

Winter bird distribution in abiotic and habitat structural gradients: A case study with mediterranean montane oakwoods¹

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Abstract: The influence of habitat structure and abiotic factors on winter bird distribution was studied at the within-habitat level in the montane Pyrenean oakwoods of central Spain. Abiotic factors associated with thermal stress were estimated based on altitude and solar radiation received by woodlands (calculated by the steepness and orientation of the terrain). This paper demonstrates the great importance of abiotic factors in influencing bird distribution. Several bird community parameters related to density and species richness decreased with altitude, while they increased with radiation incidence of oakwood plots (*i.e.*, birds avoided northern orientations where solar radiation is minimal in winter). The most important habitat structure variables related to bird distribution were the density of young and mature oaks. A thick undergrowth of thin oaks negatively influenced total bird abundance and species richness and the number of species of the ground searchers guild. Conversely, oak maturity played a positive role on total bird density and species richness and on the number of species of tree canopy gleaners and trunk foragers. Bird density and species richness were better explained by tree regression models considering complex interactions between variables than by general linear regression analyses. To enhance winter survival and habitat suitability for birds, forest management in these mediterranean endemic oakwoods should preserve the most mature forests at lower altitudes exposed to the south.

Keywords: altitude, bird distribution, habitat structure, oakwood forests, solar radiation, winter.

Résumé : L'influence de la structure de l'habitat et des facteurs abiotiques sur la distribution hivernale des oiseaux a été étudiée au niveau de l'habitat dans une chênaie de montagne des Pyrénées du centre de l'Espagne. Les facteurs abiotiques associés au stress thermique ont été estimés en tenant compte de l'altitude et de la quantité de radiation solaire atteignant la forêt (calculée à partir de la pente et l'orientation du terrain). Cette étude démontre que les facteurs abiotiques ont une grande influence sur la distribution des oiseaux. De nombreux paramètres des communautés d'oiseaux associés à la densité et à la richesse en espèces diminuaient avec l'altitude des parcelles de chênaie alors qu'ils augmentaient avec la radiation solaire (*i.e.*, les oiseaux évitaient les parcelles orientées au nord qui reçoivent une quantité minimale de radiation en hiver). Les variables structurales de l'habitat les plus importantes pour expliquer la distribution des oiseaux étaient la densité de jeunes chênes et celle de chênes matures. Un dense sous-bois de jeunes chênes avait des effets négatifs sur l'abondance totale d'oiseaux, la richesse en espèces ainsi que sur le nombre d'espèces d'oiseaux qui se nourrissent au sol. À l'opposé, la maturité des chênes avait un effet positif sur la densité totale d'oiseaux, la richesse en espèces ainsi que sur le nombre d'espèces qui se nourrissent par grappillage dans la voûte forestière et ceux qui fouillent les troncs d'arbre. La densité d'oiseaux était moins bien expliquée par des modèles généraux de régression linéaire que par des modèles de régression arborescente en considérant les interactions complexes entre les variables. Pour augmenter la survie hivernale des oiseaux et améliorer leur habitat, l'aménagement des chênaies endémiques de la région méditerranéenne devrait privilégier la conservation des forêts matures de basse altitude qui sont exposées au sud.

Mots-clés : altitude, chênaies, distribution des oiseaux, hiver, radiation solaire, structure de l'habitat.

Nomenclature: Perrins, 1998.

Introduction

Distribution and survival of birds within a landscape is constrained by multiple factors that interact in space and time (Orlans & Wittenberger, 1991). Many studies have focused largely on habitat fragmentation, structure, and floristic composition (see Wiens, 1989; Jones, 2001; Doherty & Grubb, 2002 and references therein). Vegetation characteristics and habitat size play a prominent role in defining the space that provides breeding or roosting opportunities and feeding substrates. Nevertheless, there is a paucity of works dealing with abiotic factors related to

climate, geographical location, or geomorphology (*e.g.*, climatological variables *per se*, altitude, steepness of the slope, cardinal orientation of the terrain; but see Shields & Grubb, 1974; Root, 1988a,b; Repasky, 1991; Huertas & Díaz, 2001; Martin, 2001; Canterbury, 2002). These abiotic factors, together with structural variables describing habitat characteristics, define the niche space and the physiological boundaries of performance, especially under limiting environmental conditions (*e.g.*, thermal or hydric stress; Walsberg, 1981; Hayworth & Weathers, 1984; Walsberg, 1985; 1993; With & Webb, 1993).

Influences of abiotic factors on small birds are stronger during winter in temperate latitudes, as the birds are subjected to high energetic demands (Fretwell, 1972; Grubb &

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Pravosudov, 1994). Probability of survival is determined by fat reserves that are used on a short-term basis to cope with very high metabolic costs derived from low winter temperatures, reduced and unpredictable food availability, and long winter nights (Blem, 1990). The influence of abiotic factors is especially evident in mountainous areas, where variations in altitude and exposure to sun radiation due to cardinal orientation of slopes generate a thermal mosaic. Moreover, unpredictable weather is a common characteristic of mountainous areas, where snowstorms or cold spells may drastically reduce food availability and increase metabolic demands, such that bird survival may be dramatically compromised. To survive winter conditions, birds must explore their environment in order to familiarize themselves with their habitat, tracking the changing food availability to reduce the risk of starvation (Naef-Daenzer, 2000). Nonetheless, exploration is costly in terms of the flight activity it entails and the greater exposure to predators (Ekman & Hake, 1990; Witter & Cuthill, 1993). Therefore, winter habitat selection should be the result of the interaction between the thermal environment that defines the physiological boundaries and the spatial niche characterized by the structure of the habitat that provides foraging substrata, refuge against predation, and roosting places (Cody, 1985; Wiens, 1989).

Accordingly, once birds have chosen areas where physiological stress and metabolic expenditure are minimized, habitat preferences may be exerted at smaller scales (hierarchical habitat selection; Wiens, Rotenberry & Van Horne, 1987; Kotliar & Wiens, 1990; Rolstad, Løken & Rolstad, 2000; Luck, 2002). Increase in altitude is inversely related to environmental temperature and positively associated with probability of inclement weather. On the other hand, in temperate latitudes of cold winter climate, birds should select sunlit sites (*i.e.*, habitat patches with high levels of exposure to sunlight) to gain heat from external sources, particularly radiation, which has a pronounced effect in reducing thermoregulatory costs at low temperatures (Ohmart & Lasiewski, 1971; De Jong, 1976; Lustick, Battersby & Kelty, 1978; Carrascal *et al.*, 2001). This selection can be accomplished within the range of variation in the cardinal orientations of slopes in mountain ranges, which determines the amount of solar radiation they receive (higher for southern orientations in winter time in the northern hemisphere). Therefore, birds under increased thermal expenditure in winter should exert a striking preference for lower altitudes, avoiding northern orientations where solar radiation is minimal.

The effect of altitude on bird abundance and body condition has been analyzed in some studies under winter conditions (Osborne & Green, 1992; Repasky & Schluter, 1994; Carrascal *et al.*, 1998; Carrascal, Palomino & Lobo, 2002). Less effort has been devoted to studying the effect of cardinal orientation on bird distribution in winter (but see Shields & Grubb, 1974; Huertas & Díaz, 2001). The influence of these variables on birds cannot usually be distinguished from other changing environmental attributes (*i.e.*, variation in altitude and orientation involves not only changes in temperature, but also changes in habitat structure and floristic composition; see Izco, 1984; and Costa, Morla & Sainz, 1998 for the Mediterranean region). Under these circumstances, it is highly desirable to analyze the influ-

ence of abiotic factors defining the thermal environment of birds within homogeneous habitat types. If habitat structure changes within a given habitat type (*e.g.*, gradients in shrub cover, tree height, or tree density), it is also possible to estimate the magnitude of the effects of structure *per se* and abiotic factors on habitat preferences of birds (see Seoane *et al.*, 2003; Bustamante & Seoane, 2004; Seoane, Bustamante & Díaz-Delgado, 2004; and Suárez-Seoane, Osborne & Rosema, 2004 for analysis of topographic, climatological and land-use/land-cover variables on bird distribution and abundance across gradients of different habitat types).

This paper deals with the influence of abiotic and habitat structure factors on winter bird distribution at the within-community level. The habitat studied is a montane mediterranean oak forest located in central Spain. The heterogeneity of the study area implies a large variation in altitude, cardinal orientation, and slope of the terrain, together with the environmental severity and unpredictability of a cold montane climate. The oakwoods are exclusively composed by the Pyrenean oak (*Quercus pyrenaicus*), endemic to the high plateaus and mountains of southern France and the Iberian Peninsula (Costa, Morla & Sainz, 1998). These forests also show a considerable heterogeneity in habitat structure (tree maturity, canopy cover, and development of the herbaceous and shrub layers), mainly because they have been intensively managed for charcoal and cattle grazing. However, human pressure on these woodlands has nowadays diminished, and many young oakwoods are beginning to recover. The large variation in habitat structure due to human impacts, combined with winter climate severity and the heterogeneity of the terrain (altitudes, cardinal orientation of the forest tracts, and slope of the terrain) make these forests an ideal area in which to test the role of habitat structure and abiotic factors as determinants of winter bird distribution.

Methods

STUDY AREA

The study area is located in the Sierra de Guadarrama (central Spain, Madrid province; 40° 47' 35" N, 04° 00' 40" W). Its continental climate, typical of mediterranean interior mountainous systems, includes large thermal variations, cold and wet winters, and a short vegetative period (Izco, 1984; Costa, Morla & Sainz, 1998). Oakwoods in the Sierra de Guadarrama are monospecific forests of *Quercus pyrenaica*, distributed from 900 to 1650 m asl on both slopes of the range. These forests were nearly extirpated from the Guadarrama mountains at the beginning of the 20th century (cut down for charcoal and for pasturelands for cattle grazing, especially in the valleys) but have been recovering since then. The location of these forests on the mountain range of Guadarrama, together with their past and recent history of management, have produced a large variety of oakwoods with respect to habitat structure, maturity, and geographical location (cardinal orientation, steepness of slopes, and altitude).

Fieldwork was carried out in 10 localities spanning over 900 km² (Navalperal de Pinares, Zarzalejo, Valsain, Escorial, Navacerrada, Miraflores de la Sierra, Rascafría,

Lozoya, Alameda del Valle, Canencia) from 967 to 1632 m asl. Surveys were carried out in two consecutive years (winters 2002-2003 and 2003-2004) from the second fortnight of November to the first fortnight of February. We followed a stratified random procedure, trying to sample different combinations of altitude, cardinal orientation, slope, and habitat structure in several localities throughout the study area in the two years. The sampling of different habitat configurations according to altitude, cardinal orientation, and vegetation structure was randomized across the study years and seasons. Consequently, the relationships between date, habitat-structure components (see below), altitude, cardinal orientation, and slope were very low (coefficients of determination lower than 15% for any pair of variables being correlated).

SAMPLING DESIGN

Bird censuses were made by means of stationary point counts. The radius of census plots was 50 m (0.8 ha). Each census plot was surveyed twice a day, for 10 min within the first 3 h of the morning and for 10 min in the afternoon (beginning 2 h before sunset). Thus, each census plot had an accumulated census time of 20 min, which is adequate for bird surveys of woodland birds during the non-breeding season (Shiu & Lee, 2003). These point counts do not efficiently sample all species due to interspecific differences in detectability. However, this is not a major concern in our work, as the long accumulated sampling period of 20 min maximizes the probability of detection of birds within the radius of 50 m if they are actually present. Furthermore, we were interested in relative abundances per unit of area and time, as birds wintering in these forests usually wander through oakwoods in flocks and are not territorial in this season. Bird abundances were expressed as the average of the two 10-min counts: birds·0.8 ha⁻¹ in 10 min. Census plots were separated by at least 250 m to minimize the probability of sampling the same birds more than once (especially in the case of very mobile or detectable species, e.g., corvids, woodpeckers). All visual or auditory contacts with birds were included, except when individuals flew over the census plots without stopping on them.

All samples were obtained on rainless and nearly windless days (wind speed < 3 m·s⁻¹) to reduce detectability problems (Bibby *et al.*, 2000). We sampled 149 different census plots in the two study years.

A 25-m-radius plot was placed within each census point to sample vegetation structure. Measurements defining vegetation structure were rock (ROCK), herbaceous layer (HER) and shrub layer (SHRUB) cover, average height of the shrub (H SHRUB) and tree (H TREE) layers, mean diameter of the five thickest tree trunks (DIAM), and number of trunks within three diameter classes: 5-10 cm (NT5-10), 10-30 cm (NT10-30), and more than 30 cm (NT30) at the breast level. We also recorded the number of tree trunks covered by climbers of ivy (*Hedera helix*) on at least 20% of their surface (NTIVY). All vegetation structure variables were visually estimated after previous training.

Variables summarizing geographical position of the census plots were obtained from 1:25,000 maps of the Servicio Geográfico Nacional de España, (altitude, slope,

and cardinal orientation). A sun radiation index was used on the premise that the amount of solar radiation received at a site will be influenced by the steepness and orientation of the landscape at that site (see also Gibson *et al.*, 2004). A measure of solar radiation incidence was obtained from the sinus of the angle of sun rays incidence over census plots at midday (*i.e.*, the sun was at zenith). Values ranged from 1 (perpendicular incidence, sinus of 90°) to 0 (radiation was absolutely tangential or woodland plots never received direct solar radiation). The angle of incidence (INCIDSUN) was calculated by combining the angles of cardinal orientation (CAR) and the slope of the terrain (SL) of each plot and the average sun height over the horizon at zenith in the study area (SH), according to the following formula:

$$\text{INCIDSUN} = (\text{SH} - \text{SL} \cdot \cos[\text{CAR}])$$

where SH was estimated to be 30° based on the average calendar date of the study period (December 31).

DATA ANALYSES

A principal components analysis (PCA) with a Varimax rotation was carried out with habitat variables describing the 149 census plots to obtain a reduced number of factors that summarized habitat structure. The correlation matrix between original variables was used. Multiple regression analyses (general linear models) were carried out to explore variation in total bird density and bird species richness using altitude, radiation incidence, and factors derived from principal components analysis as predictor variables (see Brotons *et al.*, 2003 for a similar approach). We checked for normality of residuals of the regression models. The principal components and multiple regression analyses were carried out using STATISTICA 6.0 (StatSoft, 2001).

Tree models were also employed to provide more detailed results describing total bird density and species richness in census plots. Tree models are non-parametric and non-linear approaches that are excellent for initial data inspection; they give a clear picture of the structure of the data, and they provide a highly intuitive insight into the interactions between variables (Hastie & Tibshirani, 1990; Breiman *et al.*, 1998; De' Ath & Fabricius, 2000; Drapeau *et al.*, 2000; Crawley, 2002). Classification and regression trees (CART) allow for the use of different types of response variables and render graphical interpretation of complex results involving interactions. They do not require the existence of linear relationships among the variables or homoscedasticity in variances. An additional advantage of this statistical tool is that interactions among explanatory variables are detected automatically in the analysis. Tree models analyze variation in a response variable that may be categorical (classification trees) or numeric (regression trees) by repeatedly splitting the data into more homogeneous groups, using combinations of categorical and/or numeric predictors. At each split the data is partitioned into two mutually exclusive groups, each of which is as homogeneous as possible. The splitting procedure is then applied to each group separately. The objective is to partition the response variable into homogeneous groups, but also to keep the tree reasonably small. The tree model is structured in a hierarchical fashion with the initial undivided data

set at the top (the root), followed by binary splits, each of which are called “nodes,” to final undivided groups of sites (“leaves”) at the bottom of the tree. The proportion of variation in the response variable that is explained by each split is indicated by the vertical length of the “branches” that extend from each node to each subsequent node or leaf. The size of the regression tree is measured by the number of leaves (final groups) in the tree. For a good general review of CART, see Efron and Tibshirani (1991), and for more detail see Breiman *et al.* (1998), Clark & Pregibon (1992), and Venables and Ripley (1994).

An important mechanism used to prevent trees from over-fitting data is tree pruning. Pruning can be employed during tree construction (pre-pruning) using stopping rules. The stopping rules in this paper were (1) minimum node size of 20 cases, (2) “leaves” (tree tips) including at least 10 cases, and (3) significant reductions in residual deviance (a measure of group heterogeneity) attained by a splitting criterion (according to a χ^2 test). Classification and regression trees were carried out using S-Plus 2000 software (MathSoft, 1999).

Assignment of bird species to four foraging guilds was obtained from Carrascal, Potti, and Sánchez-Aguado (1987) and Perrins (1998). These guilds were defined according to habitat use (ground, shrubs, trunk-thick branches, and canopy branches as the main foraging substrata). Based on the occurrence of species in census plots and their main foraging substrata, we also estimated species richness for each guild (analyzed using tree regression analyses).

Results

BIRD COMMUNITY COMPOSITION AND HABITAT STRUCTURE

Bird species densities in the whole sample of oakwoods censused are shown in Table I. The most common species (densities > 5 birds·10 ha⁻¹) were tree-branch gleaners (blue tit, *Parus caeruleus*; great tit, *Parus major*; and long-tailed tit, *Aegithalos caudatus*), followed by trunk searchers (short-toed treecreeper, *Certhia brachydactyla*; and nuthatch, *Sitta europaea*). Other common bird species were redwing (*Turdus iliacus*), mistle thrush (*Turdus viscivorus*), blackbird (*Turdus merula*), woodpecker (*Dendrocopos major*), coal tit (*Parus ater*), crested tit (*Parus cristatus*), and chaffinch (*Fringilla coelebs*).

There was a marked paucity of strictly wintering species (only redwing and goldcrest, *Regulus regulus*). The most abundant foraging guild was that of oak branch gleaners, composed of eight main species. The guild of ground foragers contained the most species (19 exclusive species), although their average densities were very low. Trunk searchers included only three main species, which attained medium densities. Finally, the shrub layer gleaners guild was composed of only a few species reaching very low densities.

Table II shows the results of principal components analysis carried out with 10 variables describing habitat structure of oakwood plots. The first component accounts for 24% of original variance, defining a gradient of increasing tree height and diameter (oak maturity). The second (17%) and the third (15%) factors order the plots according to the development of understory and herbaceous layers,

TABLE I. Density (birds·10 ha⁻¹) of bird species in the whole sample of 149 point counts (118 ha) in the Pyrenean oakwoods of the Sierra de Guadarrama. Birds were sampled in 0.8-ha census plots (radius: 50 m). The main foraging substrates of species are also provided (G: ground, S: shrubs, B: tree branches, T: tree trunk; Carrascal, Potti & Sánchez-Aguado, 1987).

Common name	Species name	foraging substrate	birds ·10 ha ⁻¹
Blue tit	<i>Parus caeruleus</i>	B	14.54
Great tit	<i>Parus major</i>	B, G	8.62
Long-tailed tit	<i>Aegithalos caudatus</i>	B, S	8.38
Short-toed treecreeper	<i>Certhia brachydactyla</i>	T, B	6.61
Nuthatch	<i>Sitta europaea</i>	T, B	5.00
Redwing	<i>Turdus iliacus</i>	G, S	2.91
Mistle thrush	<i>Turdus viscivorus</i>	G	2.07
Blackbird	<i>Turdus merula</i>	G	1.52
Great spotted woodpecker	<i>Dendrocopos major</i>	T	1.44
Coal tit	<i>Parus ater</i>	B	1.42
Chaffinch	<i>Fringilla coelebs</i>	G	1.41
Crested tit	<i>Parus cristatus</i>	B	1.18
Firecrest	<i>Regulus ignicapillus</i>	B, S	0.98
Rock bunting	<i>Emberiza cia</i>	G	0.82
Green woodpecker	<i>Picus viridis</i>	G, T	0.74
Robin	<i>Erithacus rubecula</i>	G	0.51
Azure-winged magpie	<i>Cyanopica cyanus</i>	G	0.44
Wren	<i>Troglodytes troglodytes</i>	S, G	0.43
Carrion crow	<i>Corvus corone</i>	G	0.42
Magpie	<i>Pica pica</i>	G	0.38
Chiffchaff	<i>Phylloscopus collybita</i>	B, S	0.26
Goldfinch	<i>Carduelis carduelis</i>	G	0.18
Jay	<i>Garrulus glandarius</i>	G, B	0.14
House sparrow	<i>Passer domesticus</i>	G	0.09
Cirl bunting	<i>Emberiza cirlus</i>	G	0.05
Goldcrest	<i>Regulus regulus</i>	B	0.04
Stonechat	<i>Saxicola torquata</i>	G	0.04
Blackcap	<i>Sylvia atricapilla</i>	S, B	0.04
Sardinian warbler	<i>Sylvia melanocephala</i>	S, G	0.04
Raven	<i>Corvus corax</i>	G	0.01
Starling	<i>Sturnus unicolor</i>	G	0.01
Great grey shrike	<i>Lanius excubitor</i>	G	0.01
Song thrush	<i>Turdus philomelos</i>	G	0.01

respectively. The fourth component (12%) describes the increase of ivy cover on tall trees. Finally, the fifth factor (11%) arranges oakwood plots according to rock cover on the ground.

TOTAL BIRD DENSITY AND SPECIES RICHNESS

Bird density was significantly explained by a regression model including description of habitat structure by the above-mentioned components, incidence of radiation on oakwood plots and their altitude ($F_{7, 141} = 5.71, P < 0.001; R^2 = 0.22\%$; Table III). Bird density was most strongly related to oak maturity (tree height and diameter, PC1). Bird density was also positively correlated with radiation received by oakwoods and the development of the understory layer (PC2), but was negatively affected by altitude. Figure 1 shows in more details the spatial variation in bird density using regression trees ($\chi^2 = 1108, df = 11, P < 0.001; 52.9\%$ of original deviance). Density of mature trees (> 30 cm in diameter) had a prominent, positive effect on bird abundance. Incidence of solar radiation also had a positive influence on bird abundance, while density of thin oaks (5-10 cm in diameter) had a negative one. Oakwoods with the highest bird abundances were those with more than 8.5

TABLE II. Principal components analyses performed with 10 variables defining habitat structure in 149 census plots (factors PC1-PC5). In bold type, significant correlations between variables and factors (at $P < 0.001$). Range of measured variables (MIN: minimum; MAX: maximum) is also provided. Number of trunks is expressed in number per 0.2 ha. Vegetation structure was sampled in plots of 0.2 ha (radius: 25 m).

	PC1	PC2	PC3	PC4	PC5	MIN	MAX
Rock cover (%; ROCK)	-0.04	0.03	-0.08	0.02	0.91	0	50.0
Herbaceous cover (%; HERB)	-0.24	-0.22	0.83	-0.25	0.08	0	96.0
Shrub cover (%; SHRUB)	0.03	0.90	-0.12	-0.03	-0.12	0	90.0
Average shrub height (m; H SHRUB)	-0.21	0.41	0.60	0.06	-0.26	0	2.5
Average tree height (m; H TREE)	0.52	-0.18	-0.09	0.48	-0.37	4	14.0
Number of trunks 5-10 cm in diameter (NT5-10)	-0.48	-0.10	-0.58	-0.28	0.09	0	500.0
Number of trunks 11-30 cm in diameter (NT10-30)	-0.18	-0.77	-0.16	0.09	-0.28	0	550.0
Number of trunks > 30 cm in diameter (NT30)	0.94	0.08	-0.12	-0.01	0.03	0	100.0
Average diameter of the 5 thickest oaks (cm; DIAM)	0.96	0.11	-0.07	0.04	-0.02	11	164.0
Number of trunks covered by ivy (NTIVY)	0.01	-0.04	-0.02	0.91	0.05	0	40.0
Eigenvalue	2.45	1.69	1.46	1.23	1.14		
% variance accounted for	0.24	0.17	0.15	0.12	0.11		

TABLE III. Results of regression GLM models analyzing the effect of altitude, sun radiation incidence, and habitat structure (PC1 to PC5; see Table II) on relative bird species density and richness. Sample size is 149 different census plots. SS: sums of squares; % var.: percentage of variance accounted for by each independent variable; beta: standardized regression coefficient.

	Density				Species richness			
	SS	% var.	P	Beta	SS	% var.	P	Beta
Altitude	2.01	2.8	0.027	-0.19	31.19	3.3	0.018	-0.21
Radiation incidence (sin)	2.14	2.9	0.022	0.18	21.51	2.3	0.049	0.16
Oak maturity (PC1)	6.31	8.7	0.000	0.30	20.64	2.2	0.054	0.15
Development of the shrub layer (PC2)	2.14	2.9	0.022	0.17	0.16	0	0.866	0.01
Development of the herbaceous layer (PC3)	0.04	0.1	0.755	-0.02	8.14	0.9	0.224	0.10
Ivy cover on tall trees (PC4)	0.67	0.9	0.197	0.10	39.32	4.2	0.008	0.22
Rock cover (PC5)	0.37	0.5	0.340	-0.07	8.17	0.9	0.224	-0.09

trunks larger than 30 cm·0.2 ha⁻¹, with fewer than 19 thin oaks·0.2 ha⁻¹ and less than 3.5% rock cover (10.8 birds·0.2 ha⁻¹, or 138 birds·10 ha⁻¹). If density of mature oaks did not reach that threshold, high bird abundances (average: 8.1 birds·0.2 ha⁻¹, or 103 birds·10 ha⁻¹) were also measured in plots with fewer than 14.5 thin oaks·0.2 ha⁻¹ and with high incidence levels of solar radiation (angle of incidence of sun rays at midday > 31°).

Bird species richness was significantly explained by the multiple regression in Table III ($F_{7,141} = 4.44$, $P < 0.001$; $R^2 = 0.18\%$). Richness increased with ivy cover on tall trees and radiation incidence of oakwood plots, while it decreased with altitude. Density of mature trees had a marginal ($P = 0.054$) positive effect. A regression tree performed with original variables and bird species per census plot provided a significant model ($\chi^2 = 291.3$, $df = 7$, $P < 0.001$; 41.3% of original deviance; Figure 2). Altitude was the main determinant of species richness: the lower the position of oakwoods, the higher the species richness of the bird community. Oak maturity had a positive influence in those oakwoods located above 1250 m asl, while density of young oaks had a negative influence below this altitude. The habitat characteristics of the oakwoods with the highest species richness included altitudes lower than 1250 m and number of thin trunks smaller than 27.5 trees·0.2 ha⁻¹ (average of 7.7 species per plot of 0.8 ha).

SPECIES RICHNESS OF FORAGING GUILDS

Table IV shows the habitat determinants of the spatial variation in species richness of the four main foraging guilds (see species and foraging substrata in Table I). Species rich-

ness of ground searchers is highest (3 species per 0.8 ha) at altitudes below 1245 m and in oakwoods with a very low density of young oaks (fewer than 9 oaks of 5-10 cm in diameter at breast height per 0.8 ha). Conversely, this guild is absent from the oakwoods located above 1245 m, nearly lacking a herbaceous layer (cover < 2.5%), and possessing a dense shrub stratum (cover > 76%). Tree canopy gleaners are more represented (an average of 3.5 species·0.8 ha⁻¹) in woodlands with well developed shrub and tree layers with mature oaks (at least 76% of shrub cover and more than 6.5 mature and 47.5 medium-sized oaks·0.8 ha⁻¹). Conversely, this guild is poorly represented in the oakwoods with few mature oaks and low shrub cover, located at high altitudes (more than 1295 m), and with lower incidence of solar radiation (*i.e.*, with a northern orientation). The number of species of trunk foragers is greatest in mature oakwoods receiving more solar radiation (*i.e.*, southern orientation). Finally, the scarce guild of shrub gleaners is positively associated with ivy cover on oak trunks and negatively with altitude.

Discussion

STATISTICAL TECHNIQUES AND BIRD-HABITAT RELATIONSHIPS

Regression trees have been more successful in explaining the observed variability in bird density and richness than general linear models (nearly two times more variability explained). Differences in the proportion of variance/deviance accounted for are mainly due to the fact that statistical trees identify subsets of environmental conditions in which relatively homogeneous values of the response variables

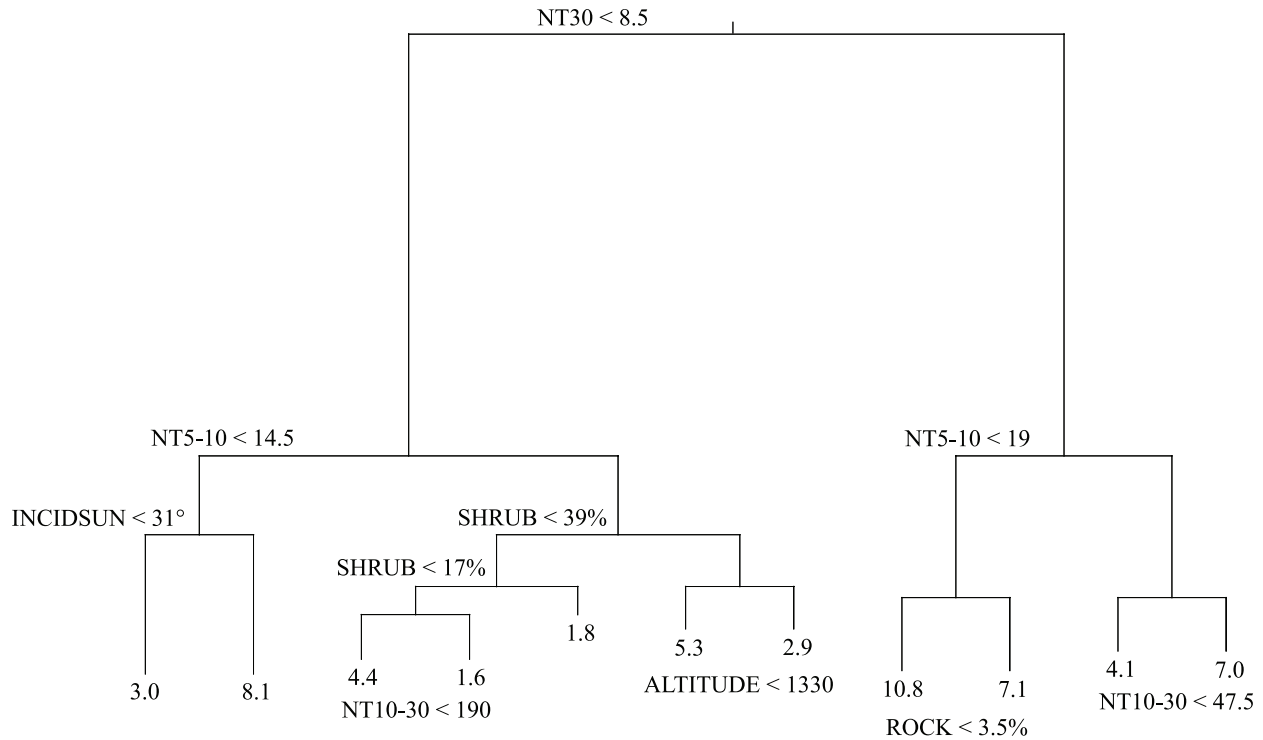


FIGURE 1. Regression tree model analyzing the relative bird density per oakwood plot (52.9% of original deviance accounted for). Splitting criteria indicate the conditions for the left branches. Numbers at terminal tips are mean density figures per 0.8 ha (minimum of 10 census plots per terminal tip). Length of the branches is proportional to deviance explained by each split. Only the main nine splitting criteria are shown. INCIDSUN: angle of incidence of sun rays on the oakwood plot. Number of trunks (several criteria beginning with NT) are expressed in number per 0.2 ha. See Table II for variable names. Sample size is 149 census plots.

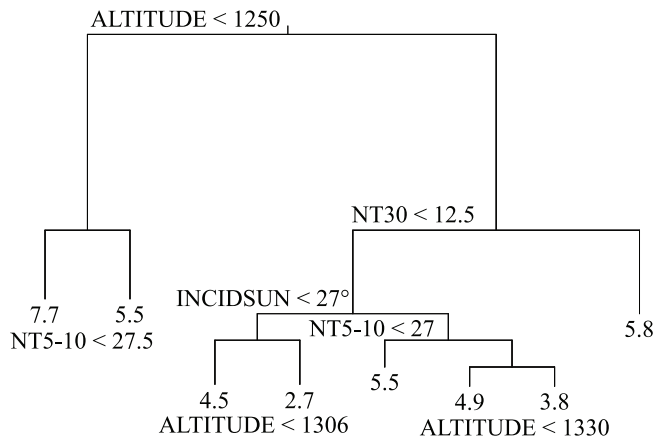


FIGURE 2. Regression tree model analyzing bird species richness per oakwood plot (41.3% of original deviance accounted for). Splitting criteria indicate the conditions for the left branches. Numbers at terminal tips are mean number of species per 0.8 ha (minimum of 10 census plots per terminal tip). Length of the branches is proportional to deviance explained by each split. INCIDSUN: angle of incidence of sun rays on the oakwood plot. Number of trunks (several criteria beginning with NT) are expressed in number per 0.2 ha. See Table II for variable names. Sample size is 149 census plots.

are observed, instead of defining common linear patterns affecting the whole pool of samples (see also De'Ath & Fabricius, 2000). For example, both statistical techniques reveal the prominent role of oak maturity on bird density, but multiple regression fails to discover the subset of environmental conditions in which this factor is responsible for

variation in species richness (see second and fourth order criteria in Figure 2). This contrast between the two statistical exploratory techniques exemplifies the advantage of regression and classification trees, which outperform typical approaches (*e.g.*, multiple regression analyses) when managing non-linear patterns found in ecological data where interactions are relevant to explaining the observed variability (see also Boone & Krohn, 2000; Olden & Jackson, 2002; Segurado & Araujo, 2004). Our results suggest that traditional, linear approaches to modelling species distributions (without the inclusion of interaction terms) provide a different representation of the importance of habitat factors in shaping species distributions relative to that provided by non-linear approaches such as classification and regression trees (Olden & Jackson, 2002).

INFLUENCE OF ABIOTIC FACTORS ON BIRD DENSITY AND SPECIES RICHNESS

Climatological and geographical variables have usually been employed in large-scale analyses of bird distribution (Root, 1988a,b; Repasky, 1991; Lennon *et al.*, 2000; Canterbury 2002; Seoane *et al.*, 2003; Seoane, Bustamante & Díaz-Delgado, 2004; Suárez-Seoane, Osborne & Rosema, 2004). Nevertheless, they have not been widely used in the study of species-specific habitat preferences and bird community parameters, where variables related to vegetation structure have played a dominant role (but see Shields & Grubb, 1974; and Huertas & Díaz, 2001). The results of this paper show the great importance of abiotic variables in explaining variation in total bird abundance and species

TABLE IV. Summary of regression trees showing the main splits modelling the influence of habitat variables on the species richness of four foraging guilds in oakwoods during winter. Tree leaves (*i.e.*, tips) providing the highest (MAX) and lowest (MIN) species richness are provided. D2%: amount of original deviance accounted for the whole tree model obtained. Birds were sampled in 0.8-ha census plots (radius: 50 m), while vegetation structure was sampled in an inner circle of 0.2 ha (radius: 25 m). AVERAGE: mean number of species per census plot (0.8 ha) in a sample of 149 census plots. Number of trunks (several acronyms beginning with NT) are expressed per 0.2 ha. See Table II for variable names. *n*: sample size for the selected conditions (*i.e.*, tips or leaves of the regression trees).

	AVERAGE	D2%	
Ground searchers	1.3	37.2	MAX: ALTITUDE < 1245, NT5-10 < 9; <i>n</i> = 10, average = 3 spp. MIN: ALTITUDE > 1245, HERB < 2.5, SHRUB > 76.5; <i>n</i> = 13; average = 0 spp.
Tree canopy gleaners	2.3	37	MAX: NT30 > 6.5, SHRUB > 76.5, NT10-30 > 47.5; <i>n</i> = 17, average = 3.5 spp. MIN: NT30 < 6.5, SHRUB < 48, ALTITUDE > 1295, INCIDSUN < 0.48; <i>n</i> = 15, average = 0.8 spp.
Trunk foragers	1.5	36.3	MAX: NT30 > 5.5, H TREE > 9.5, INCIDSUN > 0.54; <i>n</i> = 12, average = 2.7 spp. MIN: NT30 < 5.5, NT5-10 43-142; <i>n</i> = 32, average = 0.7 spp.
Shrub gleaners	0.2	35.7	MAX: NTIVY > 1.5; <i>n</i> = 12, average = 1 spp. MIN: NTIVY < 1.5, ALTITUDE > 1293; <i>n</i> = 83, average = 0.04 spp.

richness in the wintering avifauna of mediterranean continental oakwoods. They are also consistent with the fact that small passerines have very high energy requirements, especially in wintertime (Calder & King, 1974; Blem, 1990; Hedenström, 1992; Grubb & Pravosudov, 1994).

Altitude is hypothesized to influence bird distribution through its inverse relationship with ambient temperature. The basis of this association is that metabolic expenditure increases with decreasing temperature below the lower critical temperature (Calder & King, 1974), so birds should be more energetically constrained in high-altitude oakwoods than in those located in valleys. Temperature should pose an especially serious limitation in long winter nights, when minima regularly drop below 0 °C. Therefore, inhabiting lowland oakwoods during winter, avoiding those at higher altitudes, could help bird save energy in these oakwoods. In addition, frequent snowstorms or periods of harsh weather mainly strike the higher mountainous areas of Guadarrama, affecting to a lesser degree lower altitudes. A thick snow layer makes it impossible to forage on the ground, shrubs, and tree branches (Grubb, 1975; Brotons, 1997; Nakamura & Shindo, 2001), decreasing winter survival (Doherty & Grubb, 2002) and forcing birds to migrate down in altitude, leaving the higher forests (Carrascal, 1988). Therefore, due to higher energetic costs, severe weather, and/or higher climatological unpredictability, high-altitude forests are less suitable for maintaining stable bird populations. The additive consequences of these effects on populations of different species determine the marked negative relationship between altitude and species richness, in particular due to the loss of ground and shrub foragers from high-altitude oakwoods.

Diurnal metabolic costs of thermoregulation can be reduced by obtaining environmental heat from radiation (Ohmart & Lasiewski, 1971; Lustick, Battersby & Kelty, 1978; Goldstein, 1988; Carrascal *et al.*, 2001). The radiation-induced increase in operative temperature could favour a reduction of thermoregulatory costs, because below the thermoneutral zone metabolic expenditure is lower at higher temperatures (Calder & King, 1974). Besides, temperature could have a positive indirect effect on foraging efficiency due to the activation of arthropods at higher temperatures

(Carrascal *et al.*, 2001) and the reduction of snow or frost cover in areas receiving more solar radiation. Thus, birds inhabiting cold environments should select habitat patches with a higher incidence of solar radiation to reduce metabolic costs and to increase food availability while foraging (Summers & Underhill, 1996). If at the within-habitat scale, there is considerable variation in the amount of solar radiation received by different sectors according to the cardinal orientation and steepness of the slope, birds should show a striking pattern of habitat selection favouring sunny patches, all other things being equal. This form of behavioural thermoregulation could be especially relevant in mid-latitude montane regions with a large number of calm sunny days, where winter temperatures usually remain 10-20 °C below the metabolic minimum critical temperature (Carrascal *et al.*, 2001). These predictions are borne out by our results, as total bird density, global species richness, and richness of trunk foragers are higher in the woodlands receiving more solar radiation (*i.e.*, southern orientations on steep slopes where sun rays incidence is more perpendicular). Therefore, our results show, at the bird community level, the potential ecological and demographic consequences of behavioural thermoregulation by endothermic birds proposed by Carrascal *et al.* (2001); see also Huertas and Díaz (2001).

The potential positive effects of solar radiation on bird distribution and abundance are expected to disappear under cold, cloudy, and windy weather (*i.e.*, limited radiation and increased heat loss; Walsberg, 1986; Wolf & Walsberg, 1996). Faced with these stressful conditions, birds could abandon high altitudes, moving to nearby lowland areas (see Carrascal, 1988 for Guadarrama mountains), change foraging substrata towards inner tree parts (*e.g.*, thick branches and trunks) and lower portions of the forest (Grubb, 1977; Carrascal, 1987; Lens, 1996), move horizontally less often (Grubb, 1978), gather in larger flocks (Lens, 1996), or move into habitats that provide greater shelter (Petit, 1989). Nevertheless, and in spite of these habitat and foraging shifts under more severe weather conditions, the results described in this paper show clear and predictable associations between abiotic factors related to the thermal environment and the abundance and species richness of birds in a large mountainous area under typical anticyclonic winter conditions. Thus, the observed relationships could play an

important role favouring winter energy savings in southern latitudes of cold continental and/or montane climate, with low cloudiness and under windless conditions (Walsberg, 1986; Wolf & Walsberg, 1996).

A practical recommendation derived from these results is to emphasize preservation of the remnant lowland oakwoods with southern orientations in the region (see Manne, Brooks & Pimm, 1999 and Brotons *et al.*, 2003 for a global and a regional view on the importance of scarce mature lowland forests in bird conservation). These forests could serve as “better” wintering grounds, or temporal refuges against short periods of harsh weather, for the oakwood bird fauna of central Spain, being especially important for ground searchers and shrub gleaners whose winter survival is compromised if they lack oakwoods with their habitat preferences and spatial niche.

HABITAT STRUCTURE DETERMINANTS OF BIRD DENSITY AND SPECIES RICHNESS

Our results show that oakwood maturity is highly associated with bird abundance (see PC1 in Table III, and the influence of thick tree density in the first splitting criterion of the tree regression in Figure 1), but not with species richness. This result contrasts with those previously reported in woodland bird communities, where maturity of the tree layer is a common determinant of diversity (Brotons *et al.*, 2003; Wiens, 1989 and references therein). Oak maturity was positively associated with bird species richness only when oakwoods were located at high altitudes (above 1250 m), revealing the importance of this habitat attribute in the most restrictive environmental conditions according to the negative relationship between altitude and temperature.

On the contrary, a thick layer of young oaks markedly constrained bird density and species richness, especially for the occupation of oakwoods at lower altitudes, where the bird communities are denser and more diverse. A dense undergrowth probably provides fewer feeding opportunities to birds (substrates and prey; see Haveri & Carey, 2000; Hayes, Weikel & Husso, 2003; Hagar, Howlin & Ganio, 2004 for similar results in other forests). A dense, monotonous layer of young trees limits the development of the diverse shrub and herbaceous strata necessary for ground and shrub gleaners dealing with invertebrates and fruits. Moreover, high density of thin trees is usually associated with monotonous dense forests, not appropriate for those species requiring open wooded areas (see Del Moral *et al.*, 2002 for coarse-grained winter habitat preferences of birds in central Spain); examples of these species are the redwing, mistle thrush, blackbird, chaffinch, rock bunting (*Emberiza cia*), and robin (*Erithacus rubecula*). The obvious management recommendations derived from these results are to favour the presence of mature oaks (at least 40-60 oaks thicker than 30 cm at breast level per ha), especially in oakwoods located at highest altitudes, and to reduce the number of young oak trees to a maximum of 70-135 trees per ha, particularly at lower altitudes.

Bird density was positively related to shrub cover and height. The importance of the understory layer has already been noted in other studies, which highlighted its benefit

in other forest environments (Kirk & Hobson, 2001; Lohr, Gauthreaux & Kilgo, 2002; Brotons *et al.*, 2003; Jobes, Nol & Voigt, 2004). Several understory species (blackberries, dog roses, hawthorns, brooms) produce fruits that are used by birds as a primary or facultative food supply (see Jordano, 1985; and Herrera, 1984; 1998 for mediterranean environments). Some bird species are tightly associated with the availability of these fruiting species in Iberian deciduous forests (blackcap: Guitián, 1985; Tellería & Pérez-Tris, 2003). Another fruiting plant, ivy, was also very important to shrub gleaners, although it is not present in the understory layer but covers tree trunks. Ivy's fruits provide food supply for many bird species (especially redwings, blackcaps, and wrens in our study area; see also Guitián, 1987; Clergeau, 1992). A dense understory also provides predator defence, because a well-developed shrub layer constitutes an important visual obstacle to predators (Doherty & Grubb, 2000). Shrub development also positively affects tree canopy gleaners (see Table IV), which usually exploit the understory as a secondary foraging substrate (Carrascal, Potti & Sánchez-Aguado, 1987). Nevertheless, its development had a negative effect on species richness of ground searchers when shrub cover was higher than 76% (see Table IV), probably because it limits grass cover. Therefore, forest management practices should allow the development of the understory layer up to 76% of cover and also permit the existence of at least 2 trunks/0.2 ha covered by ivy.

In summary, bird distribution within the homogeneous habitat type of Pyrenean oakwoods is a predictable phenomenon where habitat structure attributes and abiotic factors related to the thermal environment play similar, important roles. In defining distribution patterns, regression tree analyses that account for complex interactions were more powerful than classical linear models (Segurado & Araujo, 2004). Birds showed a clear preference for mature forests lacking a thick undergrown stratum of young trees, but with a well-developed shrub layer. Overlapping this general pattern, there was a clear preference of wintering birds for lowland forests, avoiding northern orientations where solar radiation is minimal, showing that birds try to minimize thermal expenditure in these montane forests during winter. Although based on correlations, some practical recommendations emerge from our results: to enhance habitat suitability for oakwood birds in the study region, forest management practices ought to preserve the most mature forests at lower altitudes exposed to the south.

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