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Distributional patterns of insectivorous passerines in the Iberian Forests: does abundance decrease near the border?

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Abstract. In this paper we analyse whether the abundance of breeding insectivorous birds decreases towards the South along the Iberian forests (as predicted by the model of Brown (1984)), and try also to relate these changes of abundance to several environmental features. Abundances of six foliage insectivorous passerines that are not tree-hole nesters, *Troglodytes troglodytes* (L., 1758), *Erithacus rubecula* (L., 1758), *Sylvia atricapilla* (L., 1758), *Phylloscopus collybita* (Vieillot, 1817), *Regulus ignicapillus* (Temminck, 1820), and *Aegithalos caudatus* (L., 1758) were recorded in fifty-eight large woodlands along a 850 km belt crossing the Iberian Peninsula. By means of simple, partial and stepwise multiple regression analyses bird abundances were related with distances to the north of each woodland and with the mean scores of climatic (mean temperature and precipitation), physiognomic (tree trunk densities under 20 cm diameter and over 30 cm) and floristic (conifer *v.* broadleaved tree species) variables. Five of the six species showed significant, negative correlations between their abundances and the distances of forests to the north, thus corroborating Brown's model. *A. caudatus* did not show, however, any clear pattern of abundance distribution. Simple correlation analyses showed also the importance of climatic and physiognomic variables in predicting bird abundance. When the problem of interaction between variables was solved, all the five species showed significant positive partial correlation with precipitation, although distance continued to be important for three species (*T. troglodytes*, *R. ignicapillus* and *P. collybita*), suggesting some additional role of this variable in the processes involved in the observed distribution. The importance of precipitation and distance to the north as predictors of abundance was also showed by the stepwise regression analysis. The mean variance explained by these models was around 30%, higher than or similar to that obtained in other studies performed at the local or intrahabitat level. This suggests the potential usefulness of multivariate approaches in studies of bird distribution undertaken on large scales.

Key words. Brown's model, environmental variables, geographical distribution of abundance, Iberian forests, insectivorous passerines.

INTRODUCTION

According to Brown (1984), the spatial variation of abundance within the geographical range of each species should be determined by a combination of many physical and biotic variables that are usually autocorrelated (Hutchinson's 1957 multidimensional niche). The probability of sites having similar combinations of environmental variables should be an inverse function of the distance between them. Increasing distances from the optimal place of a species would thus entail concomitant decreases of the species abundances. Brown (1984) supported by empirical data on several taxonomic groups, also hypothesized that this distribution should adjust to a relatively symmetrical monotonic decrease of abundance from the centre of the distribution (core area) toward all the boundaries (see also Grinnell, 1922). He included two exceptions to this pattern: (a) abrupt changes in abundance that usually correspond to sharp, discontinuous changes in single environmental variables and (b) multimodal patterns of abundance due to environmental patchiness. Emlen *et al.* (1986) showed how densities of many forest birds were higher in the central portion of their ranges and lower in the periphery along a latitudinal transect in North America, although other works showed more unclear results because of a very patchy distribution of species (see Wiens, 1989, p. 276 for a review).

Here we try to corroborate whether or not birds in the Iberian forests adjust to this hypothesized pattern of abundance distribution. We also try to identify which environmental variables are responsible for the observed patterns along the Iberian Peninsula.

The Iberian Peninsula is in the southwestern part of the Palaearctic, where the climate ranges from the wetter and temperate conditions of the Eurosiberian Region in the North to the xeric and warmer conditions in the southernmost areas of the Mediterranean Region. Along this gradient, plateaux and mountains produce local patches of colder/wetter conditions leading to a mosaic of climatic environments (Font, 1983a, b; Fig. 1). This environmental

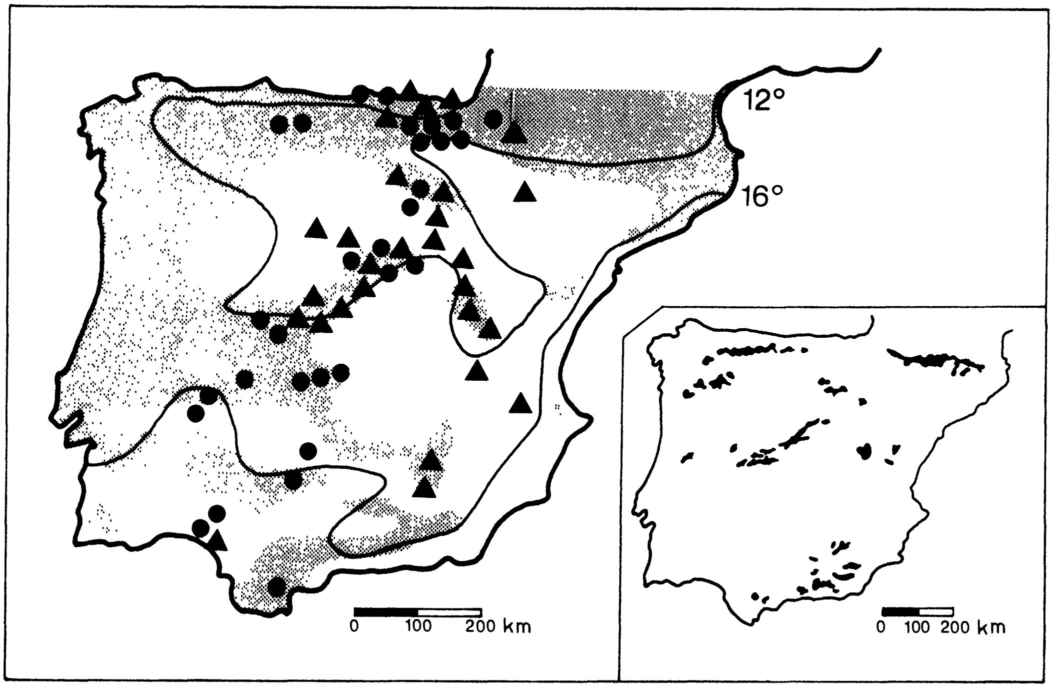

FIG. 1. Distribution of the forest censused; (●) broadleaved forests; (▲) coniferous forests. Mean annual temperature isotherms for 12°C and 16°C, areas with mean annual precipitation over 600 mm (shaded), and areas above 1500 m (small map, in black) are shown.

gradient is also related to a turnover in the composition of the forest avifauna (e.g. Harrison, 1985). According to Blondel (1985) and Blondel & Farré (1986), there is an impoverishment of forest species because of a 'peninsular effect' at the southernmost borders of the Palaearctic. This view is congruent with Brown's model because these forest passerines show a breeding range extended through the whole of the Western Palaearctic, with their core area in Central-East Europe. According to this geographical distribution, it may be also hypothesized that increasing distances to north of Iberian forests should be related to increasing difficulties of settling for northern species, the southern woodlands being the most difficult to have been reached in ecological time.

METHODS

We censused breeding birds in fifty-eight woodlands along a transect crossing the Iberian Peninsula and calculated their distance (DIST) to the northern top (Atlantic shore in the Spanish-French frontier; Fig. 1). Each woodland was sampled in early morning by means of a variable number (always over twenty) of 10 min-long unlimited distance point counts, randomly distributed along country roads and tracks across the wooded areas. Frequency of records of each species (f) in each woodland was used to obtain an index of its abundance (d) by means of the algorithm $d = -\ln(1-f)$. Blondel (1977) and Caughley (1977) have discussed the usefulness of this censusing method in extensive approaches to bird abundance.

These forests have a variable physiognomy because of human management (Tellería *et al.*, 1992). As habitat physiognomy is an important determinant in the habitat selection of birds (Hildén, 1965), we restricted our approach to those bush and foliage insectivorous birds that do not use tree-holes for nesting. These species are largely independent of some subtle features of woodlands such as the structure of canopy, abundance of old trees, ground management, etc, all of them very difficult to evaluate in studies performed at large scales. In this form, we analysed a methodological and biological homogeneous group, as has been suggested for these comparative, multispecific approaches (Clutton-Brok & Harvey, 1984).

Bird abundance was related to mean scores of some climatic, physiognomic and floristic macrohabitat variables that should reflect environmental features on a scale consistent with that of the large area covered by each census (see Rotenberry (1978) for a discussion on the uselessness of microhabitat variables in these approaches). Simple and partial correlation analysis and stepwise regression analysis (Sokal & Rohlf, 1981; Zar, 1984) were used to describe the patterns of association between environmental variables and bird abundance and to evaluate the predictive value of the environment in determining bird abundances along the studied gradient.

Climatic data were obtained from the National Climatic Atlas of Spain (Font, 1983b). We selected mean annual precipitation (MAP) and mean annual temperature (MAT) as the two most independent and comprehensive indicators of climate in the Iberian forests (Nahal, 1981). Both precipitation and temperature have been previously considered as important determinants of bird distribution (see Discussion). The structure of the sampled forests was characterized by means of the provincial statistics on timber density (ICONA, 1979, 1980; see Virkkala, 1987, for a similar approach). We selected mean densities of trees with trunks under 20 cm diameter (STD) and over 30 cm (GTD). These variables, which were log transformed to

TABLE 1. Simple and partial correlations between the abundance of species and the environmental variables studied (see Methods for symbols).

	MAP	MAT	STD	GTD	FLOR	DIST
Simple correlations						
Sylvia atricapilla (L., 1758)	0.57***	–0.04	0.32	0.24	–0.22	–0.38**
Phylloscopus collybita (Vieillot, 1817)	0.39**	0.07	0.30*	0.30*	–0.16	–0.40**
Regulus ignicapillus (Temminck, 1820)	0.40**	–0.28	0.30*	0.47***	0.32*	–0.49***
Erithacus rubecula (L., 1758)	0.54***	–0.38**	0.39**	0.39**	–0.02	–0.47***
Troglodytes troglodytes (L., 1758)	0.43***	–0.03	0.40**	0.27*	–0.13	–0.49***
Aegithalos caudatus (L., 1758)	0.06	0.01	–0.10	0.11	0.21	0.09
Partial correlations						
S. atricapilla	0.48***	0.31*	0.06	0.08	–0.10	–0.23
P. collybita	0.27*	0.41**	0.02	0.22	–0.12	–0.32*
R. ignicapillus	0.36**	0.23	0.00	–0.02	0.36**	–0.37**
E. rubecula	0.31*	–0.11	0.06	0.16	–0.11	–0.13
T. troglodytes	0.35**	0.40**	0.11	0.04	0.02	–0.39**
A. caudatus	0.14	0.07	–0.03	0.00	0.18	0.06

*=$P<0.05$, **=$P<0.01$, ***=$P<0.001$.

meet normality, are an index of the foliage abundance (the feeding substrate of the bird species selected for the analysis) in two different stages of forest development (young *v.* old forests). Finally, floristics (FLOR), an important determinant of habitat selection in some forest birds (e.g. Lack, 1971), was evaluated by means of a classification of woodlands according to the taxonomic situation of the dominant tree in coniferous (families Pinaceae and Cupressaceae) *v.* broadleaved (families Fagaceae and Myrtaceae) species (García, 1983; Castroviejo, 1986). To evaluate the effects of FLOR on bird abundance it was included as a dummy variable (1: coniferous woodlands, 0: broadleaved forests; Zar, 1984; Morris, 1987).

RESULTS

We recorded nine species of foliage insectivorous passerines. Two species (*Prunella modularis* (L., 1758) and *Sylvia borin* (Boddaert, 1783)) were discarded because their distribution was restricted to the northernmost sectors of the Iberian range (they should conform to the 'a' exception of Brown's model). Another species (*Regulus regulus* (L., 1758), whose breeding range in Spain is clearly restricted to the high mountains and thus shows a very patchy distribution (it might be included in the 'b' exception of Brown's model), was also excluded.

Five of the six remaining species showed significant negative correlations between their abundances and the distance to the core area at the 0.05 level or better (Fig. 2, Table 1), thus supporting Brown's model. The abundance patterns of these species did not adjust however to the predicted monotonic decrease of abundance, suggesting the operation of additional factors. All these species showed, for instance, high scores in one of the southernmost forests of the studied range (*Quercus suber* L. (1753) forests at the Cadiz Mountains), and one species (*Sylvia atricapilla* (L., 1758)) showed a clear multimodal pattern of abundance in which higher scores were recorded in mountain forests (Fig. 2). These results may be related to the commented patchy distribution of some environmental variables along the Iberian gradient: simple correlation analyses showed a significant positive association between the abundance of the five species and MAP, STD and GTD suggesting that abundances of these birds increase in wet forests with higher densities of trees. These associations changed, however, when we examined the interactions between these variables by partial correlation analysis: MAP became the only variable associated with the abundance of the five species, greatly reducing importance of those variables describing habitat structure (in fact they were highly correlated to MAP; Table 1). MAT became another important variable positively associated to the abundance of *S. atricapilla, Phylloscopus collybita* (Vieillot, 1817) and *Troglodytes troglodytes* (L., 1758); finally, FLOR showed positive association with the abundance of *Regulus ignicapillus* (Temminck, 1820), the sole species that was related to a particular forest type (pinewoods). According to these results, rainfall should be the main environmental correlate of the distribution of the

TABLE 2. Results of the stepwise multiple regression analysis. Dots show the selected environmental variables. The variance explained and the results of the analysis of the variance are also showed (see Methods for symbols).

	MAP	MAT	FLOR	DIST	$R2 \times 100$	*F*
S. atricapilla	o				32.18	26.57***
Ph. collybita	o	o		o	37.98	11.03***
R. ignicapillus	o		o	o	40.24	12.12***
E. rubecula	o			o	36.82	16.03***
T. troglodytes	o	o		o	42.91	13.53***
A. caudatus					00.00	00.00

***=$P<0.001$

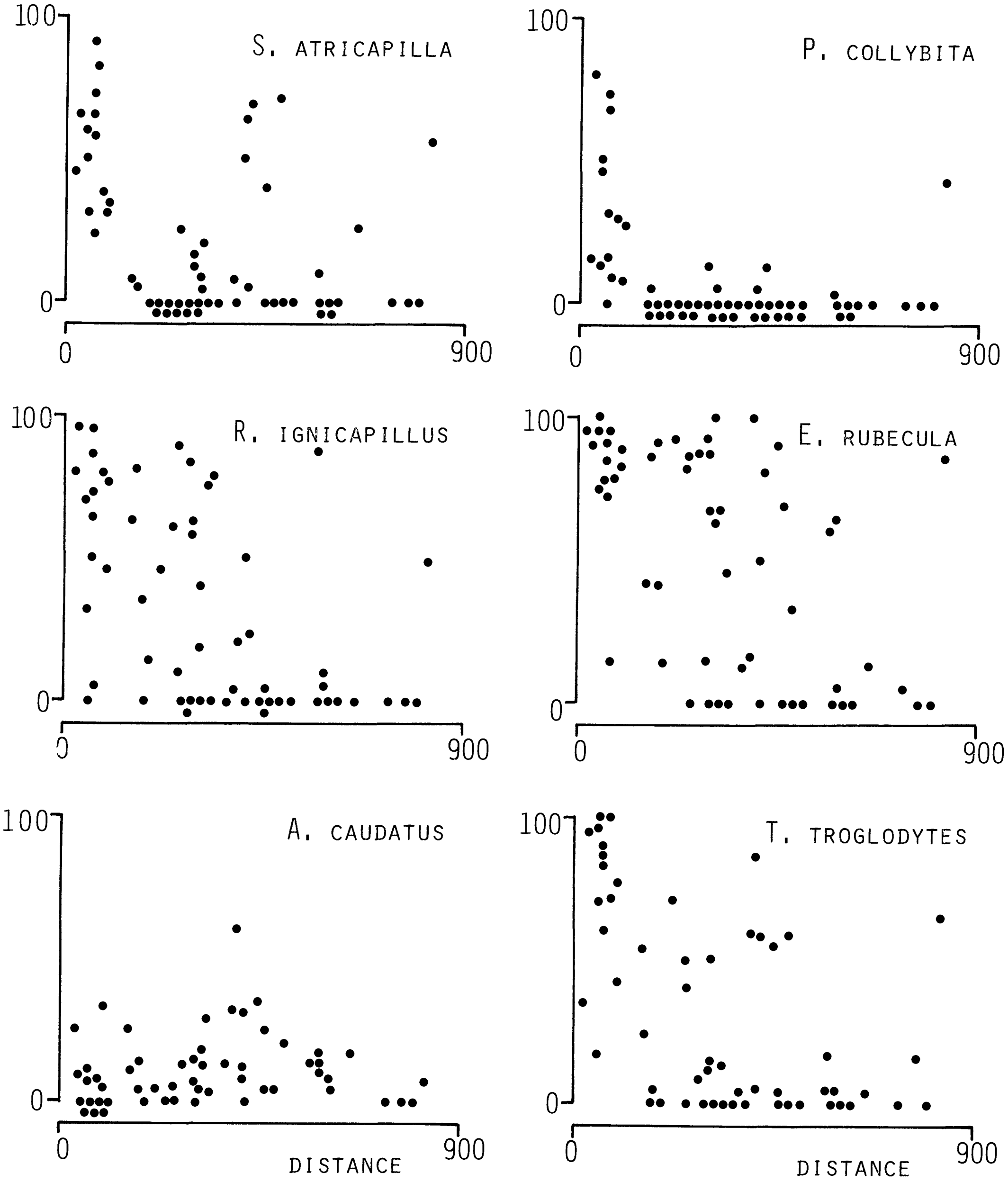

FIG. 2. Distribution of the abundance (frequency; see Methods) of six insectivorous passerines in fifty-eight forests located along a gradient spreading from Spanish-French boundary (km 0) to the southernmost tip of Spain.

species studied. However, DIST continued to be correlated to the density of some species (Table 1), suggesting some additional role in the processes involved in the observed abundance distribution along the Iberian gradient. The important role of MAP and DIST as predictors of abundance of the birds studied was also showed by the stepwise regression analysis, in which both variables were included in the models as predictors of bird abundance (Table 2).

DISCUSSION

The lack of relationships between the abundance of *Aegithalos caudatus* (L., 1758) and the distance to North along the Iberian gradient may be due to several potential shortcomings of our experimental design: (a) lack of precision of the censusing method to detect minor variations of abundance, (b) incidence of unrecorded environmental variables that may produce large amounts of 'statistical noise' and (c) lack of actual trends in the abundance of this species along the interval of the range covered by the Iberian gradient, too short to detect variations of abundance (see Wiens, 1989, for a review of these problems). The remaining species showed however clear patterns of variation in abundance along the gradient, corroborating thus the proposed model despite the incidence of environmental patchiness (Fig. 2). The decrease of abundance southwards may be due to a concomitant impoverishment of some environmental features, but it may be also related to a peninsular effect by which far woodlands should have increasing difficulties to be colonized by northern birds. Our results seem to support both views.

Rainfall patterns seem to be the main climatic factor related to abundance distribution of the birds studied. Many studies have documented close associations of individual bird species with rainfall (e.g. Serventy, 1971; Smith, 1977; Kendeigh & Fawyer, 1981; Maurer, 1985; Tellería, Suárez & Santos, 1988). A common explanation of the importance of this environmental variable is that rainfall, by controlling primary productivity and consequently the abundance of food for birds, is an important constraint on bird distribution. In the Mediterranean Region, rainfall is the most important ecological determinant of the vegetation productivity (Mooney & Kummerow, 1981). This may presumably be the ultimate causal factor constraining the distribution of many foliage insectivorous birds in the southern, xeric sectors of the studied gradient. Temperature seems to be also an important correlate of insectivorous bird abundance in the Iberian forests. Despite its importance in determining by thermal stress constraints the distribution of some species in their northern ranges (Root, 1988), it is not easy to evaluate its role in the gradient studied, in which temperatures are not so extreme (see, however, Walsberg, 1983, for a review on the subtle incidence of climate on bird distribution). Its positive partial correlation with the abundance of *S. atricapilla*, *P. collybita* and *T. troglodytes* suggest, however, that these species tend to be commoner in warm and wet forests. This could be explained according to the proposal of Emlen *et al.* (1986) that temperature may determine abundance of insectivorous birds by acting on the abundance or activity of the invertebrates they eat.

The negative association between distance to north and the abundance distribution of *P. collybita*, *R. ignicapillus* and *T. troglodytes* in the Iberian Peninsula, after removing the incidence of the rest of the environmental variables, may be explained by historical processes. According to the current knowledge on the vicissitudes of the Palaearctic avifauna since the Pleistocene (Moreau, 1954; Blondel, 1985), the withdrawal to north of glaciations was followed by forest birds that displaced their ranges northwards from the Mediterranean peninsulas, thus decreasing their abundances in their southern borders, where they distributed in some isolated patches of adequate habitats. It has been suggested that these geographical patterns should be the result of a dynamic equilibrium between the exportation of emigrants from the source areas and the importation of these individuals into sink areas where this continual migration could sustain local populations (Wiens & Rotenberry, 1981). According to predictions of island biogeographical theory applied to the distribution of species on a continental range, increasing distance to the source areas should be related to decreasing probabilities of these dispersal movements (MacArthur & Wilson, 1967) and, hence, should produce decreasing abundances of these species in the areas far from their central ranges. This dynamic process could thus account for the importance of distance to the source area as an independent determinant of the southern distribution of the northern species studied.

Results of this work show that patterns of geographical abundance of bird species are the result of the incidence of many variables. They illustrate the view that some reductionist approaches to animal distribution on large areas, in which the observed patterns are explained by means of one general environmental factor (Wright, 1983; Turner, Gatehouse & Corey, 1987; Owen, 1988), must be reviewed. It is important to increase the number of environmental features under consideration in order to perform more holistic approaches to bird biogeography (Myers & Giller, 1988). This requires the improvement of the methodology used to ascertain the true relationship of the involved variables with abundance. Multivariate analyses, for instance, a methodological approach largely used in modelling patterns of abundance at local or intrahabitat scales (see Capen, 1981), but poorly developed to date in the study of bird ranges, perhaps because of the logistic problems related to evaluation of variables across large areas, might be very promising tools. Results of the stepwise multiple regression analysis have shown in this paper its potential usefulness in predicting bird abundance along large ranges. The mean explained variance of the six analysed species was 31.69% (Table 2), higher or similar to the results obtained by this method in the modelling of bird abundance at intrahabitat or local scales (e.g. 12% for twenty-one breeding birds of an American forest; see Morrison, Timossi & Kimberly, 1987; 43% and 23% for forty-four breeding and twenty-three wintering species in an agricultural landscape of Spain, Tellería *et al.* 1988).

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