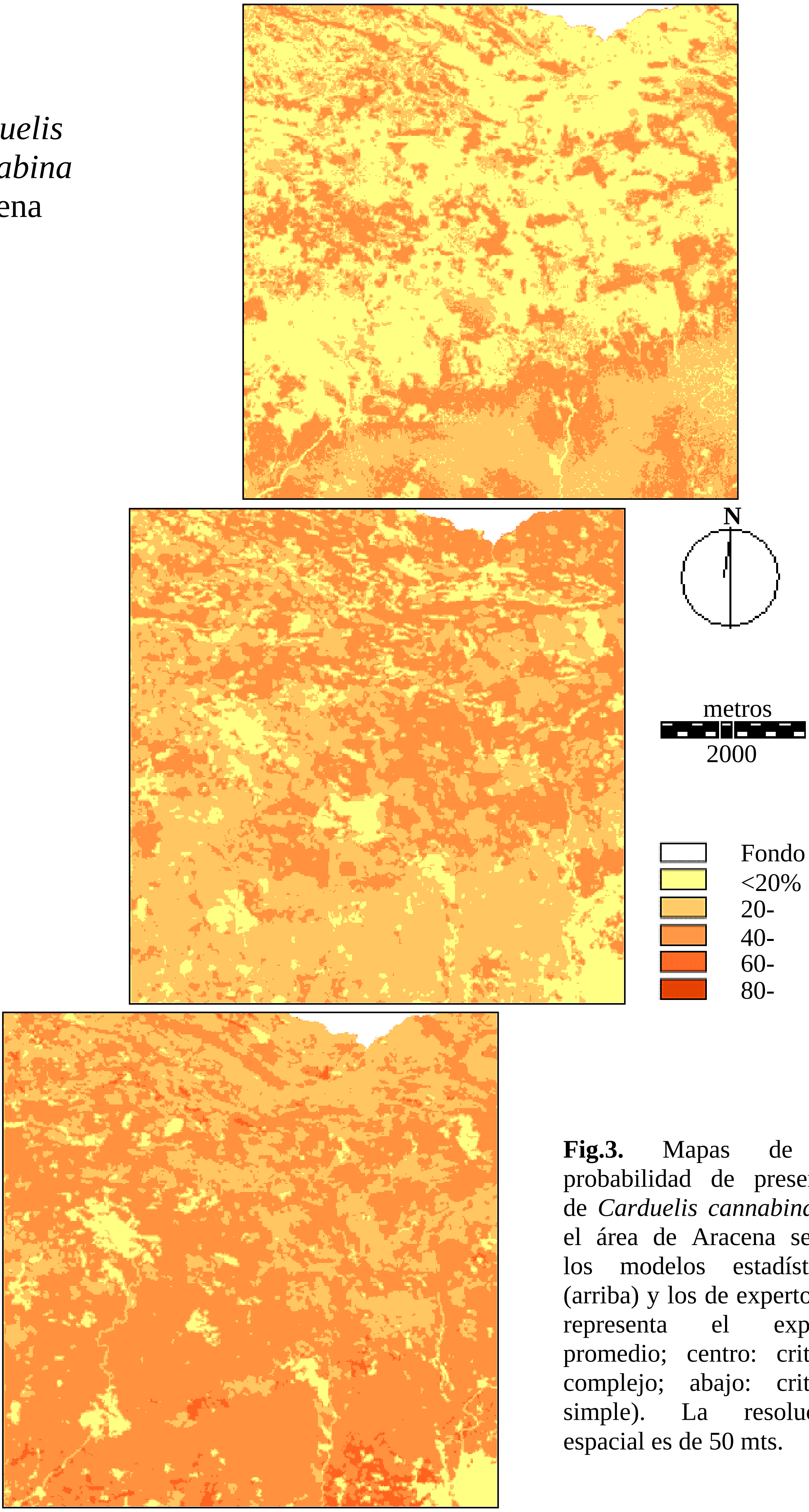
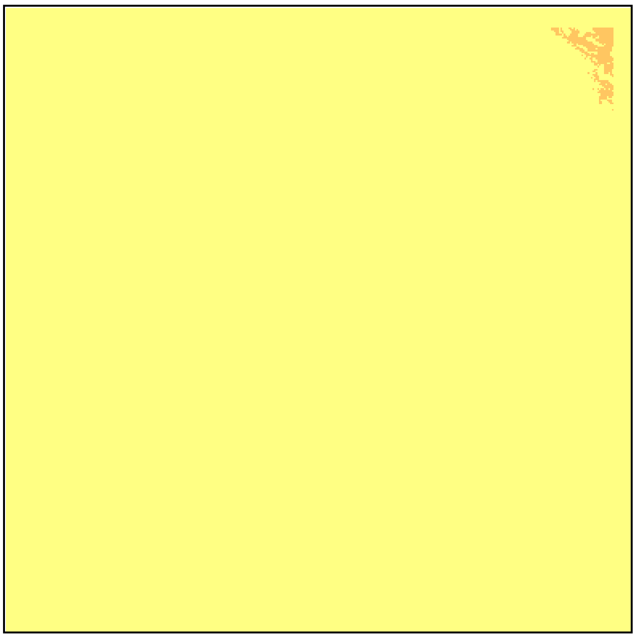
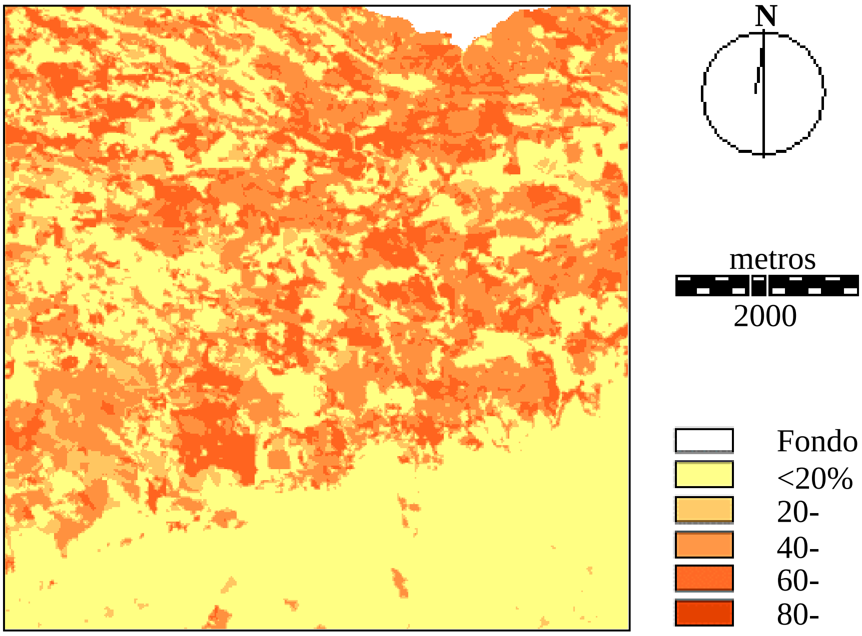


Fig.3. Mapas de la probabilidad de presencia de *Carduelis cannabina* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Certhia brachydactyla
Aracena





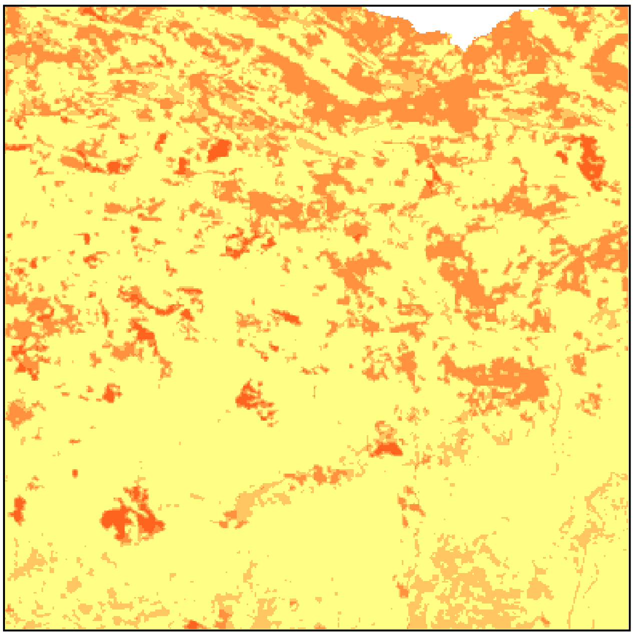


Fig.4. Mapas de la probabilidad de presencia de *Certhia brachydactyla* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Erithacus
rubecula
Aracena

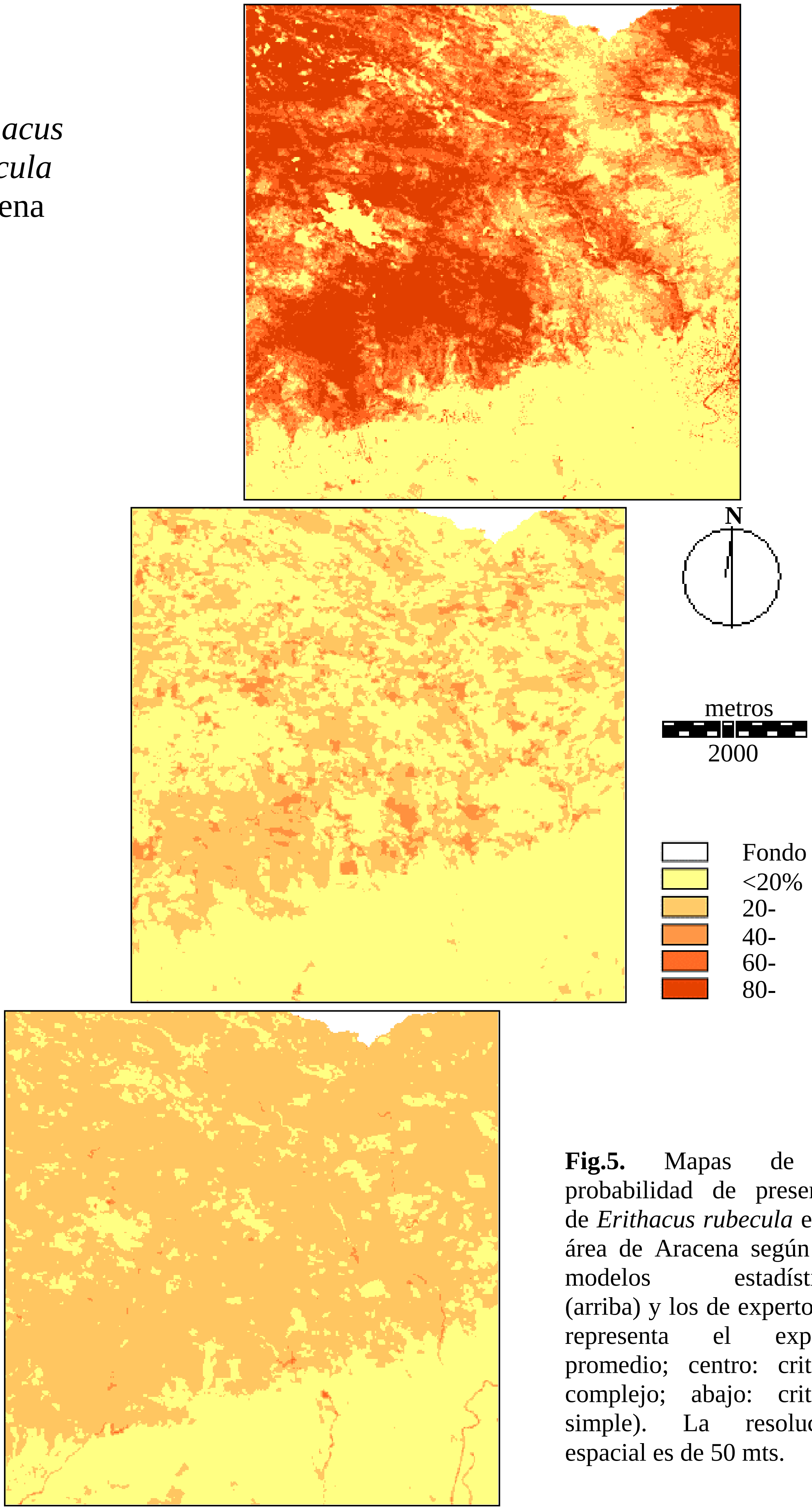


Fig.5. Mapas de la probabilidad de presencia de *Erithacus rubecula* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Galerida theklae
Aracena

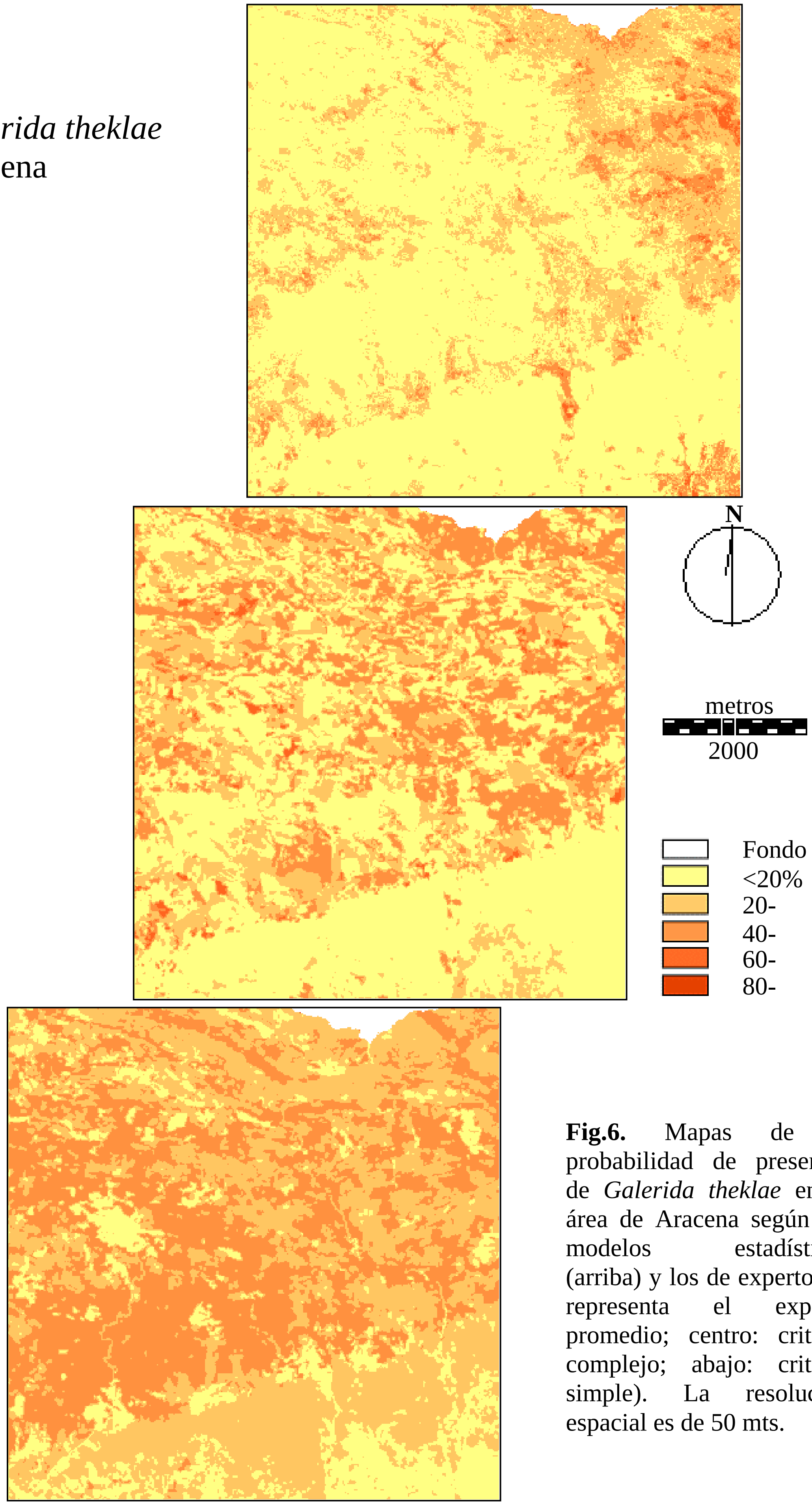


Fig.6. Mapas de la probabilidad de presencia de *Galerida theklae* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Melanocorypha calandra
Aracena

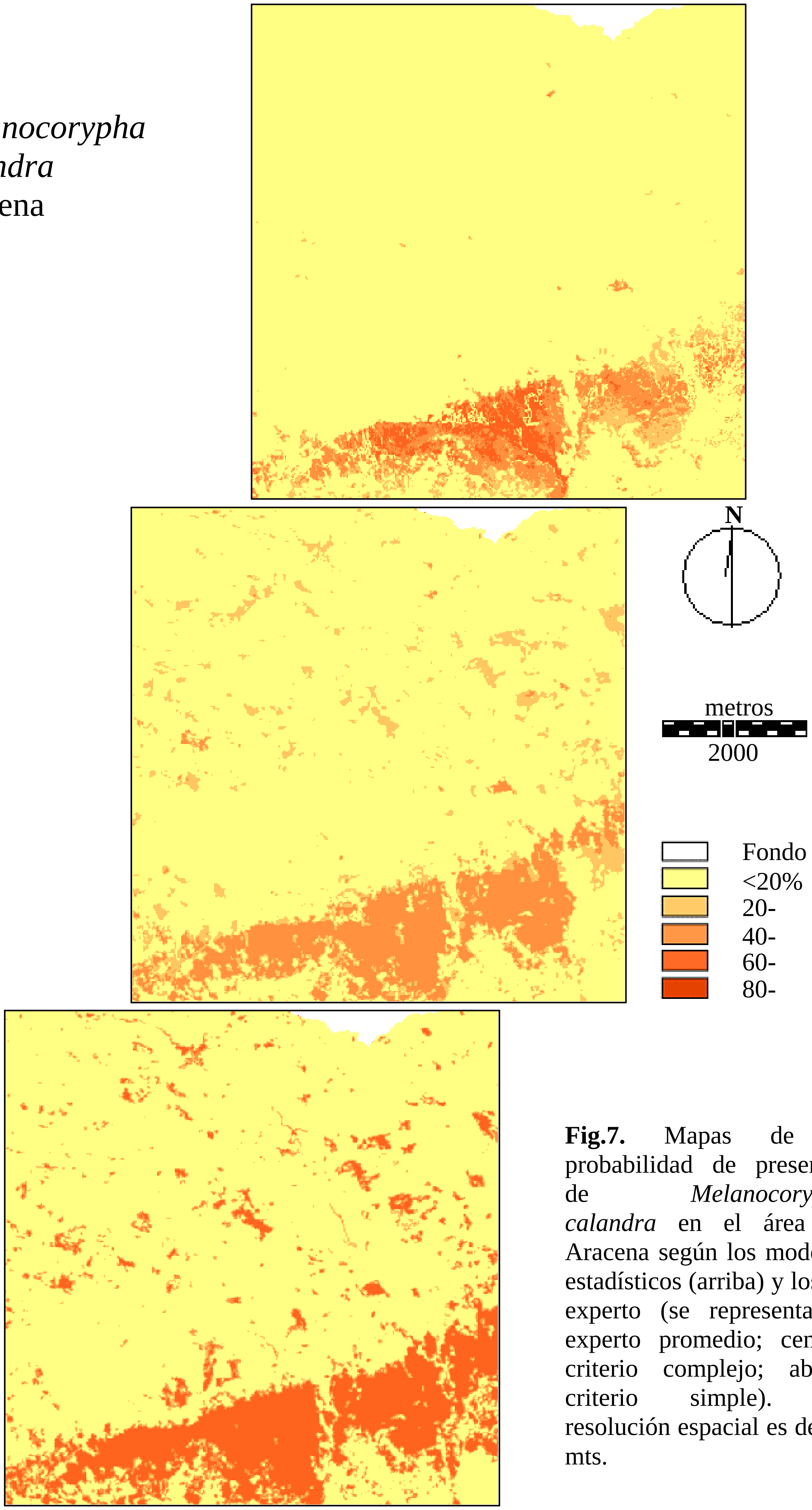


Fig.7. Mapas de la probabilidad de presencia de *Melanocorypha calandra* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Parus caeruleus
Aracena

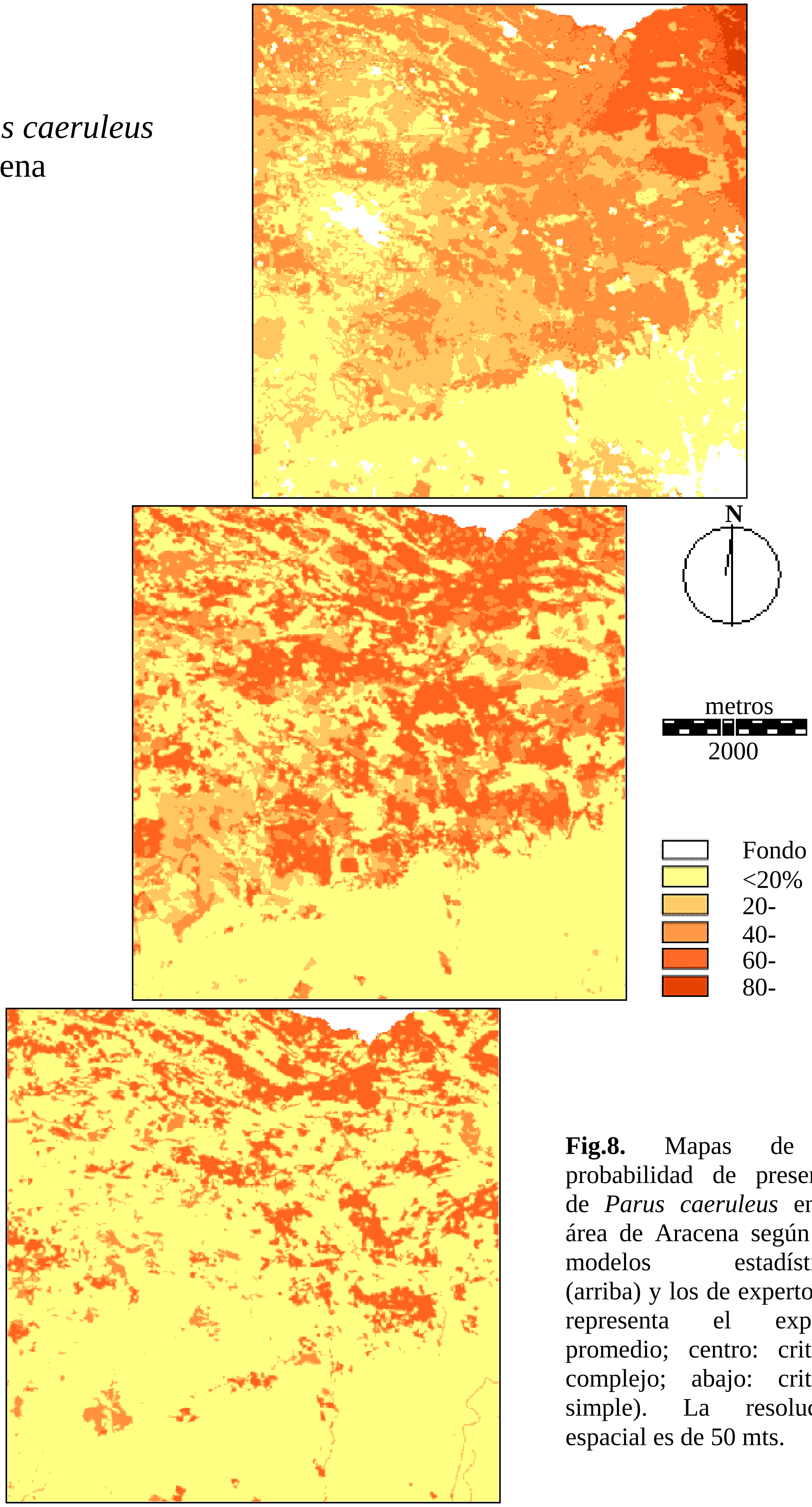


Fig.8. Mapas de la probabilidad de presencia de *Parus caeruleus* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Sitta europaea
Aracena

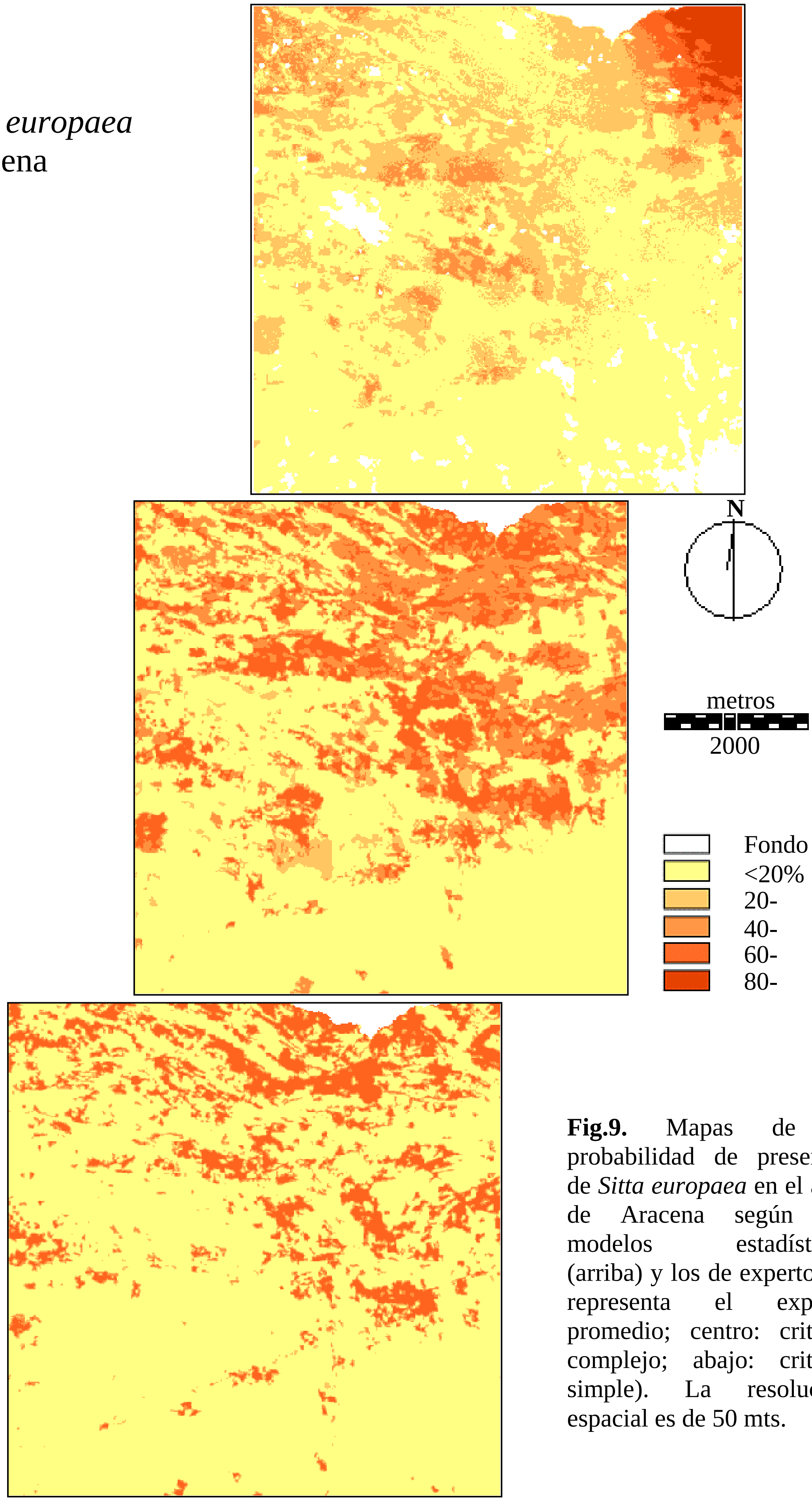


Fig.9. Mapas de la probabilidad de presencia de *Sitta europaea* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Sylvia
melanocephala
Aracena

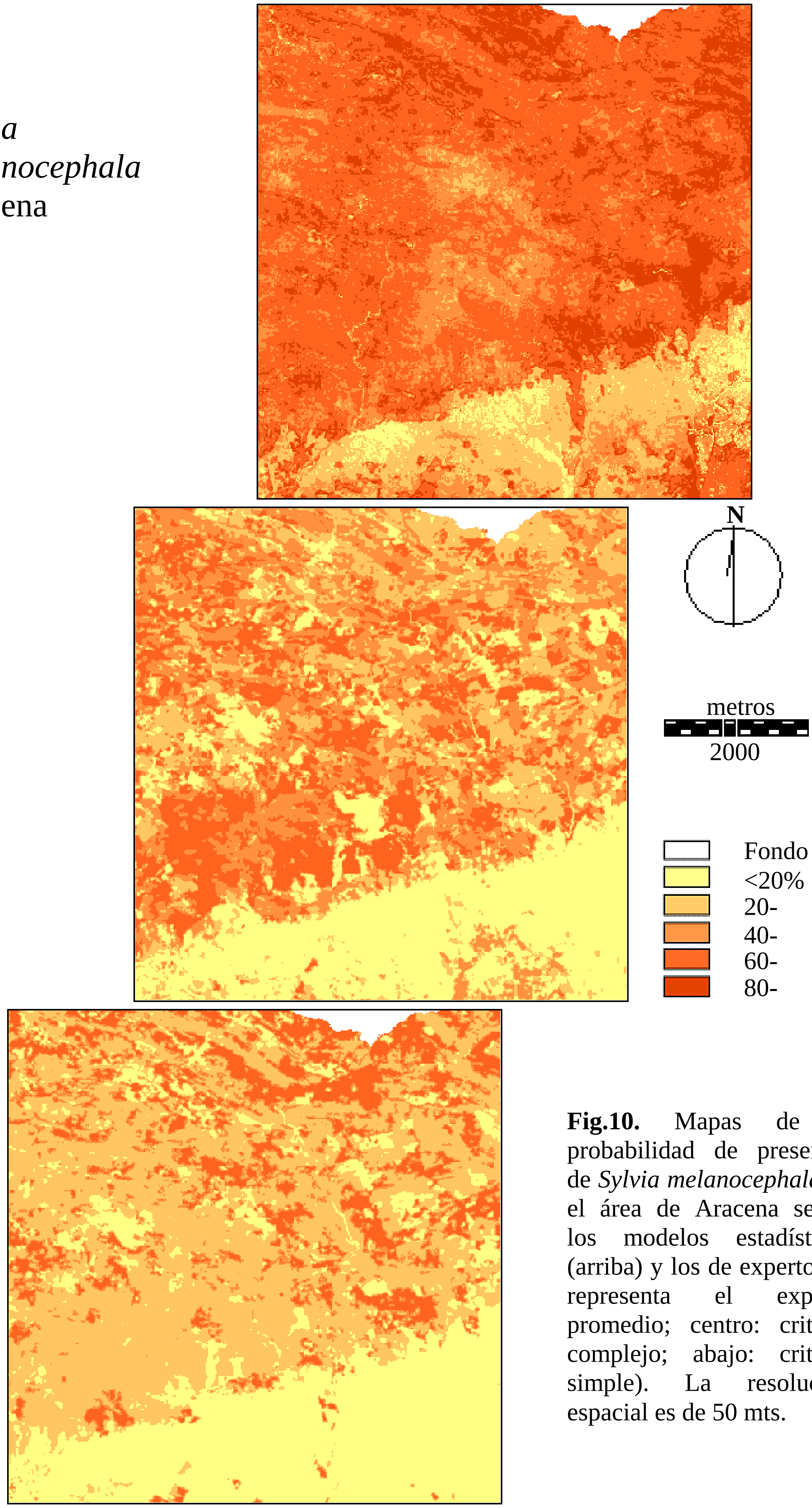


Fig.10. Mapas de la probabilidad de presencia de *Sylvia melanocephala* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Troglodytes troglodytes
Aracena

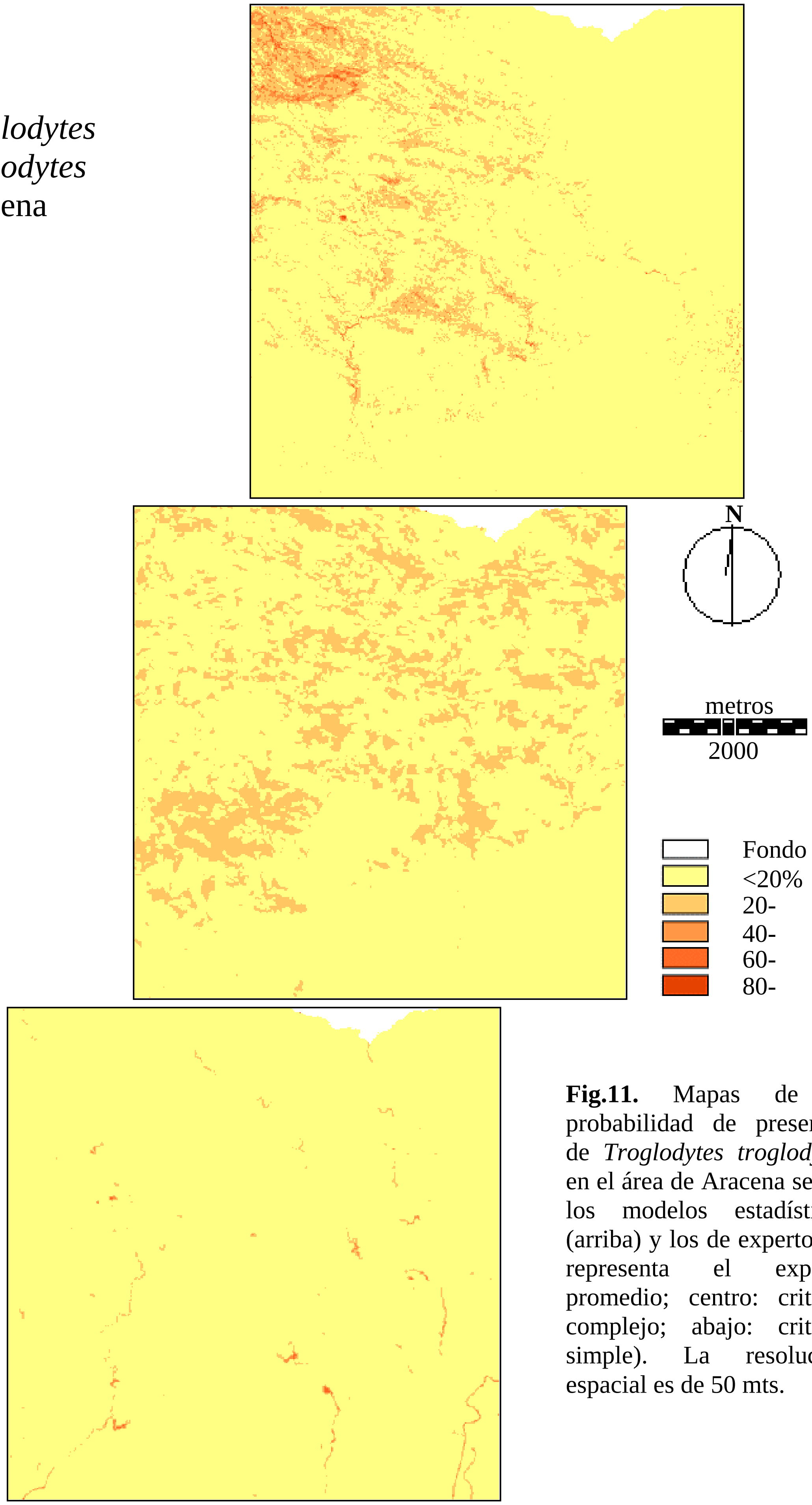


Fig.11. Mapas de la probabilidad de presencia de *Troglodytes troglodytes* en el área de Aracena según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Alectoris rufa
Grazalema

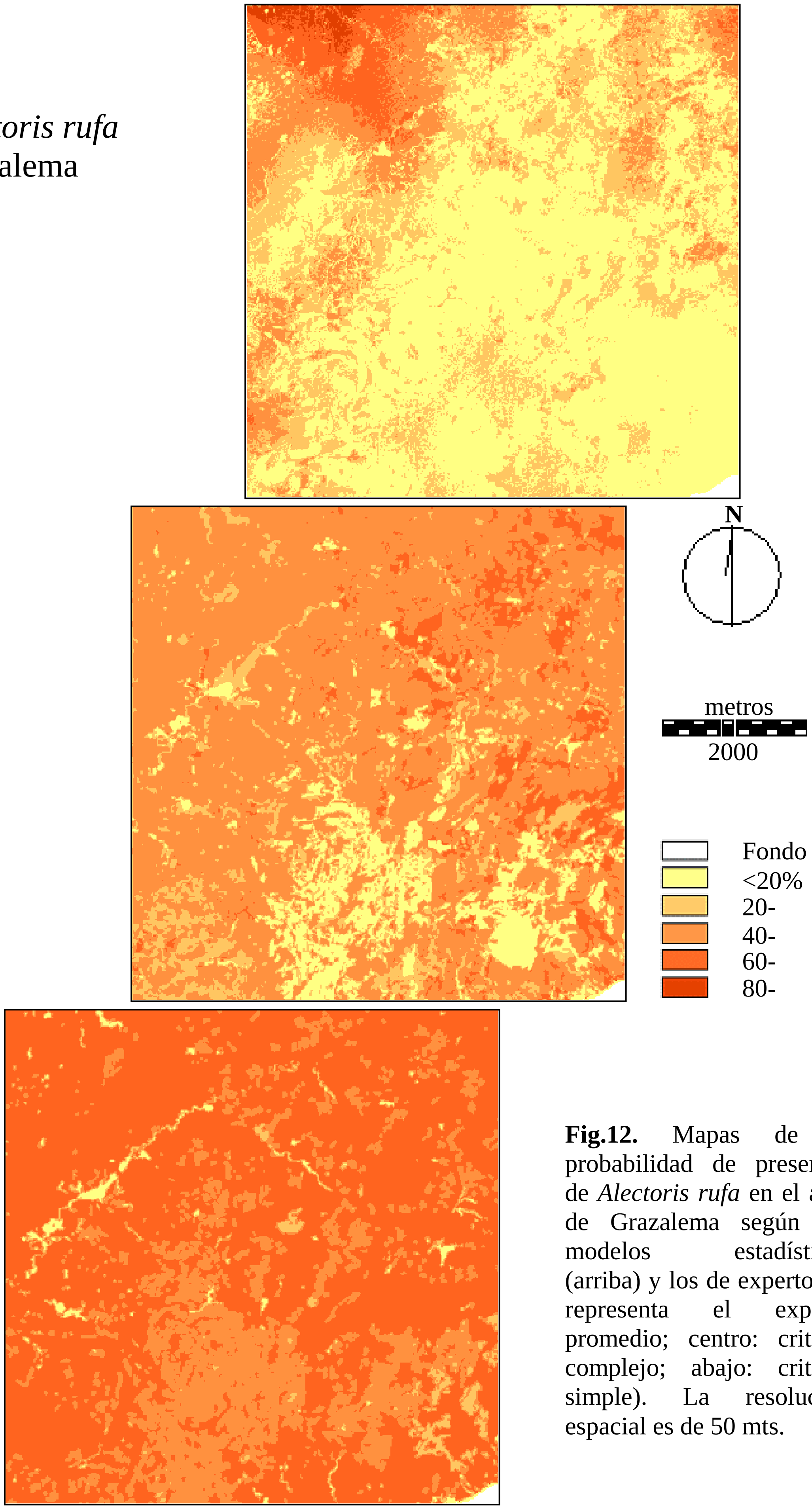
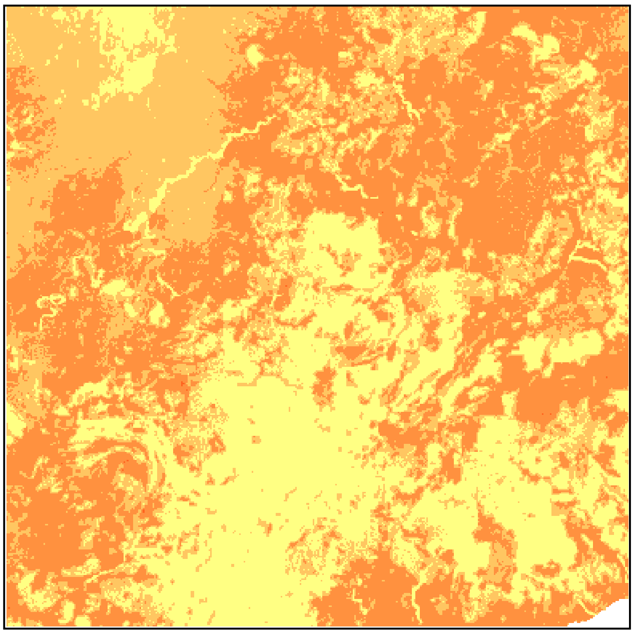
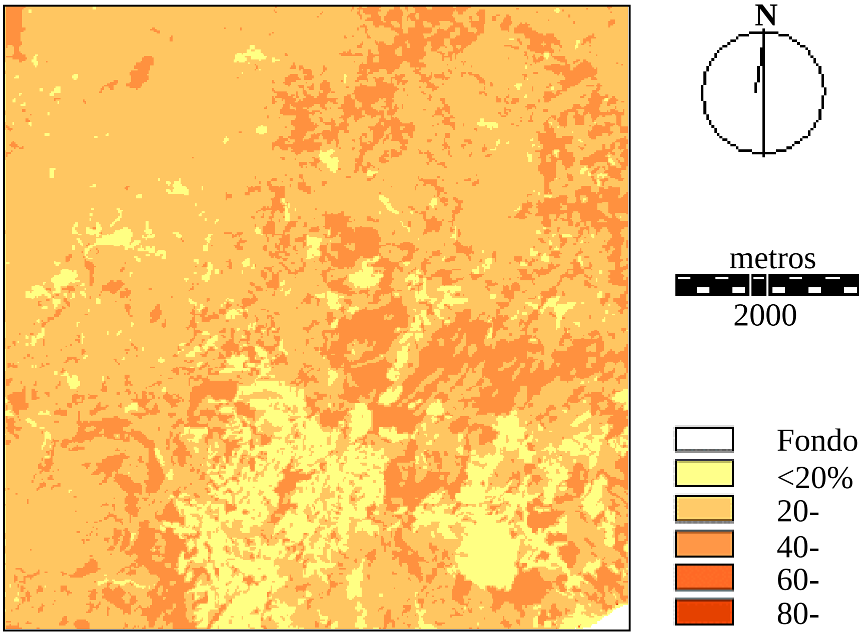


Fig.12. Mapas de la probabilidad de presencia de *Alectoris rufa* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Carduelis
cannabina
Grazalema





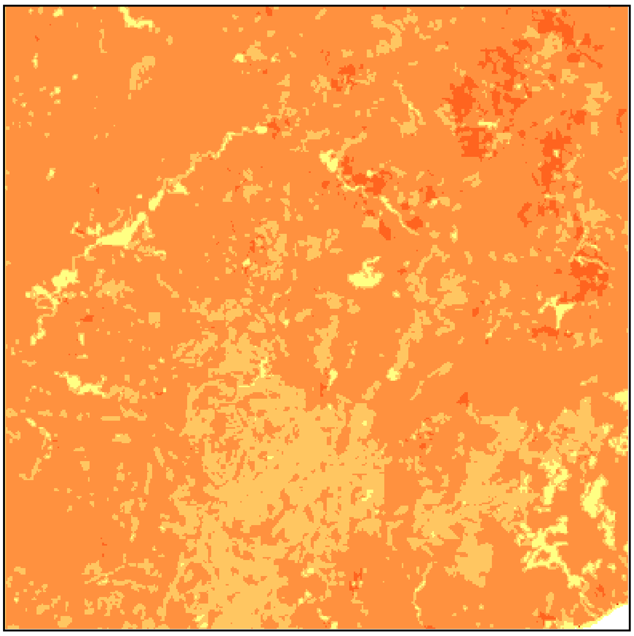
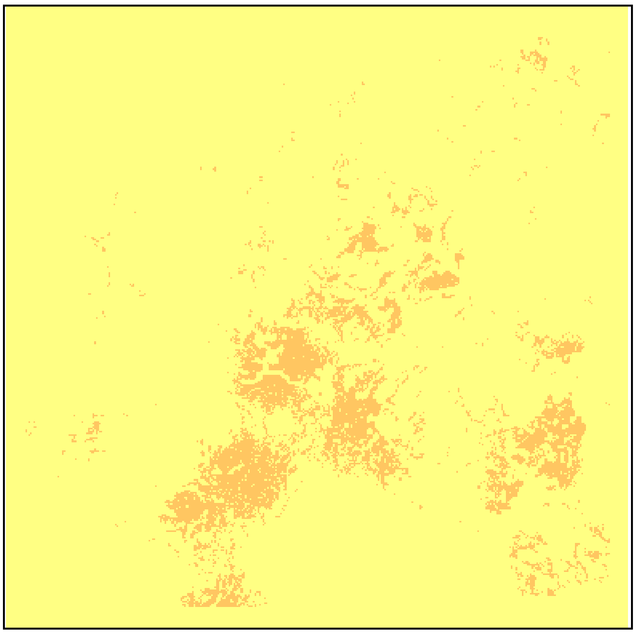
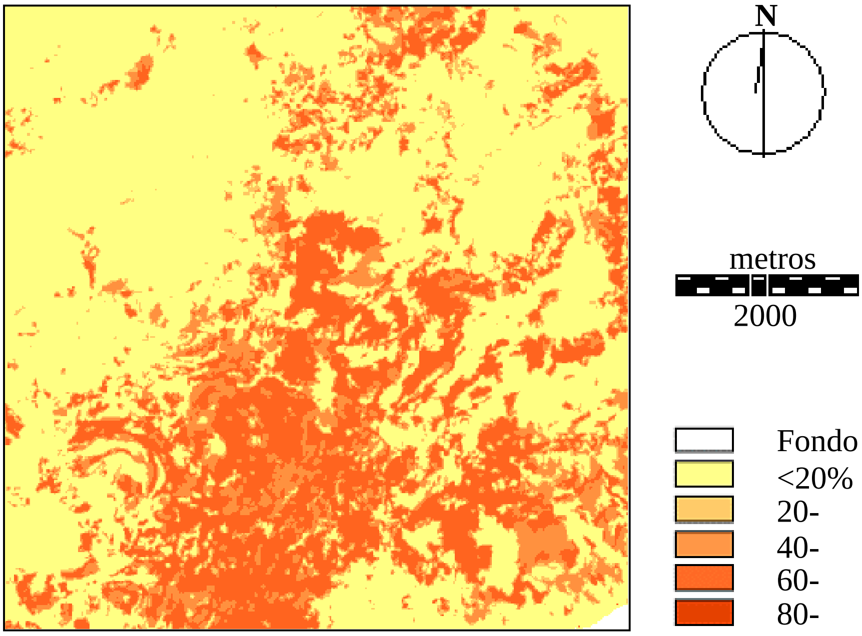


Fig.13. Mapas de la probabilidad de presencia de *Carduelis cannabina* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Certhia
brachydactyla
Grazalema





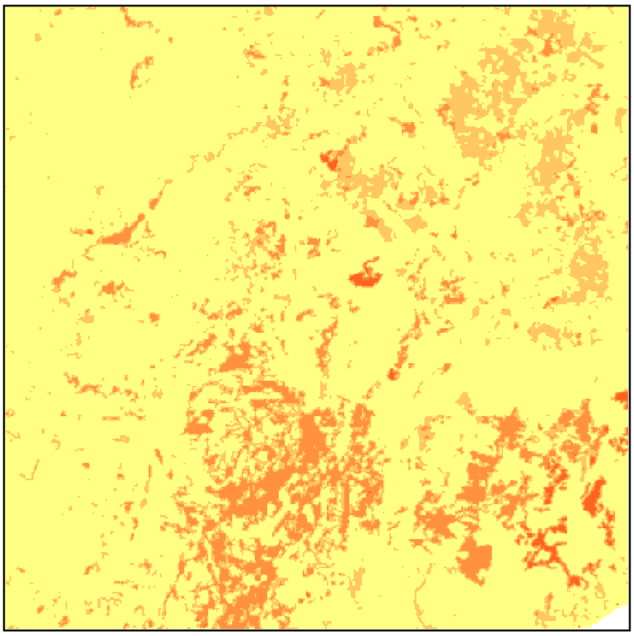


Fig.14. Mapas de la probabilidad de presencia de *Certhia brachydactyla* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Erithacus
rubecula
Grazalema

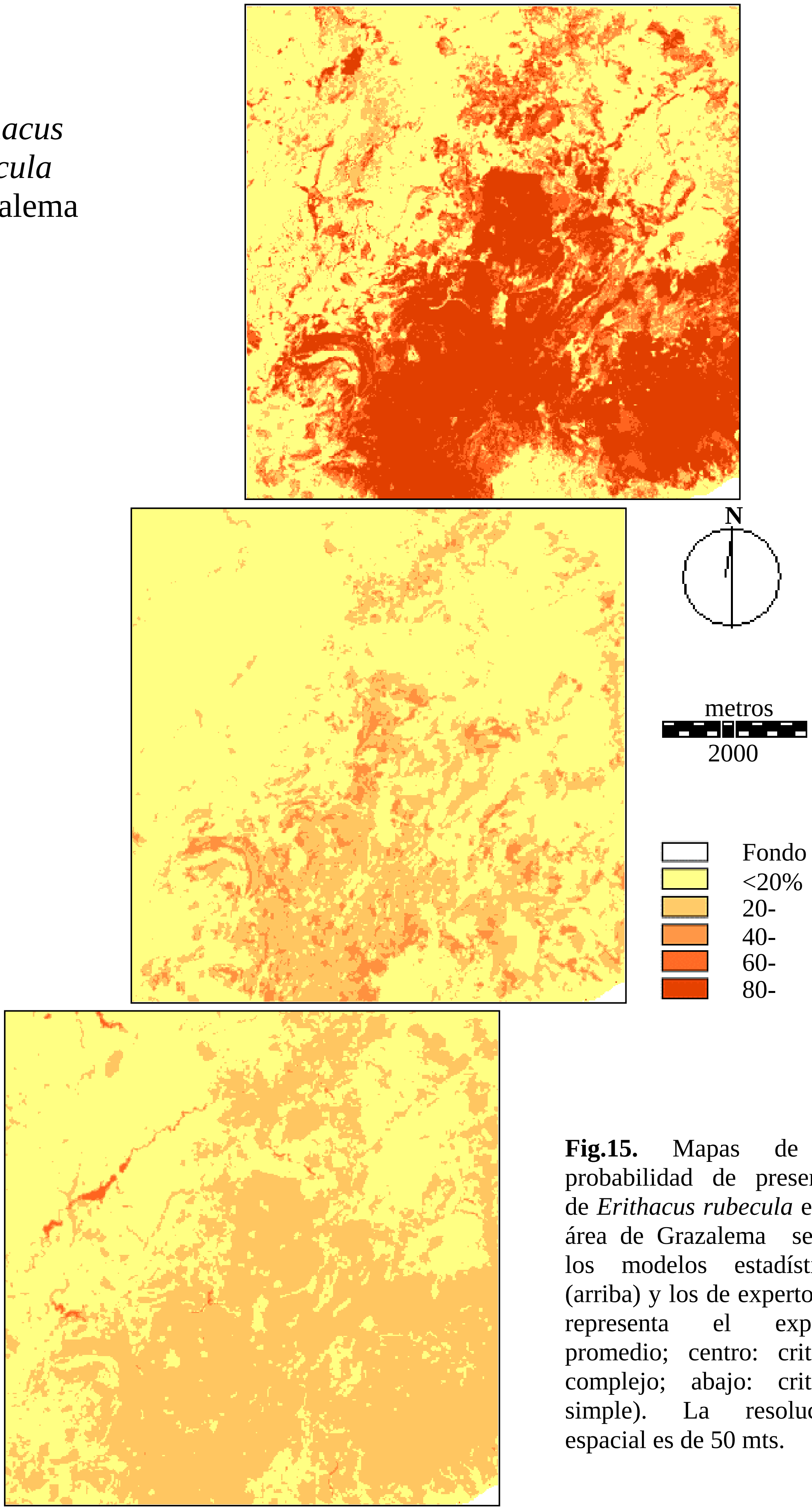


Fig.15. Mapas de la probabilidad de presencia de *Erithacus rubecula* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Galerida theklae
Grazalema

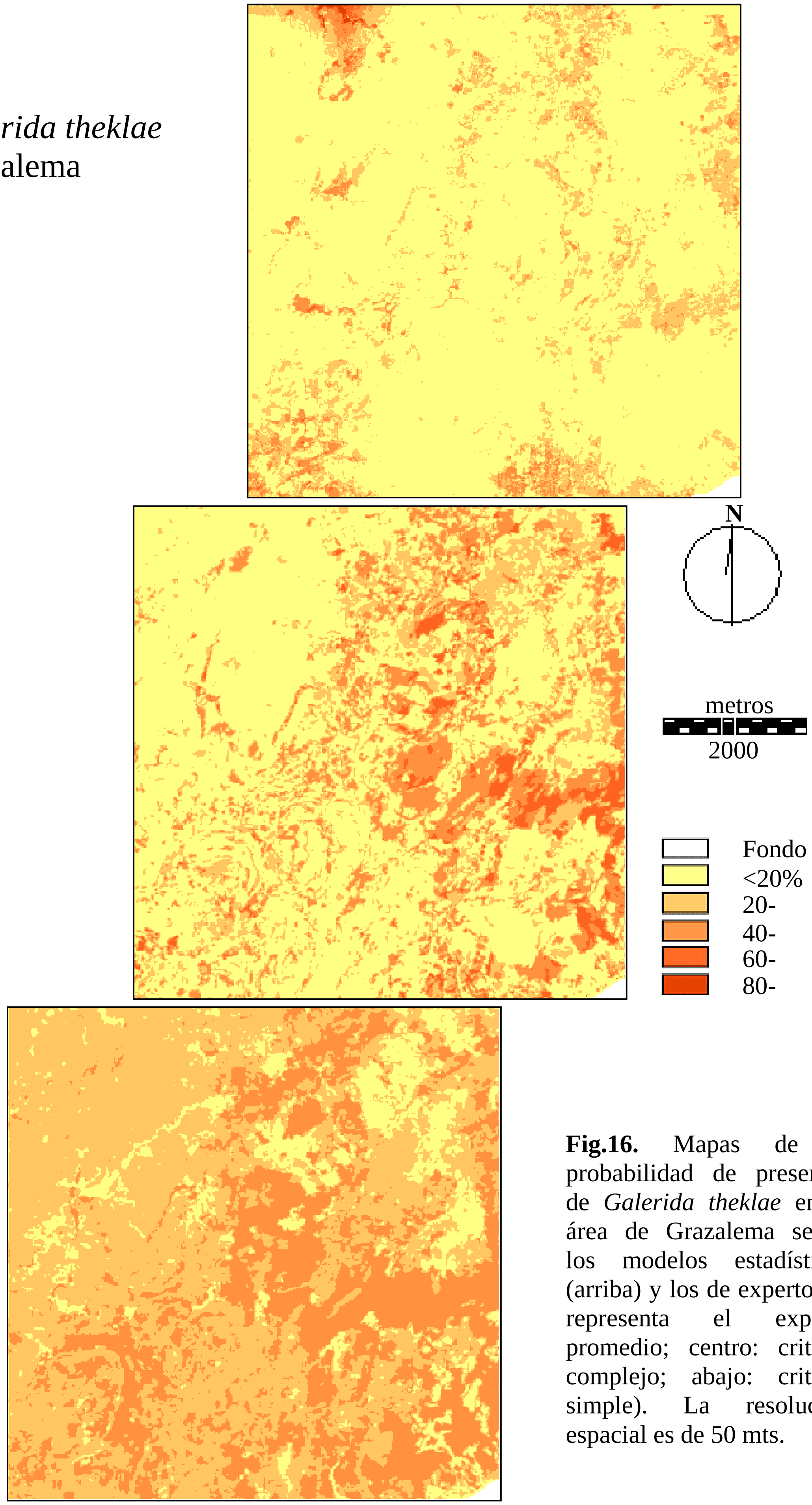


Fig.16. Mapas de la probabilidad de presencia de *Galerida theklae* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Melanocorypha calandra
Grazalema

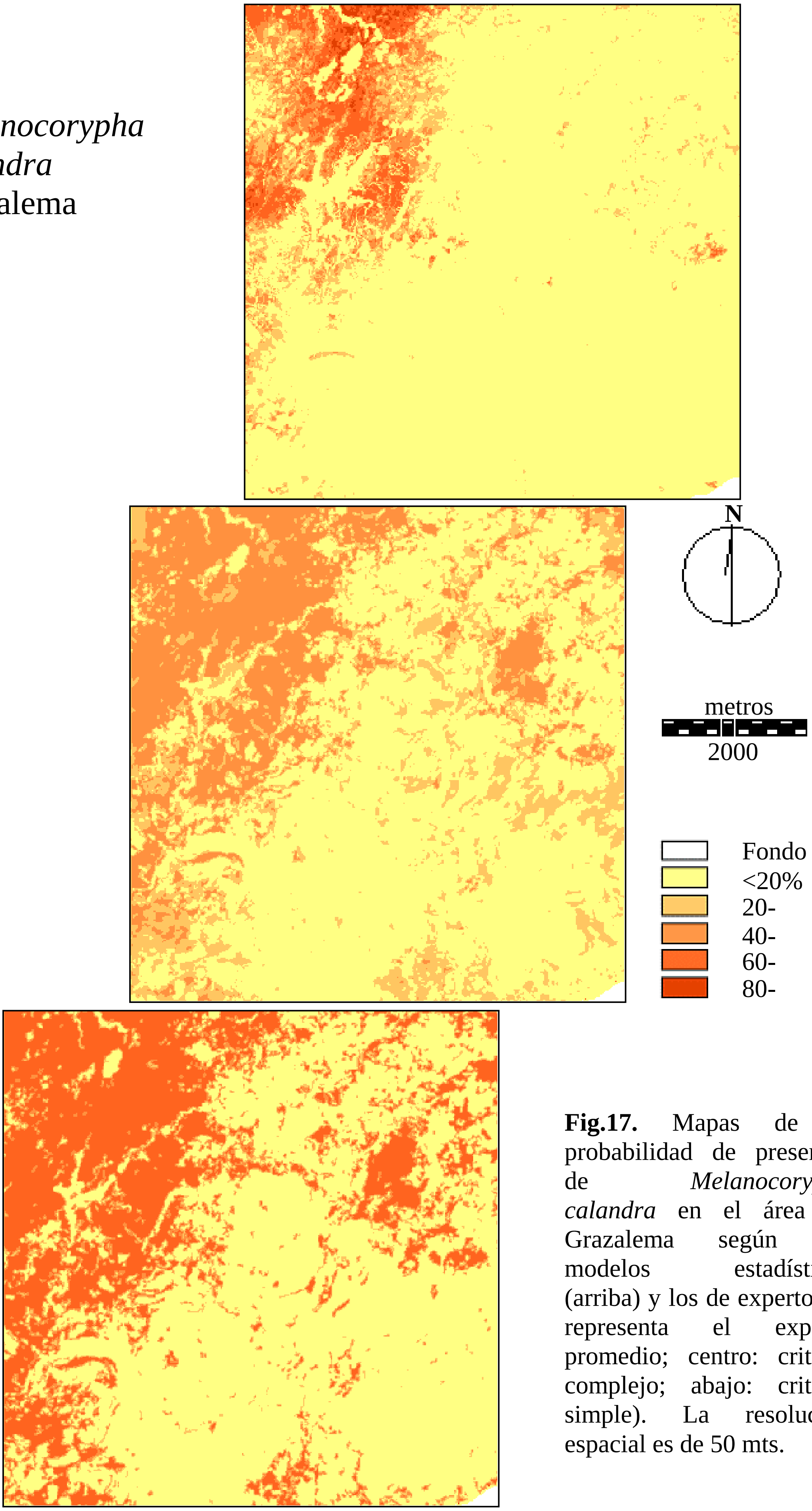


Fig.17. Mapas de la probabilidad de presencia de *Melanocorypha calandra* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Parus caeruleus
Grazalema

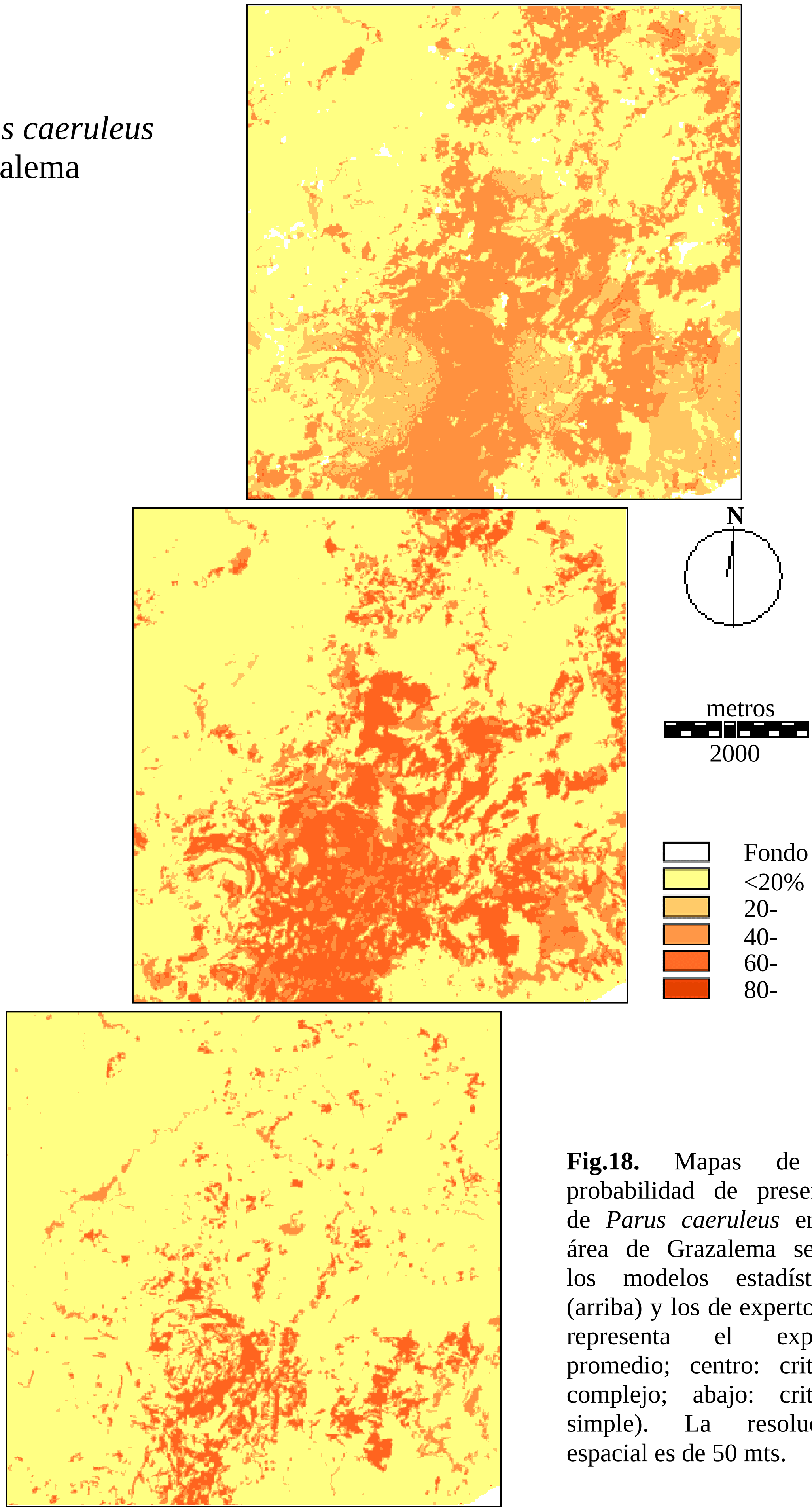


Fig.18. Mapas de la probabilidad de presencia de *Parus caeruleus* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Sitta europaea
Grazalema

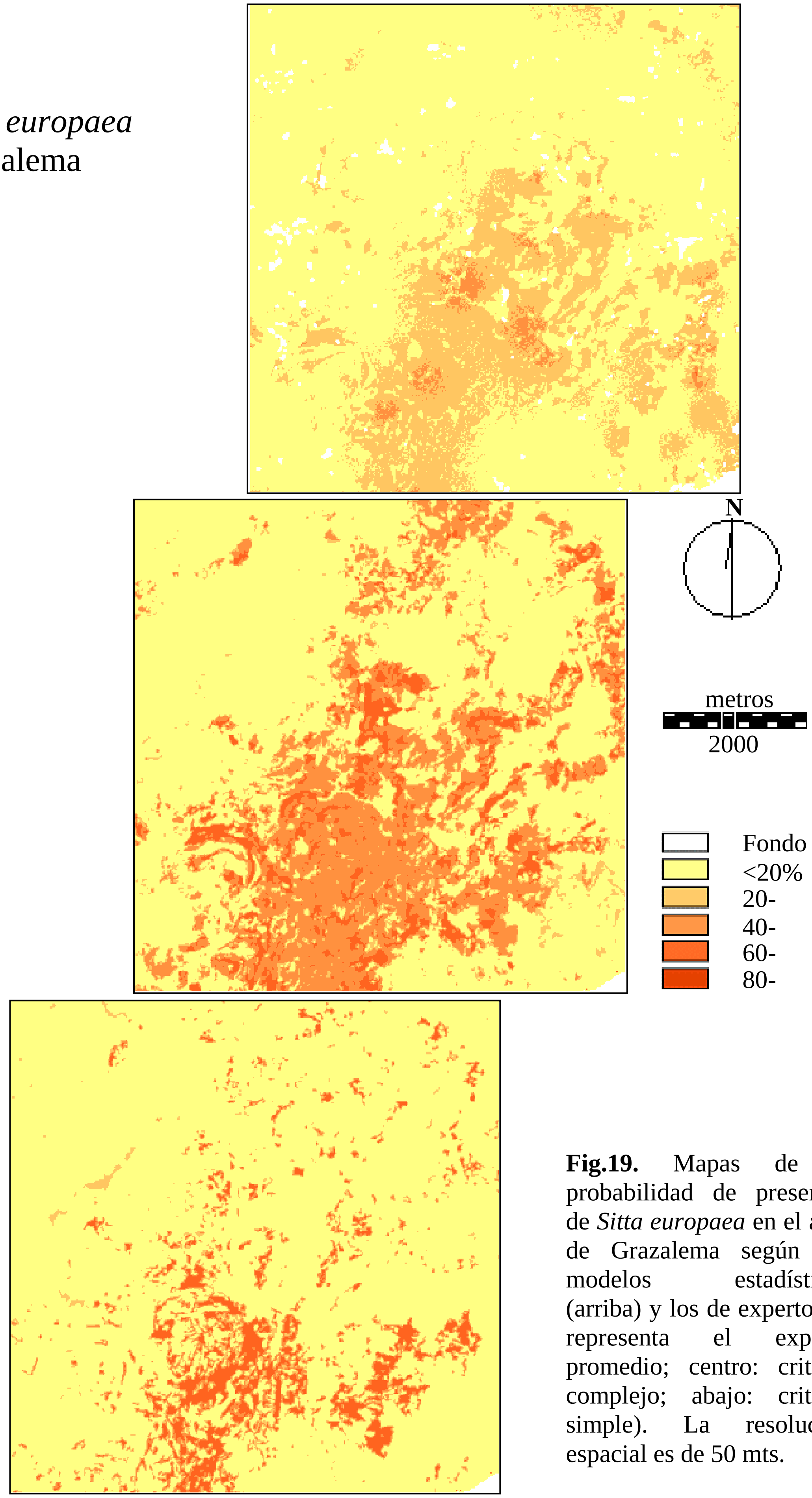


Fig.19. Mapas de la probabilidad de presencia de *Sitta europaea* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Sylvia melanocephala Grazalema

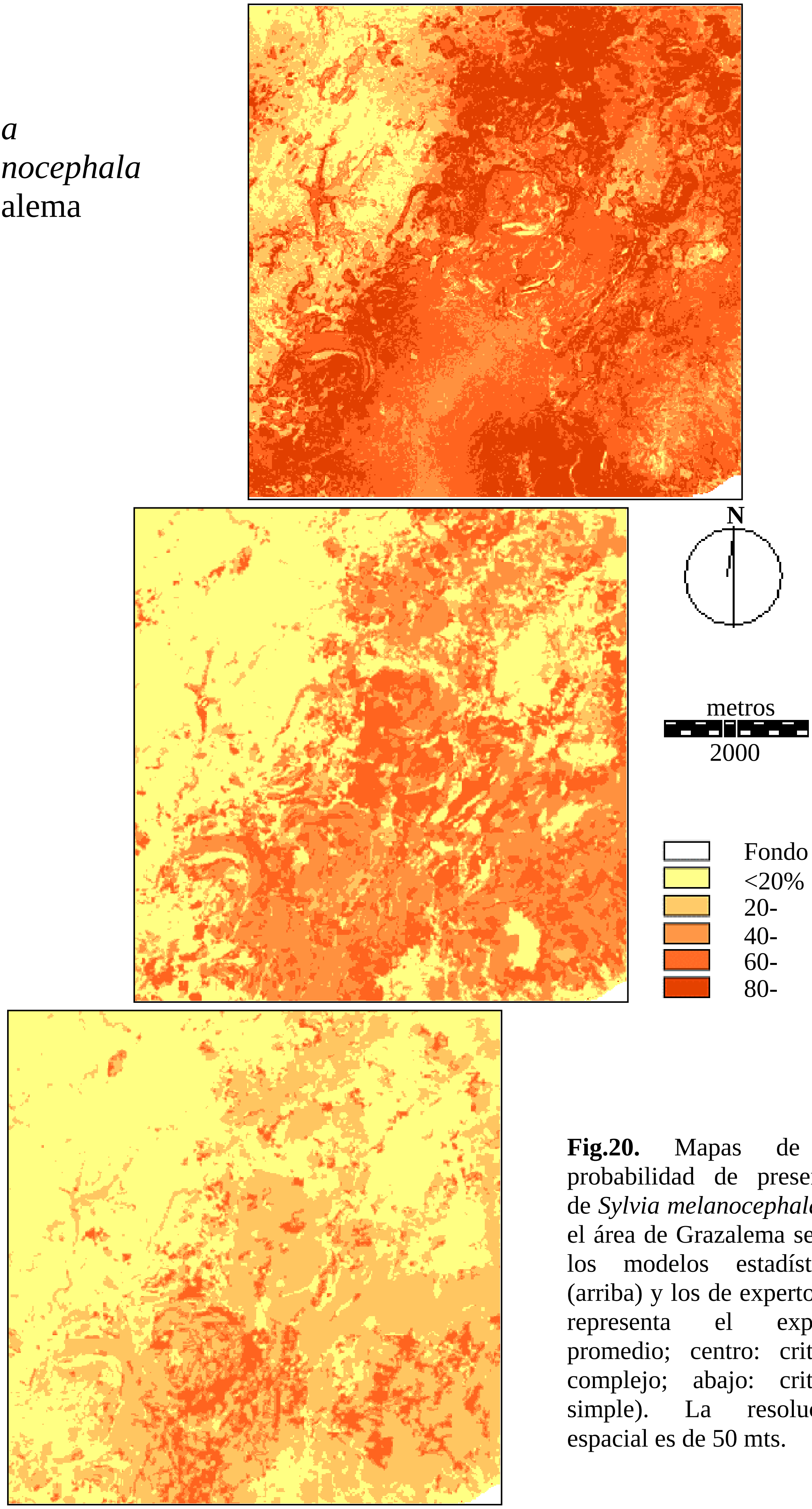
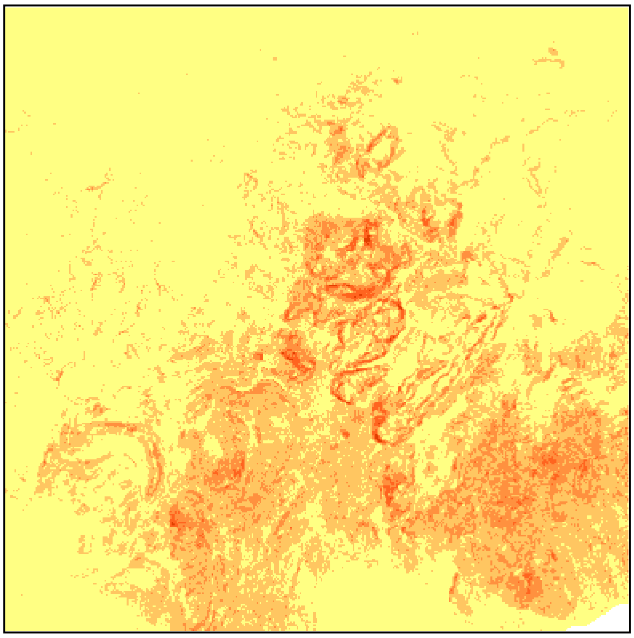
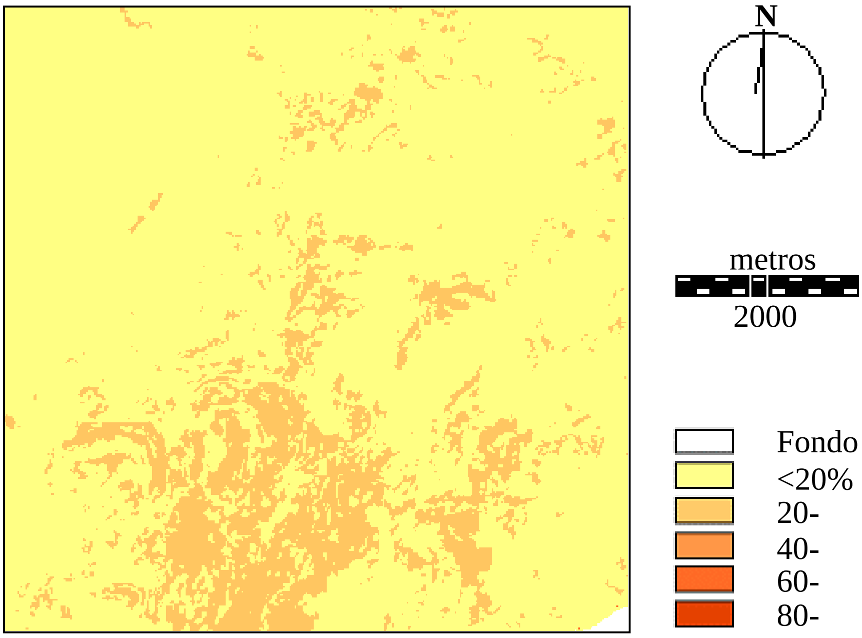


Fig.20. Mapas de la probabilidad de presencia de *Sylvia melanocephala* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

Troglodytes troglodytes
Grazalema





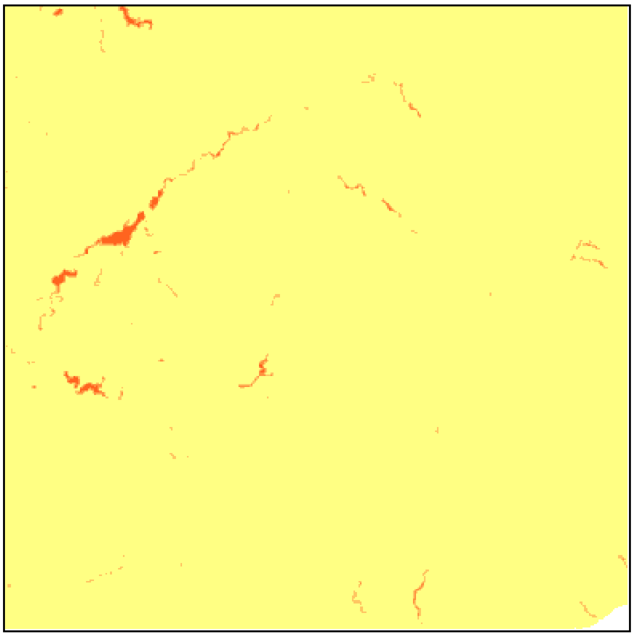


Fig.21. Mapas de la probabilidad de presencia de *Troglodytes troglodytes* en el área de Grazalema según los modelos estadísticos (arriba) y los de experto (se representa el experto promedio; centro: criterio complejo; abajo: criterio simple). La resolución espacial es de 50 mts.

SECCIÓN CUARTA

Esperanzas y desesperanzas de los modelos de distribución de especies

Facts are facts, but perception is reality:

—Conventional political wisdom

—E.J. Rykiel Jr., Relationships of scale to policy and decision making. In: ECOLOGICAL SCALE. THEORY AND APPLICATIONS (p.485). Columbia University Press. 1998.

¡Mírale!, y por eso le pagan...

—Alejandro (primavera de 1998), un amigo almeriense cuyas palabras son el eco de la sociedad en la que vivimos; un eco que yo no puedo –ni creo que deba– quitarme de la cabeza.

CONCLUSIONES

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- El modelado de la distribución de especies es una herramienta útil en numerosas aplicaciones de la biología de la conservación (ver Introducción), aunque tanto su desarrollo como su puesta en práctica cuentan con diversas limitaciones teóricas y prácticas (capítulo I).

- Los modelos empíricos estadísticos de la distribución de especies unidos a las herramientas de SIG han demostrado ser una herramienta eficaz para la generación de cartografías de especies en distintas situaciones de resolución espacial, abundancia de las especies y tipos de hábitats que frecuentan, en los ambientes altamente heterogéneos típicos de la península Ibérica (sección tercera).

- Los modelos estadísticos que se han desarrollado en esta tesis doctoral alcanzan una capacidad predictiva aceptable, y sirven para generar mapas que facilitarán la comunicación entre los investigadores y el público receptor (sección tercera).

- Parece existir un límite empírico máximo a la capacidad predictiva que alcanzan los modelos de distribución. Tal límite podría estar determinado por procesos estocásticos de tipo de dinámica de poblaciones, efectos históricos, influencia humana y factores ecológicos que no se han considerado en su construcción, como los relativos a la competencia (intra e interespecífica) o la predación (capítulo VI).

- Las especies difieren en cuanto a la capacidad predictiva que alcanzan sus modelos de distribución, pero no hemos sido capaces de predecir en qué forma las características de cada especie afectan a su suceptibilidad a ser modeladas (capítulos V y IX).

- Los modelos que aquí se han usado son de tipo empírico estadístico por lo que las relaciones que muestran entre la aparición de las especies y las variables descriptoras del medio no son causales (aunque se espera que bajo ellas subyazgan efectos causales, que se consideran muy difíciles de medir y cartografiar en áreas amplias) sino correlacionales. Esta es la causa más problable de su bajo éxito al extrapolarse a otras áreas geográficas (capítulo III).

- La cartografía temática digital existente, que se ha desarrollado con otros fines distintos al modelado de la distribución de especies, permite generar modelos de alta capacidad predictiva aunque las variables explicativas que se derivan de ella son poco detalladas (capítulo IV). Su resolución espacial (50x50 mts) es adecuada para los propósitos de modelado local (capítulos IV y IX) y regional (capítulos VII y VIII).

- La cartografía temática no es satisfactoria para reflejar aspectos del territorio que se extienden por una pequeña área, tales como los roquedos dispersos y las riberas, pero puede complementarse en estos casos con datos de teledetección (por ejemplo, imágenes de satélite).

- Los modelos de capacidad predictiva más alta se obtienen con una combinación de la cartografía temática con información topográfica, climática y la derivada de imágenes de satélite (capítulo IV). Destacan por su importancia las variables que describen el paisaje en torno a un punto de muestreo, lo que apoya la hipótesis de que las distintas especies seleccionan sus áreas de campeo teniendo en cuenta las características de las áreas vecinas (capítulos V y VI).

- Los modelos generados mediante un procedimiento muy automatizado (es decir, bajo una selección de variables determinada por criterios estadísticos) alcanzan una capacidad predictiva igual o superior a los que se generan con un protocolo supervisado, aunque existe una tendencia a que sean menos extrapolables a otras áreas geográficas (capítulo III).

AGRADECIMIENTOS

AGRADECIMIENTOS

En primer lugar, querría agradecer a mis padres la confianza que han depositado en mí pues siempre me han apoyado aún sin comprender bien mis intereses y a qué me he dedicado estos años. A ellos les debo el haber podido dedicarme al lujo de estudiar primero e investigar después en cuestiones relativas a la biología. Además, a Cristina, por todo el tiempo que no le he dado desde hace años y que siento como si yo se lo hubiera robado a nuestra juventud.

*** *** ***

Un trabajo como este, aún con sus limitaciones y errores, requiere una gran dedicación y bastante sacrificio. Sin embargo, todo el esfuerzo personal que le he dedicado no habría sido suficiente para llevarlo a cabo de no ser por ciertas personas que quiero mencionar aquí en una lista que, me temo, está abocada a la injusticia de olvidar algún nombre.

Javier Bustamante, mi director de tesis, es el responsable de darme la oportunidad de trabajar en la Estación Biológica de Doñana (EBD) y de introducirme en la cartografía de especies. Él me proporcionó un entorno de trabajo envidiable al involucrarse profundamente en todos los aspectos de la investigación que dirigía y al estar siempre dispuesto a discutir nuevas ideas, remedar errores y, en suma, a facilitar mi aprendizaje en materia de investigación científica. Lamento no haberle podido corresponder con unos resultados más relevantes. Desafortunadamente, no he tratado mis ideas y ambiciones con mucha más gente (lo que debería ser requisito obligado para todo aquel que realizara una investigación de cualquier tipo). He podido disfrutar, sin embargo, de algunas perlas de Mario Díaz, Luisma Carrascal (que colaboraban en el proyecto del que surge esta tesis doctoral) y de Daniel López Huertas, con quienes, además, he compartido fructíferas e instructivas jornadas de campo. Ricardo Díaz-Delgado (*¡aupa Atleti!*) se encargó de las labores técnicas relativas al SIG, que había comenzado Manuel Ángel de la Puente, y se mostró incansablemente receptivo ante mis dudas y problemas y pedagógico al resolverlos. Con Carlos Rodríguez, siempre amable, me unía la dirección, a veces el despacho y, sobre todo, un sentimiento semioculto de incertidumbre ante nuestro futuro como investigadores. He aprendido mucho con todos estos compañeros de trabajo.

El Laboratorio de Teledetección de la Universidad de Valladolid y el Instituto Nacional de Meteorología aportaron amable y rápidamente datos básicos que fueron muy útiles en distintos análisis (como se menciona en los capítulos correspondientes de esta tesis doctoral).

En un plano afectivo, importantísimo si —como yo— se desea conservar cierta cordura, debo agradecer a Julio Blas y a Sonia Cabezas que me hayan acogido estupendamente a mi llegada desde Madrid y que con Iván Sánchez y Juan Quetglas me desvelaran las idiosincrasias de la vida en la EBD y en Sevilla. He tenido la inmensa suerte de vivir mucho tiempo con Carlos Alonso y Juan Manuel Grande, sobrellevando los sabores y sinsabores de un precario investigador emigrado; de reencontrarme con Héctor Rodríguez, cuyas conversaciones siempre abrían una ventana al mundo exterior en mi cúpula de marfil; de conocer a Xim Cerdá y Jordi Figuerola, estimados compañeros a quien no sé si admiro más por su capacidad investigadora o por su inagotable manantial de información variada; y, en general, de disfrutar de un entorno grato de trabajo arropado, de una manera indefinible, por el heterogéneo conjunto de becarios de la EBD (David Serrano, Elena Angulo, Cristina Fuentes, José María *Cani* Fedriani, Marta Sánchez,...). Además, Frederique y Kim Jenkins suavizaron mis últimos dos meses de tesis con su paso fugaz pero amable por mi casa. Ojalá os vaya *fetén* a todos.

De mi cuatrienio en Sevilla guardaré también un recuerdo entrañable de Javier Balbontín y del resto de integrantes más o menos inconstantes del equipo “Calamaro” de futbito (Juan y Javier Balbontín, José *caracoles* Arrébola y José Sarasola, Joaquín Ayerbe, Marcelo Bertellotti, javieres de Morón y Troncoso, Antonio Manzaneda, Manolo...), con quienes atendía a la máxima de *mens sana in corpore magullado*. Además, he aprendido y disfrutado mucho con las salidas al campo —menos frecuentes de lo que yo hubiera deseado— en las que Manolo Vázquez y Nicolás Varo (de la EBD), Jesús Fernández (de GOSUR) y, especialmente, Paco Chiclana, Javier Salcedo, José Antonio Lama, Jorge Garzón y Laura Plaza (de SEO-Sevilla), me hacían de cicerone por las bonitas tierras andaluzas.

Quiero abrir un hueco aquí para mis antiguos compañeros de biológicas en la Univesidad Autónoma de Madrid (UAM): Paco Martín-Azcárate, Juancho Calleja, Laura Arqueros, y los miembros de SEO-Monticola (en especial Javier de la Puente y Ana Bermejo), con quienes crecí una pasión por interpretar y disfrutar de la naturaleza, y para mis primeros mentores, Quico Suárez y Miguel Yanes (y también Juan Manrique) con quienes balbuceé los primeros sonidos científicos, finalmente inarticulados, en mis años de facultad.

Sospecho que el personal no investigador de un instituto de investigación como la EBD es el eterno olvidado en la sección de agradecimientos de cualquier trabajo. No quiero que sea este mi caso, pues la incansable Conchita a la fotocopiadora, Mariángeles y Pedro en la biblioteca, Pepe en compras, Reyes en la secretaría y, en fin, el conjunto del personal de administración, fueron siempre atentos ante mis peticiones de copias de artículos, material de trabajo, envío de correo y demás entresijos oscuros pero necesarios en la actividad de un instituto como este. Además, Lina llenó de humanidad los pasillos con sus saludos y ánimos para acabar el trabajo. Gracias a todos.

Por último, sería injusto no mencionar el soporte fomal de Braulio Asensio (de ANALITER S.A) y las ayudas económicas que el Ministerio de Educación y Ciencia (más tarde de Educación y Cultura) y después el Consejo Superior de Investigaciones Científicas me han dado durante la realización de esta tesis. Pero vamos a dejar las cosas en su sitio: tales ayudas me dieron una cierta estrecha independencia económica, y me permitieron realizar alguna estancia breve en el extranjero y recibir gratuitamente los cursos de doctorado, sin embargo no contemplaban la cotización a la seguridad social (es decir, técnicamente no he estado trabajando y, por tanto, ni tuve derecho a vacaciones antes ni tengo derecho a subsidio de desempleo ahora, entre otros inconvenientes) a pesar de que el 1.8% de la mensualidad (entre 125 y 150.000 pts [750-900 euros] de 1998 a 2002) se pagaba como impuestos a a Hacienda (¡y, al menos en el 2002, la declaración del IRPF no resultaba negativa!). Siento, no obstante, estas becas como un privilegio no demasiado común.