Modelling Avian Distributions of the Navarrese Region in Northern Spain with a Geographic Information System

Samuel Soret-Garcia

Follow this and additional works at: https://scholarsrepository.llu.edu/etd

Part of the Biology Commons, Geographic Information Sciences Commons, and the Ornithology Commons

Recommended Citation

https://scholarsrepository.llu.edu/etd/936
ABSTRACT

MODELLING AVIAN DISTRIBUTIONS OF THE NAVARRESE REGION IN NORTHERN SPAIN WITH A GEOGRAPHIC INFORMATION SYSTEM

by

Samuel Soret-García

GIS (Geographic Information Systems) technology was used for identifying relations between environmental characteristics and the breeding distributions of nine avian species of the Navarrese region in northern Spain. Data overlays of multiple GIS layers derived the explanatory variables for modelling the breeding distributions from logistic regressions. A spatial autocorrelation analysis was conducted to characterize the distribution patterns and to incorporate spatial factors (neighborhood effects) into their analysis.

All nine patterns analyzed exhibited a high level of spatial autocorrelation. Accordingly, the basic hypothesis of spatial randomness was rejected in favor of spatial clustering for the sample data. The breeding distributions strongly corresponded with environmental factors on a regional scale and often with a spatial weighting function representing neighborhood effects. Inclusion of the spatial term produced a significant increase in the sensitivity of most models (i.e., their ability to correctly predict a breeding occurrence). The addition of non-climatic factors particularly improved the performance of models for forest species. Although patterns of association
between the environment and avian distributions are complex and species specific, some common trends emerged. (1) Climatic variables tended to be less significant than habitat structure variables in models in which both types of variables were specified. (2) Vegetation structure was the most important environmental determinant of the breeding distributions. (3) The breeding distributions which showed the closest association with climate corresponded to species which find part of their Palearctic distribution boundary within the study area. These findings seem to suggest that although climate controls directly where the boundaries of a biogeographic distribution are, habitat is more likely to determine occurrence/absence where climatic conditions are within the permitted ecological tolerance of the species. The use of GIS, spatial autocorrelation statistics and logistic regression proved to be a valid approach to address the analysis of biogeographic distributions, as shown by the significant value of the models in predicting the avian distributions analyzed.
LOMA LINDA UNIVERSITY
Graduate School

MODELLING AVIAN DISTRIBUTIONS OF THE
NAVARRESE REGION IN NORTHERN SPAIN
WITH A GEOGRAPHIC INFORMATION SYSTEM

by
Samuel Soret-García

A Dissertation in Partial Fulfillment
of the Requirements for the Degree Doctor of Philosophy
in Biology

June 1993
Each person whose signature appears below certifies that
this dissertation in his opinion is adequate, in scope and
quality, as a dissertation for the degree Doctor of
Philosophy.

Joseph G. Galusha, Professor of Biology

Leonard R. Brand, Professor of Biology

Yue-Hung Chou, Assistant Professor of Geography

H. Thomas Goodwin, Assistant Professor of Paleontology

Earl L. Lathrop, Professor of Biology
ACKNOWLEDGEMENTS

This research was partially funded by a grant from the Instituto de Estudios Riojanos, Logroño, Spain. Additional funding was provided by Geoscience Research Institute and the Loma Linda University Department of Natural Sciences. The support and funding provided by my family and wife are also greatly appreciated.

Gratitude is expressed to Dr. Richard Tkachuck for his early inspiration in this project. Dr. Joseph Galusha, committee chairman, provided crucial support during difficult moments of this research. My sincere appreciation goes to committee members, Drs. Brand, Goodwin and Lathrop for their helpful criticisms of this manuscript. Drs. Gary L. Bradley, and David L. Cowles also provided helpful input. Special thanks goes to Dr. Yue-hung Chou, from the Earth Sciences Department at the University of California, Riverside for his constant and invaluable guidance, especially in the technical portion of this research. I would also like to thank Dr. Jean Powers, Mr. Raymond Dezzani and Mr. Thomas Feldman, from the UCR GIS Laboratory for their indispensable assistance. Gratitude is also due to Mr. Jesús Elósegui Aldasoro for providing valuable information on the region of Navarre and its avifauna, including original field records. The technical assistance in creating the illustrations provided by Mr. Martin Aguirre is also greatly appreciated.
# TABLE OF CONTENTS

ACKNOWLEDGEMENTS ................................................................. iii
LIST OF FIGURES ................................................................. vi
LIST OF TABLES ................................................................. x

I. INTRODUCTION ........................................................................... 1

II. THE STUDY AREA ...................................................................... 7
   Relief .................................................................................. 10
   Climate .............................................................................. 13
   Vegetation ........................................................................... 17

III. MATERIALS AND METHODS ..................................................... 26
   The Avian Species ............................................................... 26
   The Navarrese GIS Database (NGD) ....................................... 28
   The Analytic Approach ....................................................... 56
      General Introduction ....................................................... 56
      Spatial Autocorrelation Analysis ..................................... 60
      Spatial Weighting Functions .......................................... 63
      Probabilistic Models of Avian Breeding Distributions ....... 65
      The Model-Building Process ........................................... 67

IV. RESULTS ..................................................................................... 76
   Spatial Autocorrelation ....................................................... 76
   Logistic Regression ............................................................ 78
      The Climatic Models ....................................................... 78
      The Study Models ........................................................... 79
   Comparing Predicted and Observed Distributions ............... 137

V. DISCUSSION .............................................................................. 157
   Spatial Patterns of Avian Distributions .................................. 157
Modelling Avian Distributions in Terms of Spatial and Environmental Factors .......................................................... 161

Pernis apivorus Linnaeus 1758 .................................................. 161
Falco subbuteo Linnaeus 1758 .................................................. 162
Pterocles orientalis (Linnaeus) 1758 ...................................... 164
Melanocorypha calandra (Linnaeus) 1766 .............................. 165
Lullula arborea (Linnaeus) 1758 ................................................. 166
Ficedula hypoleuca (Pallas) 1764 .............................................. 167
Sitta europaea Linnaeus 1758 .................................................. 169
Serinus citrinella (Pallas) 1764 ................................................ 170
Pyrrhula pyrrhula (Linnaeus) 1758 ............................................ 172
All species considered ............................................................ 172

VI. CONCLUSION ..................................................................... 184

APPENDIX I. ENVIRONMENTAL CHARACTERIZATION OF NAVARRE 186

APPENDIX II. BIOGEOGRAPHICAL AND ECOLOGICAL CHARACTERIZATION OF THE AVIAN SPECIES STUDIED 202

APPENDIX III. CHARACTERIZATION OF THE NAVARRESE AVIFAUNA .............................................. 210

LITERATURE CITED ................................................................ 216
<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Biogeographic regions of the western Palearctic and location of study area</td>
<td>8</td>
</tr>
<tr>
<td>2. Relief of the study area.</td>
<td>11</td>
</tr>
<tr>
<td>3. Climatic regions of Navarre</td>
<td>14</td>
</tr>
<tr>
<td>4. Map of potential vegetation</td>
<td>18</td>
</tr>
<tr>
<td>5. Distribution of grassland and scrubland.</td>
<td>20</td>
</tr>
<tr>
<td>6. Land in crops.</td>
<td>22</td>
</tr>
<tr>
<td>7. Distribution of forests</td>
<td>24</td>
</tr>
<tr>
<td>8. Construction, application and information flow in a GIS database</td>
<td>30</td>
</tr>
<tr>
<td>9. Geographic units used in this study.</td>
<td>33</td>
</tr>
<tr>
<td>10. Data organization within a GIS.</td>
<td>36</td>
</tr>
<tr>
<td>11. Annual and July isotherms maps</td>
<td>40</td>
</tr>
<tr>
<td>12. Maps of date of last frost of spring and length of frost-free period.</td>
<td>42</td>
</tr>
<tr>
<td>13. Annual isohyet map and map of mean annual potential evapotranspiration</td>
<td>44</td>
</tr>
<tr>
<td>14. Map of coldness of the spring season and map of the humidity regimes (length of the arid period)</td>
<td>46</td>
</tr>
<tr>
<td>15. Maps of annual excess and annual deficit of precipitation</td>
<td>48</td>
</tr>
<tr>
<td>16. Bioclimatic zones and map of rivers and streams</td>
<td>50</td>
</tr>
<tr>
<td>17. Distribution of Gorezynsky's K index of continentality, and map of vegetation diversity.</td>
<td>54</td>
</tr>
</tbody>
</table>
18. Hypothetical cases illustrating Complete Spatial Randomness, clustered and uniform patterns
19. Plot comparing the overall forecasting accuracy of the Climatic Model and Study Model I for Pernis apivorus
20. Plot comparing sensitivities and specificities of the Climatic Model and Study Model I for Pernis apivorus
21. Maps showing the observed and predicted distributions of Pernis apivorus
22. Plot comparing the overall forecasting accuracy of the Climatic Model and Study Model I for Falco subbuteo
23. Plot comparing sensitivities and specificities of the Climatic Model and Study Model I for Falco subbuteo
24. Plot comparing the overall forecasting accuracy of study models I and II for Falco subbuteo
25. Plot comparing sensitivities and specificities of study models I and II for Falco subbuteo
26. Maps showing the observed and predicted distributions of Falco subbuteo
27. Maps showing the observed and predicted distributions of Pterocles orientalis
28. Plot comparing the overall forecasting accuracy of study models I and II for Melanocorypha calandra
29. Plot comparing sensitivities and specificities of study models I and II for Melanocorypha calandra
30. Maps showing the observed and predicted distributions of Melanocorypha calandra
31. Plot comparing the overall forecasting accuracy of study models I and II for Lullula arborea
32. Plot comparing sensitivities and specificities of study models I and II for Lullula arborea
33. Maps showing the observed and predicted distributions of
   *Lullula arborea* ............................................................... 110

34. Plot comparing the overall forecasting accuracy of study
   models I and II for *Ficedula hypoleuca* ............................. 113

35. Plot comparing sensitivities and specificities of study
   models I and II for *Ficedula hypoleuca* ............................. 113

36. Maps showing the observed and predicted distributions of
   *Ficedula hypoleuca*. .......................................................... 116

37. Plot comparing the overall forecasting accuracy of the
   Climatic Model and Study Model I for *Sitta europaea* ............ 120

38. Plot comparing sensitivities and specificities of the
   Climatic Model and Study Model I for *Sitta europaea* ............ 120

39. Maps showing the observed and predicted distributions of
   *Sitta europaea*. ............................................................... 123

40. Plot comparing the overall forecasting accuracy of the
   Climatic Model and Study Model I for *Serinus citrinella* ....... 126

41. Plot comparing sensitivities and specificities of the
   Climatic Model and Study Model I for *Serinus citrinella* ....... 126

42. Plot comparing the overall forecasting accuracy of study
   models I and II for *Serinus citrinella*. ............................... 129

43. Plot comparing sensitivities and specificities of study
   models I and II for *Serinus citrinella*. ............................... 129

44. Maps showing the observed and predicted distributions of
   *Serinus citrinella*. .......................................................... 131

45. Plot comparing the overall forecasting accuracy of the
   Climatic Model and Study Model I for *Pyrrhula pyrrhula* ....... 135

46. Plot comparing sensitivities and specificities of the
   Climatic Model and Study Model I for *Pyrrhula pyrrhula* ....... 135

47. Maps showing the observed and predicted distributions of
   *Pyrrhula pyrrhula* .......................................................... 138
48. Map overlays of observed vs. predicted distributions for *Falco subbuteo* and *Pernis apivorus* ........................................... 144

49. Map overlays of observed vs. predicted distributions for *Pterocles orientalis* and *Melanocorypha calandra* ......................... 146

50. Map overlays of observed vs. predicted distributions for *Lullula arborea* and *Ficedula hypoleuca*. .................................. 148

51. Map overlays of observed vs. predicted distributions for *Sitta europaea* and *Serinus citrinella*. .................................... 150

52. Map overlay of observed vs. predicted distributions for *Pyrrhula pyrrhula*. ................................................................. 152

53. Frequency of significant associations between breeding distributions and explanatory variables in the effective models ........................................... 174

54. Maps showing the distribution of beech and coniferous forests in the study area. .............................................................. 192

55. Distribution of mixed coniferous-deciduous forests and of broad-leaved deciduous (other than beech and oak) forests in the study area. ........................................... 195

56. Distribution of hydric and mesic oaks in the study area. ............ 198

57. Distribution of evergreen Mediterranean oaks and of mixed oak forests over the study area. ................................................. 200
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Main descriptors of the climatic regions defined for Navarre</td>
<td>16</td>
</tr>
<tr>
<td>2. Avian species studied</td>
<td>27</td>
</tr>
<tr>
<td>3. Cartography acquired and input into GIS</td>
<td>29</td>
</tr>
<tr>
<td>4. Environmental data layers within the GIS database</td>
<td>35</td>
</tr>
<tr>
<td>5. Variables created from GIS data layers</td>
<td>38</td>
</tr>
<tr>
<td>6. Spatial autocorrelation statistics</td>
<td>77</td>
</tr>
<tr>
<td>7. <em>Pernis apivorus</em>: logistic regression statistics</td>
<td>80</td>
</tr>
<tr>
<td>8. <em>Falco subbuteo</em>: logistic regression statistics</td>
<td>86</td>
</tr>
<tr>
<td>9. <em>Pterocles orientalis</em>: logistic regression statistics</td>
<td>95</td>
</tr>
<tr>
<td>11. <em>Lullula arborea</em>: logistic regression statistics</td>
<td>105</td>
</tr>
<tr>
<td>12. <em>Ficedula hypoleuca</em>: logistic regression statistics</td>
<td>112</td>
</tr>
<tr>
<td>13. <em>Sitta europaea</em>: logistic regression statistics</td>
<td>119</td>
</tr>
<tr>
<td>14. <em>Serinus citrinella</em>: logistic regression statistics</td>
<td>125</td>
</tr>
<tr>
<td>15. <em>Pyrrhula pyrrhula</em>: logistic regression statistics</td>
<td>134</td>
</tr>
<tr>
<td>16. Model comparison statistics</td>
<td>140</td>
</tr>
<tr>
<td>17. Sensitivity, specificity, predictive value and overall forecasting accuracy of the effective models compared for two different cutpoints</td>
<td>141</td>
</tr>
<tr>
<td>18. Composition of the Navarrese breeding avifauna (by orders)</td>
<td>211</td>
</tr>
<tr>
<td>19. Families of the order passeriformes in the study area</td>
<td>211</td>
</tr>
</tbody>
</table>
20. Faunal types proposed by Voous (1960) for Europe and their proportion in the Navarrese breeding avifauna 213
I. INTRODUCTION

A remarkable feature of life on Earth is its lack of uniform distribution in the biotic fauna. Why do individuals of a given species occur in some places and not in others? This is the simplest ecological question which can be asked (Krebs, 1978). Especially striking is the fact that birds, in spite of their great mobility, have sharply demarcated spatial distributions (Van Tyne and Berger, 1961). Due to the great interest that birds have traditionally raised among biologists and naturalists, avian distributions are more accurately known than those of any other group of organisms, but much remains to be understood about their governing factors (Greenwood, 1992).

Determining the reason for distributional patterns seen in nature has been the object of study since the origins of biogeography and geographical ecology as formal disciplines in biology (Wallace, 1976). However, the question of what shapes biogeographic patterns is still being debated. Two long-held theories postulate alternatively (1) abiotic factors (Andreadwartha and Birch, 1954), such as climate, or (2) biotic interactions (MacArthur, 1958), such as competition or predation, and behavior (Bartholomew and Dawson, 1954; Sturkie, 1965) as the primary forces determining the abundance and distribution of species. Some authors have implicated both abiotic and biotic agents in accounting for distributional patterns (Brown and Gibson, 1983; Terborgh, 1985), while biogeographers have often emphasized the role of historical factors.
Abiotic factors can limit a species distribution directly by physiological demands (Boughey, 1968; Root, 1988a, 1989) --i.e., the energetic costs incurred by individuals needing to compensate for environmental stresses-- or indirectly through their impact upon habitat, food and other essential resources (Owen, 1990). Since the pervasive view among ecologists has been that biotic factors are more important than abiotic ones in limiting species distributions, much of the recent ecological research has focused on small study areas (Kareiva and Andersen, 1988; Strong and Bock, 1990), and primarily on biotic interactions (competition; e.g., Connell, 1961; Moulton and Pimm, 1983; Gurevitch, 1986; and predation; Connell 1970, 1975; Lubchenko and Menge, 1978).

Root (1988b) has pointed out that at a fine resolution level, biotic interactions are more obvious than, and therefore overshadow the relevance of, environmental factors which are important at larger scales. If as suggested by Wardle (1981) biotic interactions only influence proximate details of range boundaries, then large-scale studies are needed to examine the importance of environmental factors such as climate so that the patterns they cause are not obscured by the details of local studies (Root, 1988b).

In studies at the biogeographic level (i.e., the spatial scale roughly corresponding with the range of many species; see Davis et al., 1990), distributional patterns have usually been explained by emphasizing either ecological or historical factors (Kikkawa and Pearse, 1969; Blondel and
Choisy, 1983; Caughley et al., 1987; Root, 1988c; Ripley and Beehler, 1990; Whitehead et al., 1992). In most cases, however, environment and history act together in causing distributional patterns (Noonan, 1990; Maly and Bayly, 1991). Historical factors influence the fauna of a given region by determining its composition on a presence/absence basis, however, how species currently present are distributed within a region is most likely determined by contemporary environmental factors (Busack and Jaksic, 1982). This interaction between historical and environmental factors implies that the same distributional patterns can often be explained by using ecological or historical theories and, therefore, the real cause for the distribution cannot be determined (Endler, 1980).

Several studies (e.g., Telleria and Santos, 1985; Telleria, 1987) have examined the relation between environmental factors and species distributional patterns at a regional scale (i.e., the spatial scale intermediate between those of biogeographic and local studies). At this regional scale, the role of historical factors should be minimal unless major barriers exist preventing species dispersal. Although regional avian distributions might be determined by a single environmental factor, it is more likely that they will be determined by a group of interrelated factors (Cody, 1985). It is also likely that different species will be affected by different factors, or by the same ones but at varying degrees (Bustamante et al., 1988).
Biogeographic distributions may be viewed as patterns of plant and animal life that can be put on a map (MacArthur, 1972). As a spatial pattern, a species distribution can be studied as a variable mapped onto geographic space. Treatment of species distributions as spatial phenomena allows their formal analysis via conventional methods of hypothesis testing, a first step toward understanding the underlying processes which cause them.

As spatial phenomena, species distributions can be explained by structural and spatial factors. Structural factors of avian distributions include many environmental elements such as physiographic features, climate, etc (Andreadartha and Birch, 1954; Cox and Moore, 1985). Avian distributions may also be influenced by spatial interactions, i.e., the movement of things or information over space. Spatial interaction means that "events or circumstances at one place can affect conditions at other places if the places interact" (Odland, 1988).

One of the most obvious such factors for avian distributions is neighborhood effects because the expansion of species' ranges is often a contagious diffusion (Okubo, 1980, 1988; Ferrer et al., 1991; Van den Bosch, Hengeveld and Metz, 1992). Neighborhood effects mean that the selection of a breeding site is influenced by the presence/absence of other individuals of the same species in neighboring locations, and that this influence is a function of the distance (Margalef, 1986). Specifically, the
probability for a breeding pair to be found in a given locality will be higher
where another breeding pair of the same species exists than where it does
not and that probability decreases as the distance to the locality already
occupied increases. Neighborhood effects are the equivalent of Tobler’s
(1970) "first law of geography" that "everything is related to everything else
but near things are more related than distant things."

In this study, the view that regional patterns of distributions for given
species can be predicted from an analysis of (1) patterns in the distribution
of environmental variation and (2) spatial dependence among breeding
localities will be tested using the distributions of nine avian species in the
region of Navarre in northern Spain. The primary purpose was to find the
environmental and spatial factors which indexed the distributions most
economically. An additional goal was to illustrate a modelling strategy to
assist in that task which would transfer easily to the study of species
distributions in other areas. This modelling strategy (Chou 1989, 1990, and
1992; Chou et al. 1990) prescribes the use of inductive modelling
techniques (logistic regression and spatial autocorrelation) together with a
geographic information system.

Geographical Information Systems (hereafter GIS) are computer-based
systems specifically designed to assemble, store, manipulate, analyze and
display geographically referenced information (Burrogh, 1987; Aronoff,
1989). GIS technology has been widely used in applied ecology and various
fields of ecology and wildlife preservation (Wiggins et al., 1987; Tomlinson, 1987; Rizzo, 1988; Davis et al., 1990; Mead et al., 1988; Liebhold, 1993) and also in ornithological research (Scepan, Davis and Blum, 1987; Young et al., 1987; Shaw and Atkinson, 1988 and 1990; Miller, Stuart and Howel, 1989), but much less frequently in biogeographical analysis. This study represents one of the first attempts (e.g., Walker and Moore, 1988 and Walker, 1990) to apply GIS technology to the inductive modelling of avian distributions, i.e., systematically identifying relationships between particular biogeographic distributions and environmental parameters (Wheeler, 1988). Previous applications of GIS have usually concentrated on deductive tasks, i.e., describing and characterizing species potential habitat based on prior knowledge.

An important feature of this study was the integration of GIS technology and spatial autocorrelation statistics (Cliff and Ord, 1973, 1975, 1981; Odland, 1988; Getis, 1989) (1) to detect and describe distributional patterns, (2) to investigate the significance of neighborhood effects (i.e., the extent to which breeding data collected at certain localities depend on values at neighboring localities) and (3) to construct explanatory models with an explicitly defined term representing the neighborhood effects.
II. THE STUDY AREA

The Iberian Peninsula, which contains Spain and Portugal, clearly shows the temperate-Mediterranean climatic transition that is evident in the western Palearctic and along which two distinct biogeographic regions, namely, Eurosiberian and Mediterranean, can be recognized (Fig. 1a; Rivas-Martínez et al., 1987). The study area, i.e., the region of Navarre in northern Spain, is found precisely in the area of confluence between the Eurosiberian and Mediterranean regions within the Iberian Peninsula.

The study area (Fig. 1b) occupies an area of 10,421 Km² and lies between 41° 55’ 34” and 43° 18’ 36” north, and 1° 11’ 33” and 2° 56’ 57” east. It is bound by France to the north and it is located just a few kilometers away from the Bay of Biscay to the northwest. Maximum distances occur from northwest to southeast, 178 Km, and from northeast to southwest, 143 Km.

In Navarre it is possible to find within a comparatively small territory an impressive succession of landscapes and associated avifaunas, from the Pyrenean summits to the northeast of alpine or boreal aspect, to the semi-arid steppes to the southeast whose physiognomy and faunas resemble strikingly those of northern Africa.

In the Navarrese mountains the majestic deciduous beech forests, which harbor the same or very similar floras and faunas that can be found, for example, in the forests of Poland or Denmark reach their
Figure 1. Mediterranean and Eurosiberian regions of the western palearctic (A) according to Rivas-Martinez (1987); the shaded areas correspond to the Mediterranean region. Location of the study area within the Iberian Peninsula (B) shown in black.
southern boundary in Europe. The Ebro River Valley to the south acts as a "wedge" of the Mediterranean world, bringing plants and animals, such as the olive tree, rosemary or the Black-bellied Sandgrouse, to their most northerly outposts in the Iberian Peninsula.

This section provides succinct descriptions of the environmental and geographic framework within which the avian species of Navarre are found. Appendix I can be consulted for a more detailed environmental characterization of the study area.

Relief

Navarre is very mountainous --more than 40% of its territory lies at elevations above 600 m-- but with just modest elevations which rarely exceed 1,500 m (Ministerio de Agricultura y Gobierno de Navarra, 1986; hereafter MA & GN, 1986). Altitude decreases from east to west and, more dramatically, from north to south. The northern half of Navarre or Montaña district lies at elevations above 600 m, whereas elevations in the southern half or Ribera district are for the most part below 400 m (see Fig. 2). The highest summits (2,434 m) occur to the northeast, while the lowest elevations, approaching sea level, are found in the northern tip of the study area. The Ebro River Valley to the south lies at elevations between 200 m and 400.
Figure 2. Relief of the study area. Elevations in the white areas of the northern tip of the region ranges from sea level to 400 m. Maximum elevations in the black areas to the northeast are higher than 2,200 m.
Climate

The geographic variety of the study area and the combination of its two main climatic types, temperate and Mediterranean, over wide areas originate a pronounced mesoclimatic variation (Elias-Castillo and Ruiz-Beltrán, 1986; Elósegui, 1985). Figure 3 shows the climatic types and zones which can be recognized for Navarre (Allué-Andrade, 1966) and Table 1 contains their main descriptors. Precise information about these climatic zones can be found in Appendix I.

The northern portion (Cantabrian Zone) of the Montaña district experiences a typical oceanic climate similar to that of other temperate zones in western Europe, with mild winters, cool summers, high air humidity, abundant cloudiness, and frequent, evenly-distributed rainfall. Frosts are rare due to oceanic influence.

The Ribera district and other non-coastal areas of the Iberian Peninsula, have a continental, Mediterranean climate. In contrast to the Mediterranean climate of coastal areas in the Iberian Peninsula, the Mediterranean climate of the Ribera district is characterized by a sharp seasonal contrast of temperatures with severe winters and dry, warm summers (Font-Tullot, 1983a,b; MA & GN, 1986).

The oceanic climate becomes sub-oceanic (cooler and drier) to the south of the Montaña district (sub-Cantabrian Zone), whereas the
Figure 3. Map showing the climatic regions defined along the temperate-Mediterranean climatic transition from north to south in the study area. Temperate zones: (I) Cantabrian, (IIa) western sub-Cantabrian, (IIb) central sub-Cantabrian, (IIc) eastern sub-Cantabrian or Pyrenean. Mediterranean zones: (III) sub-Mediterranean, (IVa) Mediterranean humid (IVb) Mediterranean dry or Ribera (Allue-Andrade, 1987).
CLIMATIC ZONES

![Map showing climatic zones with zones labeled I, IIa, IIb, IIc, III, IVa, IVb. A scale bar indicates distances in Kilometers.]
Table 1. Main descriptors of the climatic regions of the study area.

<table>
<thead>
<tr>
<th>Climatic Region</th>
<th>Sub-Climatic Region</th>
<th>Climatic Type</th>
<th>Length of arid period (months)</th>
<th>Mean Annual Precipitation (mm)</th>
<th>Temp. of the coldest month (°C)</th>
<th>Temp. of the warmest month (°C)</th>
<th>Mean Annual Temp (°C)</th>
<th>Frost-Free Period (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperate</td>
<td>Cantabrian</td>
<td>Oceanic</td>
<td>0</td>
<td>1,800 - 2,800</td>
<td>6 - 8</td>
<td>18 - 21</td>
<td>12 - 14</td>
<td>140 - 220</td>
</tr>
<tr>
<td></td>
<td>Eastern sub-Cantabrian or Pyrenean</td>
<td>Pyrenean</td>
<td>0</td>
<td>1,200 - 2,000</td>
<td>1.5 - 4</td>
<td>14 - 17</td>
<td>7 - 10</td>
<td>80 - 140</td>
</tr>
<tr>
<td></td>
<td>Central sub-Cantabrian</td>
<td>Sub-oceanic</td>
<td>0 - 1</td>
<td>1,100 - 1,800</td>
<td>4 - 6</td>
<td>17 - 18</td>
<td>10 - 12</td>
<td>130 - 150</td>
</tr>
<tr>
<td></td>
<td>Western sub-Cantabrian</td>
<td>Montane sub-oceanic</td>
<td>0 - 1</td>
<td>1,100 - 1,800</td>
<td>1.5 - 4</td>
<td>15 - 17</td>
<td>8 - 10</td>
<td>70 - 140</td>
</tr>
<tr>
<td>Mediterranean</td>
<td>Sub-Mediterranean</td>
<td>Sub-humid Mediterranean</td>
<td>1 - 3</td>
<td>650 - 1,200</td>
<td>3 - 4.5</td>
<td>19 - 21</td>
<td>12 - 13</td>
<td>140 - 180</td>
</tr>
<tr>
<td></td>
<td>Mediterranean</td>
<td>Genuin Mediterranean</td>
<td>1 - 4</td>
<td>500 - 650</td>
<td>4.5 - 5</td>
<td>21 - 22</td>
<td>13 - 14</td>
<td>170 - 190</td>
</tr>
<tr>
<td></td>
<td>Mediterranean</td>
<td>Dry genuin Mediterranean</td>
<td>2 - 5</td>
<td>300 - 500</td>
<td>5 - 6.5</td>
<td>22 - 24</td>
<td>13 - 15</td>
<td>170 - 220</td>
</tr>
</tbody>
</table>
Mediterranean climate becomes sub-humid (cooler and moister) to the north of the Ribera district (sub-Mediterranean Zone).

**Vegetation**

Figure 4 depicts the potential vegetation —i.e., the inferred mature ecosystems— of the study area according to Rivas-Martínez (1987). The varied climate and orography of Navarre condition a diverse vegetation, with forests covering a vast majority of the territory and only localized areas (some alpine zones the northeast and sub-desert zones to the southeast) being devoid of trees.

Continued anthropogenic influence has altered both the extent and composition of the original vegetation (see Figures 5-7). Presently, only about 1/3 of the territory is covered by forests (Elósegui, 1985; MA & GN, 1986). Reforestations with conifers are found scattered throughout the territory and are particularly important in the Cantabrian district. Oak and beech forests of the Pyrenean valleys have been partially replaced by natural populations of Scots pine. Broad-leaved, riparian forests have been dramatically reduced as well. Only a few narrow strips of this type of forests are left along some river courses. Descriptions and maps of the present distributions of the different forest types found in Navarre can be found in Appendix I.
Figure 4. Map showing the inferred matured ecosystems of the study area (Rivas-Martinez, 1987).
Mesic oaks

Conifers

Hydric oaks

Beech

Riparian vegetation

Mediterranean oaks

Mediterranean scrubland
Figure 5. Distribution of the grassland (A) and scrubland (B) in the study area. Natural prairies and meadows predominate in northern Navarre in coincidence with the humid Cantabrian areas. Subalpine pastures (*Nardus stricta*) occur in the Pyrenean areas to the northeast, whereas Mediterranean montane pastures (*Festuca scoparia*) are found in sub-Mediterranean zones. In southern Navarre are "saltish" pastures. Fern fields and heathland are the type of humid scrubland which prevails in the Cantabrian and sub-Cantabrian regions, whereas the box shrubland is typical of central Navarre and Mediterranean maquis (mainly Kermes oak) of the southern parts.
Figure 6. Distribution of cultivated land in Navarre.
LAND IN CROPS
Figure 7. Distribution of forests over the study area.
III. MATERIALS AND METHODS

The Avian Species

Of the ornithological atlases published for several Iberian regions (De Juana, 1980; Muntaner et al., 1983; López-Beiras and Guitian, 1983; Viedma, 1983; Álvarez et al., 1985; Elósegui, 1985; Martin, 1987), the one corresponding to the region of Navarre is best suited for the study of avifaunal distributions along a temperate/Mediterranean transition. Thus, the breeding distributions analyzed in this study were based on the atlas of breeding birds of Navarre (hereafter ABN; Elósegui, 1985).

To avoid basing the statistical analysis on very small samples, the distributions of those species for which the ABN reported less than 20 breeding occurrences were not considered for inclusion. Also, species found ubiquitously over the study area were not considered for analysis since they do not constitute good examples for testing their presence or absence in relation to environmental factors. Altogether, 88 species were eliminated from the 183 described in the ABN, leaving 95 species as potential subjects of study. The breeding distributions corresponding to nine of those 95 species were analyzed in this study (Table 2). This sample, intended to be representative of the region’s avifauna and taxonomically heterogeneous, included species which (1) belonged to different avifaunal types (see Appendices II and III), (2) had different habitat requirements, diets, and nesting behaviors, (3) were different in size, (4) exhibited markedly different
Table 2. Avian species whose breeding distributions were analyzed in this study.

<table>
<thead>
<tr>
<th>ORDER</th>
<th>FAMILY</th>
<th>SPECIES</th>
<th>ENGLISH NAME</th>
</tr>
</thead>
<tbody>
<tr>
<td>Falconiformes</td>
<td>Accitripidae</td>
<td><em>Pernis apivorus</em></td>
<td>European Honey-Buzzard</td>
</tr>
<tr>
<td></td>
<td>Falconidae</td>
<td><em>Falco subbuteo</em></td>
<td>Eurasian Hobby</td>
</tr>
<tr>
<td>Columbiformes</td>
<td>Pteroclidae</td>
<td><em>Pterocles orientalis</em></td>
<td>Black-bellied Sandgrouse</td>
</tr>
<tr>
<td>Passeriformes</td>
<td>Alaudidae</td>
<td><em>Melanocorypha calandra</em></td>
<td>Calandra Lark</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Lullula arborea</em></td>
<td>Wood Lark</td>
</tr>
<tr>
<td></td>
<td>Muscicapidae</td>
<td><em>Ficedula hypoleuca</em></td>
<td>European Pied Flycatcher</td>
</tr>
<tr>
<td></td>
<td>Sittidae</td>
<td><em>Sitta europaea</em></td>
<td>Eurasian Nuthatch</td>
</tr>
<tr>
<td></td>
<td>Fringillidae</td>
<td><em>Serinus citrinella</em></td>
<td>Citril Finch</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Pyrrhula pyrrhula</em></td>
<td>Eurasian Bullfinch</td>
</tr>
</tbody>
</table>
distribution patterns and (5) exhibited variation in their numbers of breeding records. Basic biogeographical and ecological information for each of the nine species studied can be found in Appendix II and a characterization of the Navarrese breeding avifauna is provided in Appendix III to serve as a reference for the ornithological significance of the species which were studied.

The Navarrese GIS Database (NGD)

Environmental data used in this study were compiled from published maps of many types (see Table 3). Avian as well as geographic and environmental data were stored and processed within ARC/INFO (Environmental Research Systems Institute, 1987, 1991), a vector-based Geographical Information System, in a VAX8820 computer at the University of California at Riverside GIS Laboratory. GIS technology was used to accomplish: (1) the construction of a digital database containing the geographic information pertaining to the study area, (2) geographic data management (storage and retrieval), (3) spatial analyses, and (4) data display. Figure 8 shows the steps in the construction and application of the database utilized in this study.

Following the format in the ABN, the avian distributions were represented on a UTM (Universal Transverse Mercator) grid system with single cells of 10 Km X 10 Km. Since both the avian data (see Elósegui, 1985) and the environmental cartography were based on data collected
<table>
<thead>
<tr>
<th>MAP</th>
<th>SCALE</th>
<th>EXTRACTED LAYERS</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Topographic Map of Navarre</td>
<td>1:200,000</td>
<td>Drainage system Boundary</td>
<td>Regional Government of Navarre</td>
</tr>
<tr>
<td>National Topographic Map of Spain</td>
<td>1:400,000</td>
<td>Contour lines</td>
<td>National Geographic Institute of Spain</td>
</tr>
<tr>
<td>Agroclimatic Map of Navarre</td>
<td>1:600,000</td>
<td>Climatic variables</td>
<td>Ministry of Agriculture of Spain and Regional Government of Navarre</td>
</tr>
<tr>
<td>Map of the Vegetation Series of Spain</td>
<td>1:400,000</td>
<td>Potential vegetation Bioclimatic Zones</td>
<td>National Institute for Nature Conservancy of Spain</td>
</tr>
<tr>
<td>Land Use Map of Navarre</td>
<td>1:200,000</td>
<td>Land Use Vegetation</td>
<td>Ministry of Agriculture of Spain</td>
</tr>
</tbody>
</table>
Figure 8. Information flow in the GIS database constructed in this study. Headings along the top refer to the sequential steps in the design, construction and application of the database. Arrows indicate the flow of information between steps (Davis et al, 1990).
exclusively within Navarre, a layer containing the political boundary of the study area was overlaid onto the UTM grid. All the external territory belonging to those grid cells truncated by the political boundary was eliminated. The resulting layer (hereafter, base map) was a grid of 152 pixels (geographic units) with peripheral cells smaller than 100 Km² and of irregular shape (see Fig. 9). This manipulation did not affect the number of observations pertaining to each avian distribution since only the size and shape of the peripheral pixels was modified, and not the presence or absence of the species in them.

The base map was used to represent the nine breeding distributions analyzed. Each geographic unit, regardless of its size and shape, was coded for species presence or absence with 1 or 0, respectively, replicating the breeding distributions maps available in the ABN.

The NGD also included information about a wide variety of environmental factors which were digitized and stored as many individual data layers (Table 4). As depicted in Figure 10, the series of environmental layers conformed to the grid representing the avifaunal breeding distribution patterns. Creation of the environmental variables was implemented by overlaying the various environmental layers included in the NGD onto the layer containing the geographic units or base map (Table 5; Elías-Castillo and Ruiz-Beltrán, 1986).
Figure 9. UTM 10 Km X 10 Km grid used to define the geographic units in this study.
Table 4. Environmental data layers extracted by digitizing the maps detailed in Table 3.

<table>
<thead>
<tr>
<th>DATA LAYER</th>
<th>TYPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boundary</td>
<td>Line</td>
</tr>
<tr>
<td>UTM grid</td>
<td>Polygon</td>
</tr>
<tr>
<td>Geographical units</td>
<td>Polygon</td>
</tr>
<tr>
<td>Altitude</td>
<td>Line</td>
</tr>
<tr>
<td>Watershed system</td>
<td>Line</td>
</tr>
<tr>
<td>Annual mean temperature</td>
<td>Line</td>
</tr>
<tr>
<td>July mean temperature</td>
<td>Line</td>
</tr>
<tr>
<td>Date from which the probability of reaching an absolute</td>
<td>Line</td>
</tr>
<tr>
<td>minimum temperature $\leq 2^\circ$C is 50%</td>
<td></td>
</tr>
<tr>
<td>Last frost of Spring</td>
<td>Line</td>
</tr>
<tr>
<td>Length of the frost-free period</td>
<td>Line</td>
</tr>
<tr>
<td>Humidity regimes</td>
<td>Line</td>
</tr>
<tr>
<td>Annual mean precipitation</td>
<td>Line</td>
</tr>
<tr>
<td>Annual mean climatic excess of precipitation</td>
<td>Line</td>
</tr>
<tr>
<td>Annual mean climatic deficit of precipitation</td>
<td>Line</td>
</tr>
<tr>
<td>Annual mean potential evapotranspiration</td>
<td>Line</td>
</tr>
<tr>
<td>Bioclimatic Zones</td>
<td>Polygon</td>
</tr>
<tr>
<td>Potential Vegetation</td>
<td>Polygon</td>
</tr>
<tr>
<td>Landuse</td>
<td>Polygon</td>
</tr>
<tr>
<td>Vegetation</td>
<td>Polygon</td>
</tr>
</tbody>
</table>
Figure 10. Data organization within a GIS. Avian and environmental data are stored as information layers. The top layer represents a species distribution. Shaded cells denote breeding occurrences whereas empty cells symbolize the absence of the species. The stack protruding from the right side of the block represents a "core" of information and is the basic unit of analysis.
Table 5. Environmental variables created.

<table>
<thead>
<tr>
<th>Climatic variables (Elías-Castillo and Ruiz-Beltrán, 1986):</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM: Humidity regimes (length in months of arid period).</td>
</tr>
<tr>
<td>TEMP: Annual mean temperature (°C).</td>
</tr>
<tr>
<td>HTEMP: July mean temperature (°C).</td>
</tr>
<tr>
<td>SFROST: Date (days after April 10th) of last frost of spring.</td>
</tr>
<tr>
<td>DFTTEMP: Date (days after March 1st) from which the probability of reaching a minimum temperature ≤ 2°C = 50%.</td>
</tr>
<tr>
<td>FRSTFREE: Length of frost-free period (days).</td>
</tr>
<tr>
<td>BIOCLIM: Bioclimatic zones-Themicity Index (Rivas-Martínez et al., 1987).</td>
</tr>
<tr>
<td>CONT: Continentality (Gorezynsky Index; Font-Tullot, 1983).</td>
</tr>
<tr>
<td>DEFPREC: Annual mean climatic deficit of precipitation (mm).</td>
</tr>
<tr>
<td>EXPREC: Annual mean climatic excess of precipitation (mm).</td>
</tr>
<tr>
<td>PREC: Annual mean precipitation (mm).</td>
</tr>
<tr>
<td>EVTPOT: Annual mean potential evapotranspiration (mm).</td>
</tr>
<tr>
<td>Geographic variables:</td>
</tr>
<tr>
<td>ALT: Altitude (meters).</td>
</tr>
<tr>
<td>HDR350: % of geographic unit covered by a 350-meter buffer around rivers and streams.</td>
</tr>
<tr>
<td>Vegetation variables:</td>
</tr>
<tr>
<td>CULT: areal ratio of geographic unit covered by cultivated land.</td>
</tr>
<tr>
<td>Hveg: Vegetation diversity (Shannon-Weaver Index; Miller, 1986)).</td>
</tr>
</tbody>
</table>
The altitude coverage was converted into a polygon coverage for map overlay. Altitude ranges were coded by using the average between the elevation values of the contour lines delineating them (the contour line distance was 200 m). By overlaying the altitude layer onto the base map, the ALT variable, was calculated from the area-adjusted average of each geographic unit.

By overlying the climatic layers (Figures 11-15) onto the base map, ten climatic variables, TEMP, HTEMP, SFROST, FRSTFREE, PREC, REGHUM, EVTPOT, DFTEMP, DEFPREC, and EXPREC, were calculated from the area-adjusted average of each geographic unit. The meaning of the first five variables is obvious (see Table 5) but the last five require some clarification.

EVTPOT (potential evapotranspiration; Fig. 13b) is an estimate of how much moisture is lost to the atmosphere as the result of the combined action of passive evaporation and plant transpiration. DFTEMP (Fig. 14a) measures the coldness of the spring season (Elías-Castillo and Ruiz-Beltrán, 1986); the higher the value of DFTEMP the colder the spring season. REGHUM (Fig. 14b) denotes the length of the arid period. EXPREC (Fig. 15a) is a calculated measurement of how much moisture remains available after evapotranspiration. In contrast, DEFPREC (Fig. 15b) represents the water deficit when evapotranspiration exceeds precipitation.

The five bioclimatic zones described for the study area (Fig. 16a), i.e., subalpine, montane, submontane, supra-Mediterranean and
Figure 11. Maps showing the annual (A) and July (B) isotherms.
Figure 12. Maps showing the dates for the last frost of spring (A) and the duration of the frost-free period (B) in the study area.
DATE OF LAST FROST OF SPRING

<table>
<thead>
<tr>
<th>Date Range</th>
<th>0</th>
<th>20</th>
<th>40</th>
<th>60</th>
</tr>
</thead>
<tbody>
<tr>
<td>4/01 - 4/20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4/20 - 5/10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5/10 - 6/01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6/01 - 6/20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>After 6/20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

LENGTH OF FROST-FREE PERIOD

- 60 - 100 days
- 100 - 140 days
- 140 - 180 days
- > 180 days

A

B
Figure 13. Mean annual precipitation (A) and mean annual potential evapotranspiration (B).
Figure 14. Map depicting the date after which the probability of reaching a temperature $\leq 2^\circ$C is 50% (A). This variable measures the coldness of the spring season. (B) Humidity regimes (length in months of the arid period) of the study area. HU = Humid, without an arid period. Me = Humid Mediterranean, with an arid period of 1-2 months. ME = dry Mediterranean, with an arid period of 2-5 months.
DATE AFTER WHICH THE LIKELIHOOD OF REACHING FREEZING TEMPERATURES IS FIFTY PERCENT

A

B

HUMIDITY REGIMES

Before 3/01
3/01 - 3/20
3/20 - 4/10
4/10 - 5/01
After 5/01

HU
Me
ME

0 20 40 60Km
Figure 15. Maps depicting the annual mean excess (A) and the annual mean deficit (B) of precipitation in the study area.
ANNUAL MEAN EXCESS OF PRECIPITATION (mm)

ANNUAL MEAN DEFICIT OF PRECIPITATION (mm)
Figure 16. Bioclimatic zones described for the study area (A) and drainage system (B). Bioclimatic zones reflect the phenomenon of altitudinal and latitudinal thermic zonation (Rivas-Martinez, 1987).
BIOCLIMATIC ZONES

EURASIAN ZONES
- Subalpine
- Montane
- Submontane

MEDITERRANEAN ZONES
- Supramediterranean
- Mesomediterranean

DRAINAGE SYSTEM

A 0 20 40 60 Km

B
meso-Mediterranean, were coded by using a thermicity index, $It$, proposed by Rivas-Martinez (1987):

$$It = (T + m + M) \times 10$$

where $T$ is annual mean temperature, $m$ and $M$ are, respectively, the mean of the coldest month's minimum and maximum temperatures. It is essentially an estimate of seasonal and altitudinal coldness used to characterize the phenomenon of thermic zonation.

The bioclimatic zones were practically delineated in relation to changes in plant communities which present evident correlations with thermoclimatic intervals (see Rivas-Martinez, 1987 for the correspondence between latitudinal and altitudinal thermic intervals and plant communities in the study area). The Bioclimatic Zones layer (Figure 16a) was overlaid onto the base map to create the variable BIOCLIM from the area-adjusted average of each geographic unit.

For map overlay, the Drainage System coverage (see Figure 16b) was converted into a polygon coverage named Hydrology by generating a 350-m buffer around rivers and streams. By overlaying the Hydrology coverage onto the base map, the variable HDR350 is obtained as the ratio of the polygon surface covered by the river buffer within each geographic unit.
The climatic variable \( \text{CONT} \) (Fig. 17a) was created by assigning to each geographic unit a single value for the Gorezynski's continentality Index (Font-Tullot, 1983b):

\[
K = 1.7 \, \frac{A}{\sin \theta} - 20.4
\]

where \( A \) is the annual mean amplitude in temperature (difference between the mean temperatures of January and July) corresponding to each geographic unit, and \( \Theta \) is the latitude. This variable is a measurement of the seasonal thermic contrast, corrected for latitude (Font-Tullot, 1983b).

The overlay of the base map with the land use layer allowed the creation of the two vegetation variables, \( \text{CULT} \) and \( H_{\text{veg}} \). \( \text{CULT} \) (see Fig. 6) represents the percentage of each geographic unit covered by cultivated land. \( H_{\text{veg}} \) (Fig. 17b) is a Shannon-Weaver diversity index based on the number and relative abundance of the various vegetation types occurring within each geographic unit (see Miller, 1986 for a description of the methodology to calculate \( H_{\text{veg}} \)).
Figure 17. Distribution over the study area of Gorezynsky's K index of continentality (A) and vegetation diversity (B).
The Analytic Approach

General Introduction

Spatial statistics used in map pattern analysis provide the tools to understand species distributions within their spatial context. The simplest, but fundamental, hypothesis about any map pattern is that the observations represented on the map are totally unrelated, i.e., they are randomly distributed. Theoretically, a random spatial pattern arises from a \textit{homogeneous planar Poisson process} (HPP), mathematically described by the Poisson probability distribution (Boots and Getis, 1988), and in which the distribution of nesting localities are generated subject to two conditions:

1. Uniformity: the study area is completely homogeneous in all regards, i.e., each geographic unit in the study area has equal chance of being a breeding site.
2. Independence: there is no interaction among breeding sites, i.e., the selection of a breeding site in no way influences the selection of any other location as a breeding sites.

The pattern originated by a HPP process, known as Complete Spatial Randomness (CSR; Diggle, 1983), is equivalent to that which would arise by chance in a completely undifferentiated environment (Fig. 18a). CSR is unlikely to occur in real-world situations, but it is useful as a "benchmark" pattern against which other classes of patterns may be identified. Thus, in \textit{clustered patterns} (Fig. 18b) the breeding sites of a species are considerably
Figure 18. Hypothetical cases illustrating Complete Spatial Randomness (A), clustered (B) and regular or uniform patterns (C).
COMPLETE SPATIAL RANDOMNESS  CLUSTERED PATTERN  REGULAR PATTERN
more grouped than under CSR. In contrast, a regular or uniform pattern (Fig. 18c) would exhibit more dispersion than CSR.

Of great interest to the geographical ecologist is discovering how non-randomness arises in map patterns by attempting to model the processes that give rise to these patterns. Inductive spatial modelling is precisely a method of systematically identifying relationships between spatial objects by "learning" from particular instances (Wheeler, 1988; Walker and Moore, 1988). This modelling task consists basically of testing hypotheses in which either one or both assumptions of the HPP process are changed. The starting point in developing those relationships is the geographic information system. It contains topological information (i.e., the spatial arrangement of the different map entities with respect to each other) and also data describing patterns (i.e., the avian distributions) and location attributes (i.e., the environmental layers).

A major way of changing the uniformity condition is to take into consideration the environmental heterogeneity of the study area. This implies that some locations will be less likely to be breeding areas than other localities, or might even be prohibited from being so. It is expected to find more breeding sites in the favored environmental parts of the study area than elsewhere, thereby generating a clustered pattern.

One way of relaxing the independence assumption is to permit interaction among nesting sites. Spatial interaction would imply that events
or circumstances at one locality can influence conditions at other localities if the localities interact, e.g. they share a common boundary. Moreover, spatial effects among places usually vary with distance in systematic ways (Odland, 1988). By virtue of their spatial interactions, breeding localities may attract or repulse one another, implying that the location of a breeding area influences the location of other breeding areas. Attraction may result from processes such as agglomeration, association, segregation and diffusion (Okubo, 1986). In each case the result is a clustered pattern. In some circumstances, such as competition, repulsion among points will produce regular or uniform patterns.

In the two sections that follow are described the statistical techniques (1) used to test the null hypothesis that the breeding distributions studied respond to a CSR resulting from a HPP process and (2) involved in the modelling of the processes behind non-random patterns.

**Spatial Autocorrelation Analysis**

Spatial autocorrelation analysis, a method for summarizing geographic variation patterns, was used to test the null hypothesis that the avian breeding distributions studied in this research correspond to a random (CSR) model. In relation to breeding distributions, spatial autocorrelation exists if a breeding occurrence for a species in a particular location makes another breeding occurrence for the same species in neighboring locations more or
less likely (see Cliff and Ord, 1973). Formally, spatial autocorrelation statistics assess whether the observed value of a variable at one place is independent of values at neighboring places (Sokal and Oden, 1978b).

Although the concept of spatial autocorrelation (hereafter, SA) is not new to biologists, its formal treatment was undertaken by analytical geographers (Cliff and Ord, 1973; 1981). Some time ago, Sokal and Oden (1978a, b) presented an explicit application of the effects of SA to evolutionary biology and ecology. Since this key contribution, application of SA in biological studies has been significant (e.g., Sakai and Oden, 1983; Framstad, 1985; Malanson, 1985; Jensen, 1986; Sokal et al., 1987; Sokal et al., 1989; Fortin et al., 1989).

SA statistics do not possess the inherent limitation of conventional techniques of map pattern analysis (e.g., Grieg-Smith, 1964), i.e., insensitivity to the spatial arrangement of the observations. Conventional techniques (such as quadrat analysis) use frequencies to summarize map patterns. The loss of the spatial dimension in quadrat analysis (Dacey, 1966) is illustrated by the fact that quite different patterns when summarized by quadrats may be reduced to the same set of frequencies, with the result that the analysis performed on them yields identical results (Boots and Getis, 1988).

Although SA statistics are functions of the same data that are used to calculate other descriptive statistics (such as the mean or variance), they are
also functions of the arrangement of those values in a sequence. Spatial arrangement in SA is expressed by a function that assigns values to pairs of observations in order to symbolize their location with respect to one another (Odland, 1988).

In this study Moran’s I coefficient (Moran 1947, 1948, 1950) was selected to test the degree to which avian breeding distributions in the study area were spatially autocorrelated:

\[
I = \frac{N}{\sum \sum W_{ij} (X_i - \overline{X}) (X_j - \overline{X})} \sum \sum W_{ij} \frac{N}{\sum (X_j - \overline{X})^2}
\]  

(1)

where \(N\) is the number of geographic units in the base map (152 in this study); \(X_i\) and \(X_j\) are the abbreviations of the binary variable \(\text{SPEC}_i\) for the pair of observations, which equal 1 if the \(ith\) or \(jth\), respectively, geographic unit was a breeding area for the species being examined and 0 otherwise; \(\overline{X}\) is the mean; \(W_{ij}\) is a code of spatial contiguity, which equals 1 if the \(ith\) and the \(jth\) polygons share a common boundary.

Moran’s I is essentially a ratio of the covariance to the variance of the observations in space. It lies between -1 and + 1, and can be interpreted as indicating negative or positive autocorrelation in the same way as a correlation coefficient. The difference between the observed and expected values of I was evaluated by a normally distributed statistic, \(z\), such that
where the mean or expected value of Moran's I is (for formula of variance see Odland, 1988):

\[ E(I) = - \frac{1}{(N - 1)} \]  

where \( N \) is the number of geographic units (\( N = 152 \) in this study). \( E(I) \) approaches to zero as the number of geographic units approaches infinity. The procedure for deriving Moran's I and related statistics for significance testing in a geographic information system can be found in Chou (1989 and 1990).

**Spatial Weighting Functions**

Sokal and Oden (1978a,b) proposed that spatial autocorrelation could be caused by the spatial structure of the habitat but did not address purely spatial effects. However, the objective of geographical ecology is to understand biological phenomena within their spatial context. Thus, it is pertinent for a statistical investigation to include both variable relationships and spatial relationships (Odland, 1988).
Neighborhood effects is an evident spatial factor which may affect avian distributions because the expansion of a breeding range can be thought of as a contagious diffusion (Bliss, 1971; Okubo, 1980, 1988). An approach suggested by Malanson (1985; see also Odland, 1988) to incorporate spatial factors into explanatory hypotheses is to fit a regression model with a spatial weighting function or connectivity between sites and a function of dispersal (diffusion). The specification of the latter requires further study (Murray, 1989; Van den Bosch et al., 1992) and is not considered in this research. Adjacency was selected as the indicator of "neighborhood effects" given the characteristics of the data (conformed to a grid) used in this study. Since a grid is characterized by constant distance, size and border length between adjacent geographic units, problems of topological invariance with a spatial weight defined by contiguity alone are not encountered (Dacey, 1968; see also Chou, 1989 and Chou et al., 1990).

A contiguity weight was translated into a code defined as the spatial weighting function, SWF (Chou et al., 1990):

\[
SWF = \frac{\sum_{ij} W_{ij} x_j}{\sum_j W_{ij}}
\]  

(4)
where SWF is the ratio of neighboring grid cells (geographic units) in which a particular species was found to breed to the total number of neighboring grid cells \( W_{ij} \) and \( X_i \) represent the same identities as in equation 1). Thus, for example, if the \( ith \) geographic unit in the study area shares common boundaries with four adjacent polygons and a particular species was found to nest in two of the adjacent grid cells, \( SWF_i = 0.5 \). By definition SWF takes on values between 0 and 1. For a particular species, a higher SWF denotes a greater propensity for the \( ith \) geographic unit to be a breeding area.

**Probabilistic Models of Avian Breeding Distributions**

Since the breeding distributions are expressed as dichotomous variables, the typical multiple regression model was inappropriate for two reasons. First, the assumptions for hypothesis testing in regression analysis are violated for qualitative dependent variables. The distribution of errors will be described by the binomial distribution, whereas the analysis is based on the normal distribution (Hosmer and Lemeshow, 1989). Second, predicted values in multiple regression analysis are not constrained within the interval 0 to 1 (Aldrich and Nelson, 1984).

Multivariate analysis of categorical data can be adequately performed by using logit modelling techniques (Aldrich and Nelson, 1984). Logit analysis provides an interpretable linear model for a categorical dependent
variable and has the advantage that model assumptions are less stringent than those for non-logit techniques (e.g., Klecka, 1980). The logit model is similar to the linear regression model or the general linear model for ANOVA, except that the response is the log odds (i.e., the natural logarithm of the relative probability of belonging to one of two possible categories on a variable of interest) instead of a metric dependent variable.

In relation to the distributions here analyzed, it was of more interest to determine not the marginal, or unconditional, odds of occurrence for the population as a whole, but rather the conditional odds of breeding occurrence, given other characteristics (Demaris, 1992). A special case of the logit model, known as logistic regression (Hosmer and Lemeshow, 1989; Demaris, 1990, 1992), is used when the conditional log odds of a particular event is expressed as a linear function of a set of continuous predictors. Logistic regression (LR, hereafter) was selected for constructing the models for the probability of breeding occurrence.

Structure of Logistic Regression

The logistic model specifies a functional relationship between a binary dependent variable and either interval, ratio or categorical variables such that

\[ P(b)_i = \frac{\exp(U_i)}{1 + \exp(U_i)} \]  \hspace{1cm} (5)
where \( P(b) \) is the probability for a given species to breed in the \( i \)th geographic unit. The probability is a function of \( U_i \), which is specified in each model as a linear combination of input variables or attributes. A greater \( U_i \) denotes a higher probability for a geographic unit to constitute a breeding area.

The probabilistic nature of the LR model guarantees that the breeding probability for each geographic unit takes on values between 0 and 1. As \( U \) approaches positive infinity, the probability approaches 1. Likewise, as \( U \) approaches negative infinity, the probability decreases to 0. The quantity \( U \) is defined as:

\[
U_i = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \ldots + \beta_k X_k + e
\]  

(6)

where \( k \) is the total number of explanatory variables, and \( \beta_k \) is the coefficient for the \( k \)th variable to be estimated and \( e \) is the random error term.

The Model-Building Process

Explanatory models needed to be sufficiently flexible to incorporate any meaningful variable (Chou, 1991). At the same time, consideration was given to the costliness of the explanatory models. The inclusion of many variables results in cumbersome models, making their calibration --i.e., the process of giving values to the terms which appear on the model equation--
too costly. Parsimonious models should achieve a high level of accuracy while using a few critical variables.

Following the suggestion of Chou (1990) several alternative models were developed. A description of detailed operational procedures for model building in a geographic information system is provided in Chou (1991). Coefficients of the parameters were estimated from the stepwise logistic regression program available in the BMDP statistical package (BMDP P-series, 1987). During the building of each model, a $\chi^2$ test identified those variables which were statistically significant to the explanation of the breeding distributions. This model-building strategy was implemented in the four steps described below.

First, a model incorporating exclusively climatic variables was built for each species (climatic variables, described above, are listed in Table 5). All climatic parameters available in the NGD were incorporated without restriction.

Second, Study Model I was built for each species by incorporating (1) climatic factors which were statistically significant in the climatic models; (2) CONT (Gorezynski's K index of continentality; Table 5), based on the suggestion that continentality is an important factor for avian distributions in eastern Navarre (Bustamante et al., 1988); and (3) non-climatic environmental variables, i.e., ALT (altitude), HDR350 (distance to rivers), CULT (cultivated land) and $H_{\text{veg}}$ (vegetation diversity index).
Third, Study Model II was built which simply added the spatial term, SWF, to the explanatory variables retained in Study Model I. Fourth, Study Model III was a simplified version of Study Model II which specified SWF and those environmental factors which were statistically significant in Study Model II.

**Model Comparisons**

A $\chi^2$ test comparing the likelihood measures of the models was used in answering the question of whether or not Study Model II was improved by the inclusion of the spatial term (SWF):

$$C = -2 \Lambda = -2 \left( \ln L_0 / \ln L_1 \right) \approx \chi^2$$  \hspace{1cm} (7)

where $L_0$ and $L_1$ represent the likelihood measures of the simplified and the fully specified models, respectively. The log likelihood measure indicates how likely a model makes that an observed distribution pattern would have occurred. If $P(b)_i$ is the breeding probability of the $i$th geographic unit (see equation 5), then for $n$ independent, binary observations $Y_i, i = 1, 2, ..., n,$ and whether the outcome $Y_i$ be 1 (breeding) or 0 (non-breeding), the log likelihood function, $\log L,$ comes defined as (Aldrich and Nelson, 1984):

$$\log L = \sum_{i=1}^{n} n[Y_i \log P(b)_i + (1 - Y_i) \log (1 - P(b)_i)]$$  \hspace{1cm} (8)
Statistically significant differences among the models indicated by a large C statistic were further assessed by evaluating variation patterns in their forecasting accuracy.

For each species, the difference between the Climatic Model and Study Model I, and between Study Model II and Study Model III, was also examined. Since great structural differences (i.e., type and/or number of variables included) existed among the models, the C statistic was not suited for this type of comparison, and a \( \chi^2 \) statistic comparing predictive efficacies was used instead. Basically, the predictive efficacy of a model reflects its ability to assign high breeding probabilities to the breeding group (i.e., geographic units where the species was observed) and low breeding probabilities to the nonbreeding one (i.e., geographic units where the species was absent). Six probability intervals were defined (0.0–0.17, 0.17–0.33, 0.33–0.50, 0.50–0.67, 0.67–0.83, 0.83–1.0) for both the breeding and nonbreeding groups. Frequencies of geographic units assigned by each compared model to each probability interval were used for statistical comparison purposes. Thus, two \( \chi^2 \) statistics were generated, a first one for the breeding group comparison and a second one for the nonbreeding group comparison. Statistically significant differences indicated by large \( \chi^2 \) statistics for the Climatic-Model I and/or Model II-III comparisons were pondered by examining variation patterns in their forecasting accuracy.
The forecasting accuracy of a model is sensitive to the cut-off probability ("cutpoint") assumed to indicate breeding occurrence or absence (breeding probabilities above the cutpoint are classified as breeding whereas those below it are classified as nonbreeding), being higher for middle cutpoints than for either low or high cutpoints. This implies that the improvement of a model may be barely noticeable for middle points but may be significant for low and/or very high cutpoints. Therefore, the impact of differences among models were examined across cutpoints (i.e., 0.0 to 1.0). The issue of the relation between predictive ability and cutpoints is further discussed in the following section.

Model Testing

Four outcomes are possible in dichotomous classification. In this study, geographic units were classified as follows: (1) those where the presence of the species was both observed and predicted, (2) those where the absence of the species was both observed and predicted, (3) those where the presence of the species was observed but not predicted and (4) those where the absence of the species was observed but not predicted. The accuracy of the models in replicating the real distributions can be assessed by comparing the breeding probability function \( P(b) \) with the observed distributions. A model should ideally allocate all of the predictions into groups 1 and 2.
The Percentage of Correct Estimation (PCE), used as an approximation of overall forecasting accuracy, was calculated for each model as:

\[ \text{PCE} = \frac{\text{TCP}}{\text{TCP} + \text{TIP}} \]

where TCP is the total number of correct predictions for both the breeding and nonbreeding groups, whereas TIP is the total number of incorrect predictions for both groups. A PCE = 0.50 indicates that a model can at best forecast accurately 50 percent of a given distribution pattern. Obviously, PCE index values of or near 0.50 are unsatisfactory because they are only slightly better than a random guess.

The magnitude of the PCE index varies with the cutpoint assumed to indicate breeding occurrence or absence. For the same cutpoint, the better the model, the higher the PCE index. The PCE index reported for each species corresponded to the highest one obtained across cutpoints, indicating the maximum level of forecasting accuracy for each model. A drawback of the PCE index is that separate comparisons of observed breeding occurrences and absences with their respective estimated probabilities, \( P(b) \), are not possible. However, these types of comparisons may be of higher interest than just knowing the overall accuracy of the models, especially if the consequences of misclassifying a presence are graver than those of misclassifying an absence.
As the cutpoint is decreased, the ability of a model to accurately predict a breeding occurrence increases as the capability to accurately predict an absence decreases, whereas if the cutpoint is increased the situation is reversed. However, the success of predicting either the breeding occurrence or absence of a particular species depends only on the number of breeding and nonbreeding observations when using the PCE index (Walker and Moore, 1988; Walker, 1990). Thus, the PCE index gives only an overall measure of correct estimations, without revealing the proportion of correct predictions corresponding to the breeding and nonbreeding groups. To evaluate their relative contribution to the PCE index, the sensitivity, specificity and predictive value of the effective models were also examined.

Sensitivity (Sens) is the probability that an actual breeding locality will be classified correctly whereas specificity (Spec) is the probability that an actual nonbreeding locality will be classified as "nonbreeding" (Ahlbom and Norell, 1990):

\[
Sens = \frac{CPB}{CPB + ICB}
\]

\[
Spec = \frac{CPNB}{CPNB + ICNB}
\]

where CPB and CPNB are the number of correct predictions for the groups breeding and non-breeding, respectively. ICB and ICNB are the number of incorrect predictions incurred for the same groups.
Predictive value (PV), which is a practical application of Bayes’ theorem, refers formally to the probability for a geographic unit, among those classified in the group breeding, to actually constitute a breeding site. In other words, PV represents the proportion of the predicted breeding occurrences which are really so:

\[
PV = \frac{Sens \times I}{(Sens \times I) + [(1 - Spec) \times (1 - I)]}
\]

\[
I = \frac{R}{N}
\]

where I is incidence (i.e., the proportion of geographic units in the sample where a given species breeds), R is the number of breeding records and N the sample size or number of geographic units (N = 152 in this study). The predictive value of a model will be low when the number of breeding records is low, even for high values of sensitivity and specificity. As with sensitivity, the predictive value varies with the cutpoint but in the opposite direction. While sensitivity increases by lowering the cutpoint, the predictive value of a model increases by raising it.

Study Model III was used to estimate the probability of breeding occurrence for each geographic unit. Based on these probability values, all
geographic units were classified into four categories of breeding probability: low (0-30%), medium (30-60%), high (60-90%) and very high (> 90%). To facilitate the visualization of the comparison between the predicted and the observed breeding distributions, individual maps were made to represent the spatial distribution of the predicted breeding probabilities over the study area. These maps were then overlaid onto the maps depicting the observed breeding distributions.
IV. RESULTS

Spatial Autocorrelation

The nine breeding distributions studied generated positive Moran’s I coefficients (Table 6), ranging from $I = 0.367$ (Pernis apivorus) to $I = 0.792$ (Pterocles orientalis). All I coefficients were much greater than their expected values (P-value < 0.0001 in all nine instances), indicating highly significant clumping or aggregation of the breeding sites.

The breeding distributions of the six passerine species (Table 2) generated higher I coefficients than those of the two raptor species (Pernis apivorus and Falco subbuteo), but it was the distribution of Pterocles orientalis (Black-bellied Sandgrouse), a non-passerine, which produced the highest I coefficient ($I = 0.792$). Melanocorypha calandra exhibited the largest I coefficient ($I = 0.784$) among the passerines and the second largest among the nine species. Although taxonomically distant, Pterocles orientalis (Columbiformes) and Melanocorypha calandra (Passeriformes) have ecological affinities as open-habitat species and share similar nesting behaviors and granivorous diets.

The distributions of small-sized, gregarious species exhibited higher Moran’s I values than those of the large-sized, solitary species (i.e., the two raptors, Falco subbuteo and Pernis apivorus).

When habitat preferences (see Appendix I) were taken into account, open-space species (Pterocles orientalis and Melanocorypha calandra) had
Table 6. Spatial autocorrelation statistics. The value $Z$ in the third column is a normal deviate ($Z = 1.645$ at the $\alpha = 0.05$ significance level).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>MORAN'S $I$</th>
<th>$Z$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pterocles orientalis</em></td>
<td>0.792</td>
<td>12.857*</td>
</tr>
<tr>
<td><em>Melanocorypha calandra</em></td>
<td>0.784</td>
<td>12.703*</td>
</tr>
<tr>
<td><em>Pyrrhula pyrrhula</em></td>
<td>0.735</td>
<td>11.899*</td>
</tr>
<tr>
<td><em>Sitta europaea</em></td>
<td>0.722</td>
<td>11.702*</td>
</tr>
<tr>
<td><em>Serinus citrinella</em></td>
<td>0.647</td>
<td>10.557*</td>
</tr>
<tr>
<td><em>Ficedula hypoleuca</em></td>
<td>0.563</td>
<td>9.271*</td>
</tr>
<tr>
<td><em>Lullula arborea</em></td>
<td>0.521</td>
<td>8.469*</td>
</tr>
<tr>
<td><em>Falco subbuteo</em></td>
<td>0.501</td>
<td>8.145*</td>
</tr>
<tr>
<td><em>Pernis apivorus</em></td>
<td>0.367</td>
<td>6.021*</td>
</tr>
</tbody>
</table>

*p < 0.0001
the highest values of Moran’s I, followed by forest species (*Phyrrula pyrrhula, Sitta europaea, Serinus citrinella* and *Ficedula hypoleuca*) then by species which prefer semi-open forest habitats (*Lullula arborea, Falco subbuteo* and *Pernis apivorus*).

**Logistic Regression**

**The Climatic Models**

In general, the Climatic models produced large PCE indices (see 2nd column in Tables 7-15), indicating high levels of forecasting accuracy. The Climatic Model for *Falco subbuteo* generated the lowest PCE index (PCE = 0.78), those for *Pernis apivorus, Lullula arborea* and *Ficedula hypoleuca* produced PCE indices ≥ 0.86, whereas those for the remaining five species exhibited higher ones (PCE ≥ 0.90). The climatic model for *Pterocles orientalis* generated the highest level of forecasting accuracy, with PCE = 0.94.

The leading explanatory climatic variables were REGHUM (length of arid period), FRSTFREE (length of frost-free period) and BIOCLIM (seasonal and altitudinal coldness). REGHUM was statistically significant at $\alpha = 0.1$ for six species, while FRSTFREE and BIOCLIM each were in four instances. HTEMP (summer mean temperature), PREC (annual mean precipitation), EVTPOT (potential evapotranspiration) and CONT (continentality index) were each statistically significant at the $\alpha = 0.1$ for two species, while SFROST
(last frost of spring), DFTEMP (coldness of the spring season) and EXPREC (annual precipitation surplus) only for one.

The Study Models

For each species, I will deal with the following issues: How much did the addition of non-climatic factors improve Study Model I? 2) Did the inclusion of the spatial term improve Study Model II? 3) How was Study Model III (the effective model) affected by the elimination of nonsignificant variables?

*Pernis apivorus*

Coefficients and statistics corresponding to the study models for *Pernis apivorus* can be found in Table 7. The inclusion of non-climatic variables improved the predictive efficacy of Study Model I for the nonbreeding group but not that for the breeding group (see Table 16). This improvement, however, was not translated into large differences in overall forecasting accuracy, sensitivity or specificity (see Figures 19 and 20).

There was no significant difference between Model I and Model II as denoted by a small $C$ statistic (see Table 16). Inclusion of SWF did not improve Model II relative to Model I, as shown by (1) little change in the log likelihood function and (2) the fact that forecasting accuracy of Model II remained the same as in Model I (PCE = 0.87).
Table 7. *Pernis apivorus*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM</td>
<td>- 0.8069*</td>
<td>- 0.8417**</td>
<td>- 0.8345**</td>
<td>- 0.7733**</td>
</tr>
<tr>
<td>TEMP</td>
<td>- 0.0848</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HTEMP</td>
<td>0.7898</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SFROST</td>
<td>- 0.0044</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DFTEMP</td>
<td>- 0.0613</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>- 0.0215</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DEFPREC</td>
<td>0.0015</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>- 0.0066</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PREC</td>
<td>0.0022</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EVTPOT</td>
<td>- 0.0343***</td>
<td>- 0.0170†</td>
<td>- 0.0169†</td>
<td>- 0.0140†</td>
</tr>
<tr>
<td>EXPREC</td>
<td>- 0.0052**</td>
<td>- 0.0057‡</td>
<td>- 0.0057‡</td>
<td>- 0.0060‡</td>
</tr>
<tr>
<td>CONT</td>
<td>0.0743</td>
<td>0.1216</td>
<td>0.1210</td>
<td></td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>- 0.0003</td>
<td>- 0.0003</td>
<td></td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>- 0.7093</td>
<td>- 0.7088</td>
<td></td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>2.987**</td>
<td>2.968**</td>
<td>3.507†</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>0.0112</td>
<td>0.0112</td>
<td></td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td></td>
<td>0.0670</td>
<td>0.1208</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>19.47**</td>
<td>14.46***</td>
<td>14.36‡</td>
<td>13.77‡</td>
</tr>
<tr>
<td>LOG LIKELIHOOD</td>
<td>- 50.562</td>
<td>- 49.975</td>
<td>- 49.974</td>
<td>- 51.088</td>
</tr>
<tr>
<td>PCE</td>
<td>0.85</td>
<td>0.87</td>
<td>0.87</td>
<td>0.87</td>
</tr>
</tbody>
</table>

*P < 0.1; **P < 0.05; ***P < 0.01; †P < 0.001; ‡P < 0.0001
Figure 19. Plot comparing the overall forecasting accuracy of the Climatic Model and Study Model I for *Pernis apivorus*.

Figure 20. Plot comparing the sensitivities and specificities of the Climatic Model and Study Models I as a function of the cutpoint for *Pernis apivorus*. 
SWF did not reach statistical significance ($\alpha = 0.10$) in Model II, nor in Model III and was outperformed by EVTPOT, EXPREC, REGHUM and $H_{veg}$. The latter variables exhibited the highest levels of significance ($P < 0.05$ in all cases) across all study models. The overall forecasting accuracy ($PCE = 0.87$) remained the same even for Model III in which only four variables were specified.

Elimination of four variables (see Table 7) did not reduce significantly the predictive efficacy of Study Model III, relative to Study Model II, for either the breeding nor the nonbreeding group (see Table 16). Model III was used to predict the breeding distribution of *Pernis apivorus* (Fig. 21) according to the following equation:

$$U_i = 13.77 - 0.7733 \text{REGHUM}_i - 0.014 \text{EVTPOT}_i - 0.006 \text{EXPREC}_i + 3.507 H_{veg} + 0.1208 \text{SWF}_i$$

*Falco subbuteo*

The coefficients and statistics of the different models built for *Falco subbuteo* are in Table 8. Inclusion of non-climatic variables into Model I improved its predictive efficacy, relative the Climatic Model, for both the breeding and nonbreeding groups as indicated by the high significance of the $\chi^2$ statistic (see Table 16). This improvement was reflected in a considerably higher overall forecasting accuracy for cutpoints between 0.3 and 0.4 (Fig. 22), which corresponded to the largest improvement (17%, for
Figure 21. Breeding (A) and predicted (B) distributions of the European Honey-Buzzard (*Pernis apivorus*).
EUROPEAN HONEY-BUZZARD

*(Pernis apivorus)*

Breeding

Absent

A

B

0 20 40 60Km

> 0.9

0.6 - 0.9

0.3 - 0.6

< 0.3
Table 8. *Falco subbuteo*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM</td>
<td>-0.1724</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>TEMP</td>
<td>0.1270</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>HTEMP</td>
<td>-0.1190</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SFROST</td>
<td>0.0153</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DFTEMP</td>
<td>0.0344</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>0.0547*</td>
<td>-0.0080</td>
<td>-0.0142</td>
<td>-</td>
</tr>
<tr>
<td>DEFPREC</td>
<td>0.0066</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>-0.0030</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PREC</td>
<td>0.0002</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EVTPOT</td>
<td>-0.0095</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EXPREC</td>
<td>-0.0021</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CONT</td>
<td>0.1766</td>
<td>0.1713**</td>
<td>0.0578</td>
<td>-</td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>-0.0011</td>
<td>-0.0019</td>
<td>-</td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>3.900***</td>
<td>3.109*</td>
<td>3.041**</td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>2.7390**</td>
<td>2.711**</td>
<td>2.571**</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>-0.0468***</td>
<td>-0.0302</td>
<td>-</td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td>-</td>
<td>3.846†</td>
<td>4.263†</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>-4.508</td>
<td>-3.127</td>
<td>-1.445</td>
<td>4.832†</td>
</tr>
<tr>
<td>LOG LIKELIHOOD</td>
<td>-77.515</td>
<td>-75.051</td>
<td>-61.327</td>
<td>-63.566</td>
</tr>
<tr>
<td>PCE</td>
<td>0.78</td>
<td>0.80</td>
<td>0.83</td>
<td>0.82</td>
</tr>
</tbody>
</table>

*P < 0.05; **P < 0.01; ***P < 0.001; †P < 0.0001
Figure 22. Plot comparing the overall forecasting accuracy of the Climatic Model and Study Model I for *Falco subbuteo*.

Figure 23. Plot comparing the sensitivities and specificities of the Climatic Model and Study models I for *Falco subbuteo*. 
cutpoint = 0.4) in specificity (Fig. 23). Sensitivity was slightly higher for low (0.0-0.3) and significantly better for high cutpoints (0.6-0.9), with the largest difference (15%) observed at cutpoint 0.7.

Comparison of Models I and II generated a large $C$ statistic (see Table 16). The highly significant outcome ($P < 0.001$) of this test indicated the considerable improvement of Model II over Model I which translated into a higher overall forecasting accuracy (from $PCE = 0.80$ for Model I to $PCE = 0.83$ for Model II). Fig. 24 shows how the overall forecasting accuracy of Model II was higher than that of Model I across the whole range of cutpoints. This difference was particularly great for cutpoints above 0.4. The reason for this increase in the overall forecasting accuracy of Model II, relative to Model I can be ascertained by examining Fig. 25. While the specificity of Model II remained at or above that of Model I across the range of cutpoints, its sensitivity was lower for cutpoints below 0.4 but higher for cutpoints above 0.4. For cutpoints higher than 0.4 the increase in sensitivity of Model II was particularly great. This indicates that the increase in the overall forecasting ability of Model II at higher cutpoints was mainly due to the increase in its sensitivity than to the increase of its specificity. SWF improved more the capacity of Model II to correctly predict the breeding occurrences of *Falco subbuteo* than that to correctly predict its
Figure 24. Plot comparing the overall forecasting accuracy of study models I and II for *Falco subbuteo*.

Figure 25. Plot comparing the sensitivities and specificities of study models I and II for *Falco subbuteo*. 
absence. This effect was particularly remarkable at high cutpoint values, precisely where the sensitivity of a model is the lowest.

Significance tests for individual variables clearly suggest that SWF was the most important variable in both Model II and Model III (P < .0001 in both cases). The exceptionally high significance of SWF reduced the statistical significance of other variables in Model II. Only $H_{\text{veg}}$ maintained its significance in Model II in relation to Model I. In Model III SWF also outperformed the other two variables, i.e., CULT and $H_{\text{veg}}$, by a great margin (Table 8, 3rd column).

Comparison of Models II and III did not generate a significant $\chi^2$ statistic indicating that the elimination of four nonsignificant variables in Model III did not affect its predictive efficacy. The PCE index of Model III, relative to Model II, decreased only from 0.83 to 0.82 (Table 8).

The predicted breeding distribution in Fig. 26 was obtained by calibrating Study Model III:

$$U_i = 4.832 + 3.041 \text{CULT}_i + 2.571 H_{\text{veg}}, + 4.263 \text{SWF}_i$$

*Pterocles orientalis*

Table 9 shows the coefficients and statistics of the models built for *Pterocles orientalis*. All three comparisons, i.e., Climatic/Model I and Model I/Model II and Model II/Model III generated nonsignificant ($\alpha = 0.05$) $\chi^2$ statistics (see Table 16). This indicated that (1) the addition of non-climatic
Figure 26. Breeding (A) and predicted (B) distributions of the Eurasian Hobby (*Falco subbuteo*).
EURASIAN HOBBY
(Falco subbuteo)

Breeding
Absent

0.6 - 0.9
0.3 - 0.6
< 0.3
Table 9. *Pterocles orientalis*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM</td>
<td>1.239*</td>
<td>0.4717</td>
<td>0.4818</td>
<td>-</td>
</tr>
<tr>
<td>TEMP</td>
<td>1.366</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>HTEMP</td>
<td>5.8970**</td>
<td>11.28†</td>
<td>10.77†</td>
<td>6.8220†</td>
</tr>
<tr>
<td>SFROST</td>
<td>0.5721**</td>
<td>0.4815***</td>
<td>0.4682***</td>
<td>0.4147***</td>
</tr>
<tr>
<td>DFTEMP</td>
<td>-0.2478</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>0.1441</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DEFPREC</td>
<td>0.0557*</td>
<td>0.0171</td>
<td>0.0125</td>
<td>-</td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>0.0064</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PREC</td>
<td>0.0156*</td>
<td>0.0072</td>
<td>0.0069</td>
<td>-</td>
</tr>
<tr>
<td>EVTPOT</td>
<td>-0.0399**</td>
<td>0.0230</td>
<td>0.0223</td>
<td>-</td>
</tr>
<tr>
<td>EXPREC</td>
<td>-0.0117</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CONT</td>
<td>-0.4335</td>
<td>-1.354**</td>
<td>-1.3010*</td>
<td>-0.8312</td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>0.0010</td>
<td>0.0001</td>
<td>-</td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>13.260†</td>
<td>12.970†</td>
<td>8.9210†</td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>-1.2480</td>
<td>-1.4020</td>
<td>-</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>-0.0762*</td>
<td>-0.0659</td>
<td>-</td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td>-</td>
<td>1.0560</td>
<td>2.1120</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>-162.3**</td>
<td>-217.8†</td>
<td>-207.7†</td>
<td>-143.1†</td>
</tr>
<tr>
<td>LOG LIKELIHOOD</td>
<td>-23.512</td>
<td>-12.925</td>
<td>-12.834</td>
<td>-15.830</td>
</tr>
<tr>
<td>PCE</td>
<td>0.94</td>
<td>0.97</td>
<td>0.97</td>
<td>0.95</td>
</tr>
</tbody>
</table>

*P < 0.1; **P < 0.05; ***P < 0.01; †P < 0.001; ‡P < 0.0001
parameters did not improve Model I; (2) the inclusion of the spatial terms did not improve Model II; and (3) exclusion of seven nonsignificant variables in Model III did not result in a decrease of predictive efficacy.

The predicted distribution obtained for *Pterocles orientalis* from Model III appears depicted in Figure 27:

\[ U_i = -143.1 + 8.921 \text{CULT}_i + 0.4147 \text{SFROST}_i - 0.8312 \text{CONT}_i + 2.112 \text{SWF}_i \]

*Melanocorypha calandra*

Coefficients and statistics corresponding to the explanatory models built for *Melanocorypha calandra* appear in Table 10. Addition of non-climatic variables did not improve significantly the predictive efficacy of Model I in relation to the Climatic Model as indicated by a nonsignificant $\chi^2$ statistic (Table 16).

The $C$ statistic (Table 16) used to evaluate the differences between Model I and Model II generated a highly significant value ($\alpha = 0.005$). This evidenced the notable increase in the log likelihood of Model II (Table 10). Differences between Models I and II can be better assessed by looking at Figures 28 and 29. The overall forecasting accuracies of Model I and Model II were very similar (Fig. 28). By inspecting Figure 29, it can be seen that both sensitivity and specificity for Model II were higher than those of Model I almost through the entire range of cutpoints. Differences in sensitivity were
Figure 27. Breeding (A) and predicted (B) distributions of the Black-bellied Sandgrouse (*Pterocles orientalis*).
BLACK-BELLIED SANDGROUSE

(Pterocles orientalis)

Breeding
Absent

A

B

0 20 40 60Km

> 0.9
0.6 – 0.9
0.3 – 0.6
< 0.3
Table 10. *Melanocorypha calandra*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM</td>
<td>0.2324</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>TEMP</td>
<td>-0.239</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>HTEMP</td>
<td>0.2006</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SFROST</td>
<td>0.1258</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DFTEMP</td>
<td>0.0320</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>0.0785</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DEFPREC</td>
<td>-0.0056</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>0.0398**</td>
<td>0.0249**</td>
<td>0.0096</td>
<td>-</td>
</tr>
<tr>
<td>PREC</td>
<td>-0.0065</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EVTPOT</td>
<td>-0.0110</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EXPREC</td>
<td>-0.0041</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CONT</td>
<td>0.7581*</td>
<td>0.7527†</td>
<td>0.4403**</td>
<td>0.5031**</td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>-0.0055</td>
<td>-0.0047</td>
<td>-</td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>6.9380†</td>
<td>7.2910‡</td>
<td>7.2820‡</td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>1.8590</td>
<td>3.510</td>
<td>-</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>-0.0912***</td>
<td>-0.0929***</td>
<td>-0.0859‡</td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td>-</td>
<td>4.5430**</td>
<td>5.4170‡</td>
</tr>
<tr>
<td>PCE</td>
<td>0.91</td>
<td>0.94</td>
<td>0.95</td>
<td>0.97</td>
</tr>
</tbody>
</table>

*P < 0.1; **P < 0.05; ***P < 0.01; †P < 0.001; ‡P < 0.0001
Figure 28. Plot comparing the overall forecasting accuracy of study models I and II for *Melanocorypha calandra*.

Figure 29. Plot comparing the sensitivities and specificities of study models I and II for *Melanocorypha calandra*. 
even larger than those in specificity and occurred at high cutpoints, where
the sensitivity of a model tends to be the lowest. The most pronounced
improvement (11%) in sensitivity occurred at cutpoint = 0.7. Larger
differences in sensitivity indicated that the better overall forecasting
accuracy of Model II, relative to Model I, was more closely linked to its
higher sensitivity at high cutpoints than to the improvement of its speci-
ficity.

Comparison of Models II and Model III generated a nonsignificant $\chi^2$
statistic for both the breeding and nonbreeding groups (Table 16). This
indicated that both models exhibited similar predictive efficacies, even
though Model III included three variables less than Model II. Figure 30
shows the predicted distribution for Melanocorypha calandra obtained by
Model III:

$$U_i = -15.060 + 7.282 \text{CULT}_i + 0.5031 \text{CONT}_i - 0.0859 \text{HDR350}_i +$$
$$+ 4.263 \text{SWF}_i$$

_Lullula arborea_

Coefficients and statistics related to the models for _Lullula arborea_ can
be found in Table 11. The nonsignificant $\chi^2$ statistic obtained for the
comparison between the Climatic Model and Study Model I (Table 16)
Figure 30. Breeding (A) and predicted (B) distributions of the Calandra Lark *Melanocorypha calandra*
CALANDRA LARK
(Melanocorypha calandra)

A

B

Breeding
Absent

> 0.9
0.6 - 0.9
0.3 - 0.6
< 0.3

0 20 40 60Km
Table 11. *Lullula arborea*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM</td>
<td>-1.1060**</td>
<td>-1.292†</td>
<td>-0.7444*</td>
<td>-0.5908**</td>
</tr>
<tr>
<td>TEMP</td>
<td>0.1272</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>HTEMP</td>
<td>-0.3287</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SFROST</td>
<td>0.0745</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DFTEMP</td>
<td>0.0224</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>0.00750**</td>
<td>0.0040</td>
<td>0.0051</td>
<td>-</td>
</tr>
<tr>
<td>DEFPREC</td>
<td>0.0003</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>-0.0100**</td>
<td>-0.0130***</td>
<td>-0.0083*</td>
<td>-0.0089*</td>
</tr>
<tr>
<td>PREC</td>
<td>-0.0050**</td>
<td>-0.0036†</td>
<td>-0.0026**</td>
<td>-0.0028***</td>
</tr>
<tr>
<td>EVTPOT</td>
<td>-0.0115</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EXPREC</td>
<td>0.0017</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CONT</td>
<td>0.4020**</td>
<td>0.0693</td>
<td>-0.0048</td>
<td>-</td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>0.0007</td>
<td>0.0011</td>
<td>-</td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>1.9970</td>
<td>2.1770</td>
<td>-</td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>3.912†</td>
<td>3.4320***</td>
<td>2.8340**</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>-0.0114</td>
<td>-0.0084</td>
<td>-</td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td>-</td>
<td>2.537***</td>
<td>2.500***</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>1.2580</td>
<td>4.674</td>
<td>1.067</td>
<td>3.216*</td>
</tr>
<tr>
<td>LOG LIKELIHOOD</td>
<td>-60.026</td>
<td>-60.928</td>
<td>-56.653</td>
<td>-58.119</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>0.86</td>
<td>0.86</td>
<td>0.87</td>
<td>0.87</td>
</tr>
</tbody>
</table>

*P < 0.1; **P < 0.05; ***P < 0.01; †P < 0.001; ‡P < 0.0001
indicated that addition of non-climatic variables did not improve the predictive efficacy of Model I.

Improvement of Model II, relative to Model I, by the addition of the spatial term, SWF, was indicated by a highly significant C statistic (Table 17). The differences between the models were reflected in the increase of the log likelihood functions of Models II and III, relative to Model I. Figure 31 shows that the difference in the overall forecasting accuracy exhibited by Models I and II across the whole cutpoint range was not very large. It widened in favor of Model II for low cutpoints (0.0 - 0.4), almost disappeared for cutpoints between 0.4 and 0.7, and increased again in favor of Model II for high cutpoints (0.7 - 0.1). In Fig. 32 it can be seen that for low cutpoints, the advantage of Model II was due to its larger specificity (i.e., its ability to correctly classify the absence of a species). The largest difference in specificity (9%) was observed for a cutpoint = 0.3. For high cutpoints, however, it was linked to its higher sensitivity (i.e., its ability to correctly predict the breeding occurrence of the species). The largest difference (10%) in sensitivity occurred at a cutpoint = 0.9.

Comparison of Models II and III yielded a nonsignificant $\chi^2$ statistic, indicating that reduction in the number of variables from 10 to 5 in Model III, relative to Model II, did not result in a significant loss in predictive efficacy.
Figure 31. Plot comparing the overall forecasting accuracies of study models I and II for *Lullula arborea*.

Figure 32. Plot comparing the sensitivities and specificities of the study models I and II for *Lullula arborea*. 
This was reflected in the identical PCE indices obtained for both models (Table 11).

Calibration of Model III for *Ullula arborea* produced the predicted breeding distribution depicted in Figure 33:

\[ U_i = 3.216 + 2.834 H_{\text{veg}} - 0.5908 \text{REGHUM} - 0.0089 \text{BIOCLIM} - 0.0028 \text{PREC} + 2.50 \text{SWF}, \]

*Ficedula hypoleuca*

Table 12 contains the coefficients and statistics of the models built for *Ficedula hypoleuca*. Statistical comparison (Table 16) of the Climatic Model and Model I did not indicate a significant difference in predictive efficacy between the models by the addition of non-climatic parameters. Their PCE indices only differed by 1% (Table 12). As denoted by the C statistic (Table 17), Models I and II were statistically different at \( \alpha = 0.05 \). Improvement in the overall forecasting accuracy of Model II relative to Model I (see Fig. 34) was more noticeable for cutpoints between 0.4 and 0.7. For low cutpoints differences in overall forecasting accuracy were small, while for high ones they were nonexistent. While differences between the specificities of Models I and II were consistently small throughout the entire range of cutpoints, those between their sensitivities increased significantly for cutpoints between 0.4 and 0.7 (Fig. 35). From this trend, it can be inferred that the small differences in overall forecasting accuracy at low
Figure 33. Breeding (A) and predicted (B) distributions of the Wood Lark (*Lullula arborea*).
WOOD LARK
(Lullula arborea)

Breeding
Absent

A

B

> 0.9
0.6 - 0.9
0.3 - 0.6
< 0.3

0 20 40 60 Km

N
Table 12. *Ficedula hypoleuca*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM</td>
<td>-2.5110**</td>
<td>1.0520</td>
<td>-0.4685</td>
<td>-</td>
</tr>
<tr>
<td>TEMP</td>
<td>1.1810</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>HTEMP</td>
<td>-0.6024</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SFROST</td>
<td>-0.0084</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DFTEMP</td>
<td>0.0959</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>-0.0048</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DEFPREC</td>
<td>0.0212</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>0.0112</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PREC</td>
<td>-0.0006</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EVTPOT</td>
<td>0.0067</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EXPREC</td>
<td>0.0029</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CONT</td>
<td>0.0511</td>
<td>-0.0609</td>
<td>-0.0421</td>
<td>-</td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>-0.0017**</td>
<td>-0.0002</td>
<td>-</td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>-6.273</td>
<td>-4.5540</td>
<td>-</td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>0.2677</td>
<td>1.3830*</td>
<td>2.7110***</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>-0.0007</td>
<td>0.0047</td>
<td>-</td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td>-</td>
<td>2.621†</td>
<td>4.0780‡</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>-15.210</td>
<td>2.5300</td>
<td>-1.7570</td>
<td>-4.8320‡</td>
</tr>
<tr>
<td>LOG LIKELIHOOD</td>
<td>-37.207</td>
<td>-38.530</td>
<td>-35.548</td>
<td>-37.993</td>
</tr>
<tr>
<td>PCE</td>
<td>0.87</td>
<td>0.88</td>
<td>0.90</td>
<td>0.90</td>
</tr>
</tbody>
</table>

*P < 0.2; **P < 0.1; ***P < 0.001; †P < 0.05; ‡P < 0.0001
Figure 34. Plot comparing the overall forecasting accuracy of study models I and II for *Ficedula hypoleuca*.

Figure 35. Plot comparing the sensitivities and specificities of study models I and II for *Ficedula hypoleuca*.
cutpoints were related to higher specificities and that the larger differences observed at higher cutpoints were in connection with higher sensitivities. The largest difference in sensitivity (36.5%) was observed for a cutpoint = 0.6. The importance of SWF (P-value < 0.0001) in Models II and III was evidenced by the way it outperformed other variables. Only $H_{vag}$ remained statistically significant at $\alpha = 0.05$ in Model III, although it was much less significant than the spatial term SWF (Table 12).

Models II and III were not statistically different (Table 16), indicating that the elimination of four variables in Model III did not result in a decrease in predictive efficacy. The PCE indices for both models were the same (0.90), in spite of the fact that Model III included only two explanatory variables ($H_{vag}$ and SWF), whereas Model I included six.

The low correlation found for most of the variables in the explanatory models was probably due to the peculiarly fragmented distribution exhibited by this species (Fig. 36a), which makes it difficult to establish explicit associations with environmental factors. In addition, the small number of breeding records (22) for this species (the smallest among the nine species) also may have reduced the accuracy of the correlations between the distribution and environmental factors. The predicted distribution of *Ficedula hypoleuca* obtained by calibrating Model III can be found in Figure 36b:

$$U_i = -4.832 + 2.711 H_{vag} + 4.078 \text{SWF}_i$$
Figure 36. Breeding (A) and (B) predicted distributions of the European Pied Flycatcher (*Ficedula hypoleuca*).
EUROPEAN PIED FLYCATCHER
(*Ficedula hypoleuca*)

- **A**: Breeding
- **B**: Absent

- > 0.9
- 0.6 - 0.9
- 0.3 - 0.6
- < 0.3

Scale: 0 - 60 Km
Table 13 contains the coefficients and statistics for the study models for *Sitta europaea*. Addition of non-climatic parameters into Model I was accompanied by a significant improvement in predictive efficacy for the breeding group as denoted by a highly significant $\chi^2$ statistic (Table 16). This improvement was translated into a higher overall forecasting accuracy across cutpoints, but was particularly noticeable for high ones (Fig. 37).

Figure 38 shows the impact on sensitivity and specificity by the addition of non-climatic predictors into Model I. For cutpoints from 0.1 to 0.6, Model I exhibited considerably higher specificities than the Climatic Model but very similar sensitivities. However, for cutpoints from 0.6 to 0.9, this trend was reversed as Model I showed significantly higher sensitivities and only slightly better specificities. The largest differences in specificity and sensitivity were 12% (cutpoint = 0.2) and 14% (cutpoint = 0.9), respectively.

The $C$ statistic used to examine the differences among Model I and Model II was nonsignificant at the $\alpha = 0.05$ level (Table 16). This indicated that the inclusion of the spatial term, SWF, did not improve Model II relative to Model I. Likewise, Models II and III were not statistically different (Table 16), indicating that elimination of four variables from Model II to Model III did not result in a significant decrease in predictive efficacy. The PCE index values for the three study models were identical and high (PCE = 0.95), denoting a very satisfactory level of overall forecasting accuracy, particularly
Table 13. *Sitta europaea*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEMP</td>
<td>-1.223</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>HTEMP</td>
<td>0.3532</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SFROST</td>
<td>-0.0796</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DFTEMP</td>
<td>0.1235</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>0.1056**</td>
<td>-0.0203</td>
<td>-0.0232</td>
<td>-</td>
</tr>
<tr>
<td>DEFPREC</td>
<td>0.0088</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>-0.0414**</td>
<td>-0.0186*</td>
<td>-0.0211**</td>
<td>-0.0272***</td>
</tr>
<tr>
<td>PREC</td>
<td>-0.0022</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EVTPOT</td>
<td>-0.0246</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EXPREC</td>
<td>0.0016</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CONT</td>
<td>-0.0933</td>
<td>-0.3143***</td>
<td>-0.3697***</td>
<td>-0.4185***</td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>0.0003</td>
<td>0.0005</td>
<td>-</td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>1.0810</td>
<td>0.6203</td>
<td>-</td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>5.4940†</td>
<td>5.741†</td>
<td>5.4630†</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>0.0333</td>
<td>0.0351</td>
<td>-</td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td>-</td>
<td>-1.528</td>
<td>-0.8627</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>35.69</td>
<td>12.900</td>
<td>16.47**</td>
<td>15.950</td>
</tr>
<tr>
<td>LOG LIKELIHOOD</td>
<td>-32.582</td>
<td>-27.103</td>
<td>-26.779</td>
<td>-28.569</td>
</tr>
<tr>
<td>PCE</td>
<td>0.93</td>
<td>0.95</td>
<td>0.95</td>
<td>0.95</td>
</tr>
</tbody>
</table>

*P < 0.1; **P < 0.05; ***P < 0.01; †P < 0.001; †P < 0.0001
Figure 37. Plot comparing the overall forecasting accuracy of the Climatic Model and Study Model I for *Sitta europaea*.

Figure 38. Plot comparing the sensitivities and specificities of the Climatic Model and Study Model I for *Sitta europaea*. 
in the case of Model III which included only five variables, four less than Model II. The predicted distribution corresponding to *Sitta europaea*, obtained from the calibration of Model III, is depicted in Figure 39:

\[
U_i = 15.95 + 5.463 H_{\text{veg}} - 3.219 \text{REGHUM} - 0.0272 \text{BIOCLIM} - 0.4185 \text{CONT} - 0.8627 \text{SWF},
\]

*Serinus citrinella*

Coefficients and statistics for the three study models corresponding to *Serinus citrinella* are listed in Table 14. Inclusion of non-climatic parameters into Model I resulted in an improvement in predictive efficacy for the breeding group as indicated by a highly significant \( \chi^2 \) statistic (Table 16). The better predictive efficacy of Model I, relative to the Climatic Model, was reflected in a higher overall forecasting accuracy almost throughout the entire range of cutpoints (the only exception to this trend occurred for a cutpoint of 0.5 where overall forecasting accuracies for both models were the same). This increase was slightly higher at high cutpoints (Fig. 40). Figure 41 shows that differences in specificity between Model I and the Climatic Model were larger at low cutpoints but smaller nonetheless than those in sensitivity observable at high cutpoints. Thus the largest increases (5-9%) in specificity occurred between cutpoints ranging from 0.0 to 0.2, whereas the largest differences (17-26%) in sensitivity were observed for cutpoints between 0.7 to 0.9.
Figure 39. Breeding (A) and predicted (B) distributions of the Eurasian Nuthatch (*Sitta europaea*).
EURASIAN NUTHATCH
(Sitta europaea)
Table 14. *Serinus citrinella*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM</td>
<td>-3.524**</td>
<td>-2.966</td>
<td>-2.745</td>
<td>-</td>
</tr>
<tr>
<td>TEMP</td>
<td>-1.751</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>HTEMP</td>
<td>1.718</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SFROST</td>
<td>0.0047</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DFTEMP</td>
<td>0.1298*</td>
<td>0.1282</td>
<td>0.1181</td>
<td>-</td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>0.0624</td>
<td>0.0876**</td>
<td>0.0812*</td>
<td>0.0123</td>
</tr>
<tr>
<td>DEFPREC</td>
<td>-0.0081</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>-0.0025</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PREC</td>
<td>0.0009</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EVTPOT</td>
<td>0.0054</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EXPREC</td>
<td>-0.0022</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CONT</td>
<td>-0.1318</td>
<td>0.0311</td>
<td>0.0703</td>
<td>-</td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>0.0100‡</td>
<td>0.0093†</td>
<td>0.0062***</td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>-4.645</td>
<td>-2.128</td>
<td>-</td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>2.276**</td>
<td>2.157*</td>
<td>3.1250***</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>0.0322</td>
<td>0.0316</td>
<td>-</td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td>-</td>
<td>2.4360*</td>
<td>4.7770‡</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>-10.64</td>
<td>-23.200***</td>
<td>-23.490**</td>
<td>0.0013</td>
</tr>
<tr>
<td>LOG LIKELIHOOD</td>
<td>-37.260</td>
<td>-27.446</td>
<td>-25.827</td>
<td>-30.689</td>
</tr>
<tr>
<td>PCE</td>
<td>0.90</td>
<td>0.92</td>
<td>0.93</td>
<td>0.91</td>
</tr>
</tbody>
</table>

*P < 0.1; **P < 0.05; ***P < 0.01; †P < 0.001; ‡P < 0.0001
Figure 40. Plot comparing the overall forecasting accuracy of the Climatic Model and Study Models I for *Serinus citrinella*.

Figure 41. Plot comparing the sensitivities and specificities of the Climatic Model and Study Model I for *Serinus citrinella*. 
The $C$ statistic used to detect differences between Models I and II was significant at the $\alpha = 0.1$ level (Table 16). The test indicated a slight improvement of Model II due to the inclusion of the SWF term. The PCE index increased from 0.92 to 0.93. However, the PCE index (0.91) generated by Model III with only four variables, five less than Model II, was satisfactory. Figure 42 shows that the overall forecasting accuracy levels of Models I and II, as a function of the cutpoint, were nearly the same, with a minor differences for low and middle cutpoint values. These small differences were accounted for by the increase in the sensitivity of Model II (Fig. 43) related to the inclusion of the term SWF. The largest increase in sensitivity was 8% (cutpoint = 0.5). Differences in specificity between Models I and II were imperceptible (Fig. 43).

Statistical comparison did not show significant differences between Models II and III, indicating that elimination of four variables did not result in a decrease in predictive efficacy. Calibration of Model III produced the distribution of breeding probability for *Serinus citrinella* depicted in Figure 44:

$$U_i = 0.0013 + 3.125 \text{H}_{\text{veg}} + 0.0062 \text{ALT}_i + 0.0123 \text{FRSTFREE}_i + 4.777 \text{SWF}_i$$
Figure 42. Plot comparing the overall forecasting accuracy of study models I and II for *Serinus citrinella*.

Figure 43. Plot comparing sensitivities and specificities of study models I and II for *Serinus citrinella*. 
Figure 44. Breeding (A) and predicted (B) distributions of the Citril Finch (*Serinus citrinella*).
CITRIL FINCH
(Serinus citrinella)

Aur > 0.9
0.6 - 0.9
0.3 - 0.6
< 0.3

Breeding
Absent

A

B

0 20 40 60Km

N
"Pyrrhula pyrrhula"

Table 15 contains the coefficients and statistics of the study models for *Pyrrhula pyrrhula*. The $\chi^2$ statistic obtained in the comparison of the Climatic and Study Model I was significant for the breeding group (Table 16), indicating an improvement in predictive efficacy for this breeding group by the addition of non-climatic variables. This improvement was translated into a higher overall forecasting almost across the entire range of cutpoints (Fig. 45). Variation in specificity and sensitivity (Fig. 46) followed a pattern very similar to that observed for the Eurasian Nuthatch. Specificity for Model I was notably higher than that of the Climatic Model at lower cutpoints, whereas sensitivity was increased considerably at higher cutpoints. The largest differences in specificity and sensitivity were 11.5% (cutpoint = 0.3) and 14% (cutpoint = 0.5), respectively.

The results of the C test (Table 16) indicated that the inclusion of the SWF term was not translated into an improvement of Model II relative to Model I. Both models generated a high level of overall forecasting accuracy (PCE = 0.97).

Elimination of six variables did not decrease the predictive efficacy of Model III relative to Model II (see Table 16). It was particularly impressive that Model III, with a specification of only four variables could accurately forecast 97% of the spatial pattern exhibited the distribution of *Pyrrhula pyrrhula*. REGHUM, HTEMP and $H_{\text{veg}}$ were consistently significant
Table 15. *Pyrrhula pyrrhula*: estimated coefficients of the climatic and study models. PCE is the maximum percentage of correct estimation.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CLIMATIC MODEL</th>
<th>MODEL I</th>
<th>MODEL II</th>
<th>MODEL III</th>
</tr>
</thead>
<tbody>
<tr>
<td>REGHUM</td>
<td>-5.707*</td>
<td>-2.620**</td>
<td>-4.137**</td>
<td>-2.520**</td>
</tr>
<tr>
<td>TEMP</td>
<td>-1.967</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>HTEMP</td>
<td>-2.370*</td>
<td>-2.969***</td>
<td>-3.397***</td>
<td>-1.362‡</td>
</tr>
<tr>
<td>SFROST</td>
<td>-0.01</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DFTEMP</td>
<td>0.0916</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>FRSTFREE</td>
<td>0.1136**</td>
<td>0.0759</td>
<td>0.0813</td>
<td>-</td>
</tr>
<tr>
<td>DEFPREC</td>
<td>0.0033</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>BIOCLIM</td>
<td>-0.0171*</td>
<td>0.0072</td>
<td>0.0074</td>
<td>-</td>
</tr>
<tr>
<td>PREC</td>
<td>-0.0023</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EVTPOT</td>
<td>0.0231</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EXPREC</td>
<td>0.0046</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>CONT</td>
<td>0.5155</td>
<td>0.8455*</td>
<td>0.9980*</td>
<td>0.1800</td>
</tr>
<tr>
<td>ALT</td>
<td>-</td>
<td>0.0002</td>
<td>0.0003</td>
<td>-</td>
</tr>
<tr>
<td>CULT</td>
<td>-</td>
<td>-2.608</td>
<td>-3.095</td>
<td>-</td>
</tr>
<tr>
<td>Hveg</td>
<td>-</td>
<td>5.809†</td>
<td>6.182†</td>
<td>7.9380‡</td>
</tr>
<tr>
<td>HDR350</td>
<td>-</td>
<td>0.0259</td>
<td>0.0301</td>
<td>-</td>
</tr>
<tr>
<td>SWF</td>
<td>-</td>
<td>-</td>
<td>-2.325</td>
<td>-2.004</td>
</tr>
<tr>
<td>CONSTANT</td>
<td>34.94***</td>
<td>32.48***</td>
<td>41.35***</td>
<td>26.48†</td>
</tr>
<tr>
<td>PCE</td>
<td>0.92</td>
<td>0.97</td>
<td>0.97</td>
<td>0.97</td>
</tr>
</tbody>
</table>

*P < 0.1; **P < 0.05; ***P < 0.01; †P < 0.001; ‡P < 0.0001
Figure 45. Plot comparing the overall forecasting accuracy of the Climatic Model and Study Model I for *Pyrrhula pyrrhula*.

Figure 46. Plot comparing sensitivities and specificities of the Climatic Model and the Study Model I for *Pyrrhula pyrrhula*. 
(α = 0.05) in all three study models. In Models II and III SWF was not
statistically significant (α = 0.1). \( H_{\text{veg}} \) outperformed the other variables both
in Model I and Model II. Its statistical significance was even larger
(P < 0.0001) in Model III as was that of HTEMP, which went from
P < 0.01 in Model II to P < 0.0001 in Model III. Model III was calibrated to
generate the predicted distribution of *Pyrrhula pyrrhula* (see Fig. 47) over the
study area:

\[
U_i = 26.48 + 7.938 \, H_{\text{veg}} - 2.52 \, \text{REGHUM} - 1.362 \, \text{HTEMP} -
\]
\[ - 2.004 \, \text{SWF}, \]

Comparing Predicted and Observed Distributions

Assuming that predicting an absence when a presence is documented
is more costly than vice versa, visual inspection of Fig. 21, 26, 30, 34, 33,
36, 39, 44 and 47 evidenced a more accurate reconstruction of the
observed distributions when \( P(b) \geq 0.3 \) is taken to represent a breeding
occurrence, and therefore \( P(b) < 0.3 \) is considered to mean the absence of
the species, than for higher values of \( P(b) \). Two different cutpoints
(Cp = 0.3 and Cp = 0.5) were used to further compare changes in the
predictive ability of the models. Table 17 gives results of such comparison,
showing changes in the forecasting accuracy, sensitivity, specificity and
predictive value of the effective models.
Figure 47. Breeding (A) and predicted (B) distributions of the Eurasian Bullfinch (*Pyrrhula pyrrhula*).
EURASIAN BULLFINCH

(Pyrrhula pyrrhula)

Breeding
Absent

A

B

> 0.9
0.6 - 0.9
0.3 - 0.6
< 0.3

0 20 40 60Km
Table 16. Statistics of the tests used for model comparison purposes. The first four columns refer to the $\chi^2$ statistic comparing predicted breeding probabilities for groups breeding (Br) and nonbreeding (NBr) between the Climatic Model and Study Model, and between Study Model II and Study Model III (unless specified, degrees of freedom, df = 5). In the last column are listed the results of the C test comparing likelihood measures among Study Model I and Study Model II. $C = -2 \ln \left( \frac{L_i}{L_o} \right) \approx \chi^2$ (degrees of freedom, df = 1), where $L_o$ and $L_i$ represent the log likelihood measures of Model I and Model II, respectively. An asterisk denotes a statistically significant value.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>Climatic/Model I</th>
<th>Model II/Model III</th>
<th>C_{II}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Br</td>
<td>NBr</td>
<td>Br</td>
</tr>
<tr>
<td><em>Pernis apivorus</em></td>
<td>1.534</td>
<td>11.907*</td>
<td>1.881</td>
</tr>
<tr>
<td><em>Falco subbuteo</em></td>
<td>26.712*</td>
<td>39.724*</td>
<td>5.400</td>
</tr>
<tr>
<td><em>Pterocles orientalis</em></td>
<td>10.331</td>
<td>6.813</td>
<td>4.695</td>
</tr>
<tr>
<td><em>Melanocorypha calandra</em></td>
<td>6.811</td>
<td>8.257</td>
<td>4.878</td>
</tr>
<tr>
<td><em>Lullula arborea</em></td>
<td>10.361</td>
<td>7.946</td>
<td>3.534</td>
</tr>
<tr>
<td><em>Ficedula hypoleuca</em></td>
<td>2.574</td>
<td>5.705</td>
<td>8.885</td>
</tr>
<tr>
<td></td>
<td>(df = 3)</td>
<td>(df = 4)</td>
<td>(df = 4)</td>
</tr>
<tr>
<td><em>Sitta europaea</em></td>
<td>25.385*</td>
<td>6.227</td>
<td>4.692</td>
</tr>
<tr>
<td></td>
<td>(df = 4)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Serinus citrinella</em></td>
<td>21.156*</td>
<td>4.230</td>
<td>6.782</td>
</tr>
<tr>
<td><em>Pyrrhula pyrrhula</em></td>
<td>15.338*</td>
<td>9.582</td>
<td>9.867</td>
</tr>
</tbody>
</table>

$\chi^2_{0.05,5} = 11.070; \chi^2_{0.05,4} = 9.488; \chi^2_{0.05,3} = 7.815; \chi^2_{0.05,1} = 3.84; @P < 0.1$
TABLE 17. Sensitivity, specificity, predictive value and overall forecasting accuracy of the effective models for two different cutpoints (0.3 and 0.5). V corresponds to the number of variables specified in the effective models, BR is the number of breeding records for each species distribution, PCE is the percentage of overall correct estimation and Cp is cutpoint.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>V</th>
<th>BR</th>
<th>SENSITIVITY</th>
<th>PREDICTIVE VALUE</th>
<th>SPECIFICITY</th>
<th>PCE(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cp = .3</td>
<td>Cp = .5</td>
<td>Cp = .3</td>
<td>Cp = .5</td>
</tr>
<tr>
<td>Pernis apivorus</td>
<td>5</td>
<td>38</td>
<td>79.0</td>
<td>68.4</td>
<td>80.0</td>
<td>93.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>56.8</td>
<td>76.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Falco subbuteo</td>
<td>3</td>
<td>61</td>
<td>83.6</td>
<td>72.1</td>
<td>73.6</td>
<td>86.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>51.4</td>
<td>78.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pterocles orientalis</td>
<td>5</td>
<td>42</td>
<td>95.2</td>
<td>93.0</td>
<td>94.5</td>
<td>96.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>91.2</td>
<td>92.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Melanocorypha calandra</td>
<td>4</td>
<td>54</td>
<td>96.3</td>
<td>92.6</td>
<td>90.0</td>
<td>93.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>83.9</td>
<td>89.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lullula arborea</td>
<td>5</td>
<td>71</td>
<td>88.6</td>
<td>81.4</td>
<td>76.8</td>
<td>87.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>77.0</td>
<td>85.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ficedula hypoleuca</td>
<td>2</td>
<td>22</td>
<td>63.6</td>
<td>54.5</td>
<td>90.0</td>
<td>97.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>51.8</td>
<td>75.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sitta europaea</td>
<td>5</td>
<td>70</td>
<td>98.6</td>
<td>94.3</td>
<td>90.2</td>
<td>93.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>89.6</td>
<td>93.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serinus citrinella</td>
<td>4</td>
<td>35</td>
<td>88.6</td>
<td>80.0</td>
<td>90.6</td>
<td>94.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>73.8</td>
<td>82.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pyrrhula pyrrhula</td>
<td>5</td>
<td>69</td>
<td>98.6</td>
<td>93.0</td>
<td>91.2</td>
<td>96.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>90.3</td>
<td>95.3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
For a cutpoint of 0.3, the effective models for *P. orientalis, M. calandra, S. europaea*, and *P. pyrrhula* and generated very high sensitivity values (> 95%) indicating a great ability to correctly predict breeding observations, as well as high specificity values (> 90%) indicating ability to correctly classify most absences. At the same cutpoint, the effective models for *Falco subbuteo, Lullula arborea* and *Serinus citrinella* generated moderately high sensitivities (83.6% - 88.6%) and moderate to high specificities (73.6% - 90.6%) indicating an acceptable level of accuracy to predict the breeding occurrence of the species. The models for *Pernis apivorus* and *Ficedula hypoleuca* generated the lowest sensitivities (79% and 63.6%, respectively). These low sensitivities may be related to the low number of breeding records (38 and 22, respectively) available for these species, since the success of predicting a breeding occurrence depends on the number of observations. However, *S. citrinella* with relatively few breeding records (35) exhibited a moderately high sensitivity (88.6%).

By raising the cutpoint, the sensitivity of a model decreases as its specificity increases. Thus, when 0.5 was adopted as cutpoint, there was an increase in the specificity of all models but it was most dramatic (increases ≥ 11%) for *Pernis apivorus, Falco subbuteo, and Lullula arborea*. On the other hand, there was a decline in the sensitivity of all models with sharpest decreases for *Pernis apivorus, Falco subbuteo, Lullula arborea, Ficedula hypoleuca* and *Serinus citrinella*. 
The higher specificities obtained under cutpoint = 0.5 in relation to cutpoint = 0.3 were translated into only modest increases (0 to 7.4%) in overall forecasting accuracy of the effective models. The model for *Pernis apivorus* exhibited the highest increase (7.4%) in overall forecasting accuracy, whereas those for *Sitta europaea* and *Pyrrhula pyrrhula* remained identical. In all cases, except *F. subbuteo*, the magnitude of the increases in overall forecasting accuracy of the models was considerably smaller than that of the decrease in the sensitivity values obtained by raising the cutpoint from $P(b) = 0.3$ to $P(b) = 0.5$. The small increases in overall forecasting accuracies contrasted with the more significant decreases in sensitivity were indicative that species' spatial patterns could be more effectively reconstructed when $P(b) = 0.3$ was used as cutpoint.

The maps displayed in Figures 48-52 were produced by overlying the observed distributions onto the predicted distributions with the cutpoint as 0.3. Different shading patterns were used to denote the four possible groups of grid cells which form when each geographic unit is classified into either the group breeding or nonbreeding.

A double cross-hatch pattern represented those grid cells in which a breeding occurrence was both observed and predicted by the model. The larger the number of double cross-hatched cells, the higher the sensitivity of the models. Solid black represented breeding occurrences which were not
Figure 48. Maps comparing the predicted and observed distributions of *Pernis apivorus* (A) and *Falco subbuteo* (B).
Observed and Predicted
Predicted but not observed
Observed but not predicted
Figure 49. Maps comparing the predicted and observed distributions of *Pterocles orientalis* (A) and *Melanocorypha calandra* (A).
Figure 50. Maps comparing the predicted and observed distributions of *Lullula arborea* (A) and *Ficedula hypoleuca* (B).
Observed and Predicted
Observed but not predicted
Predicted but not observed

0 20 40 60Km
Figure 51. Maps comparing the predicted and observed distributions of *Sitta europaea* (A) and *Serinus citrinella* (B).
EURASIAN NUTHATCH

CITRIL FINCH

A  

B

Observed and Predicted
Predicted but not observed
Observed but not predicted

0 20 40 60Km

151
Figure 52. Map comparing the predicted and observed distributions of *Pyrrhula pyrrhula*. 
predicted by the model. The actual breeding distribution for a given species was made up of the solid-black cells plus those with double cross-hatch. A single cross-hatch pattern denoted grid cells for which a breeding occurrence was predicted but not observed. A high proportion of double cross-hatch cells relative to single cross-hatch cells indicated a high predictive value for the model (see Table 17 for the predictive values of each model). Empty grid cells corresponded to those cases in which the species was neither observed nor its presence predicted by the model. This group of cells indicated the specificity of the model.

High accuracy of a model would be denoted by a map pattern characterized by the lack of cells with solid-black shading --i.e., a high sensitivity-- and by a low ratio of cells with single cross-hatch shading to cells with double cross-hatch shading --i.e, a high predictive value.

The map patterns in Figures 49a, 49b, 51a and 52 indicated a high level of accuracy in replicating the observed distributions of *Pterocles orientalis*, *Melanocorypha calandra*, *Sitta europaea* and *Pyrrhula pyrrhula*. In all four cases, the number of cells with incorrectly predicted presences (hatched) or absences (solid) were both small, indicating considerable success in correctly predicting the breeding distributions and a high predictive value, respectively. The group of single-shading cells can be interpreted as potential habitat areas, i.e., areas environmentally suitable but vacant. When compared to the four above-mentioned species, the map
patterns depicted in Figures 48a, 48b, 50a, 50b and 51b reflected a level of forecasting accuracy less satisfactory for *Pernis apivorus*, *Falco subbuteo*, *Lullula arborea*, *Ficedula hypoleuca* and *Serinus citrinella* as the presence of black grid cells was more common, an indication of a lower capability to correctly predict a breeding occurrence.

The ability of the models to correctly predict a breeding occurrence, could have been significantly increased by lowering the cutpoint (see Methods section). For example, if instead of $P(b) = 0.3$, $P(b) = 0.1$ is used as cutpoint, the sensitivity for the model corresponding to *Pernis apivorus* increases from 79% to 95%, and that of the model for *Ficedula hypoleuca* from 63.6% to 82%. In the extreme, a $P(b) = 0.0$ could be used as cutpoint ($P(b) > 0.0$ denotes a breeding occurrence) to ensure that 100 percent of the breeding occurrences are correctly predicted. However, the predictive value of a model (the probability that a predicted occurrence corresponds to an actual breeding occurrence) of a model decreases as its sensitivity increases. This effect can be well illustrated by the significant decrease ($\geq 19\%$) in the predictive value for the models corresponding to *Pernis apivorus*, *Falco subbuteo* and *Ficedula hypoleuca* when the cutpoint is reduced from $P(b) = 0.5$ to $P(b) = 0.3$ (Table 17). Thus, if the cutpoint and correlated predictive value of a model is lowered too much the imprecision of the model makes it difficult to distinguish "potential" occurrences from real
absences. At a practical level, this means a higher uncertainty about the breeding status of those grid cells shown with single shading (i.e., cells for which the occurrence of a species was predicted but not observed). In other words, a lower predictive value means a higher probability that the single-shading cells represent wrongly classified presences rather than potential habitat areas.

Although the ability to correctly predict the presence of a given species is of critical importance in the task of reconstructing its breeding distribution, the ultimate goal is to reproduce, with maximum accuracy, the whole distribution pattern --i.e., those areas where the species breeds and those from where it is precluded. Consequently, a model which identifies very accurately where a species breeds, but frequently fails in predicting where it does not, cannot be considered to be an appropriate representation of the processes from which the distribution pattern arises.
V. DISCUSSION

Spatial Patterns of Avian Distributions

Results of the spatial autocorrelation analysis indicated that the species patterns here analyzed are not explained by a CSR model and, accordingly, the basic hypothesis of spatial randomness is rejected in favor of spatial clustering for the sample data (see Taylor et al., 1978). However, the degree of "clumping" was not the same for all the species. Different types of processes which may be involved in causing such patterns are suggested below.

Since many geographic phenomena extend over space to occupy "regions" rather than point locations, events and processes at one place are not likely to be independent of conditions at neighboring localities (Odland 1988). Spatial autocorrelation of the avian distributions may simply indicate the underlying spatial autocorrelation of their governing environmental factors. Thus, it would be expected to find species "clustered" around favorable areas and absent from the unfavorable ones. This is illustrated, for example, by the close association between the breeding distribution of the Citril Finch (Fig. 44a) and high elevation areas (see Fig. 2).

The different degrees of spatial autocorrelation exhibited by the avian distributions can be explained, at least in part, in terms of differences in habitat structure. In general, forests in the study area tend to be more
patchy than the open-space habitats which prevail in southern Navarre. While habitat continuity will tend to produce "compact-looking" avian distributions, habitat patchiness will tend to produce dispersion of the breeding occurrences. Thus, the open-space species, i.e., the Black-bellied Sandgrouse and the Calandra Lark, exhibited distribution patterns with little dispersion and generated the largest Moran’s I coefficients, indicating the highest level of spatial autocorrelation in the sample. Forest or semi-open forest species (the other seven study species) produced smaller Moran’s I coefficients, indicating lower levels of spatial autocorrelation.

This effect can also be illustrated by comparing the distributions of the two species belonging to the Family Alaudidae (Calandra Lark and Wood Lark) as well as those of the Family Fringillidae (Citril Finch and Eurasian Bullfinch). The Wood Lark prefers semi-open habitats such as sparse forests and forest edges, and these habitats have a more patchy spatial distribution than those preferred by the Calandra Lark (open fields, lowland grassy steppes, etc). While the Wood Lark generated the third lowest Moran’s I, the Calandra Lark produced the second highest one. Likewise, the Citril Finch, which nests in a very restrictive habitat (coniferous forests near the timberline), exhibited a lower Moran’s I than did the Eurasian Bullfinch, a species which occupies various types of forests across a wider range of elevations.
Spatial interaction may also cause spatial autocorrelation. Spatial interaction, i.e., the transfer of things or information over space, means that events and processes at a particular location can affect conditions at other locations if the locations interact (Odland 1988). For example, two zones of identical structural conditions may differ in their propensities to be the breeding grounds for a species due to different surrounding conditions, for example, the presence or absence of potential colonizing individuals of the same species at a neighboring area.

The expansion of many breeding ranges is basically a contagious diffusion (Okubo, 1980, 1988; Ferrer et al., 1992). A founding population invades a region and disperses from a localized area of colonization. As the population size increases, empty areas are invaded from neighboring localities already occupied. If enough time elapses, most of the potential breeding range will be occupied. The only constraints to range expansion will be interspecific competition and/or environmental conditions incompatible with its ecological requirements. This process will result in a highly clustered distribution pattern. For migratory species, however, the breeding range is the result of an invasive process in which the entire population participates "simultaneously." This process is constrained by the ecological tolerance of the species but there is also an element of randomness involved. For instance, just by chance, breeding localities which are occupied during a breeding season may be empty during the
following one, and vice versa. The resulting distribution pattern will exhibit less "clumping" than those of sedentary species.

The distributions of the migratory species in the sample, (European Honey-Buzzard, Eurasian Hobby, European Pied Flycatcher and Wood Lark, some of whose populations in the study area are sedentary) were precisely the ones which generated the lowest Moran’s I coefficients, indicating less clustering than that observed for the sedentary species.

The fact that territories of the two raptors, the European Honey-Buzzard and the Eurasian Hobby are larger than those of the other seven species, together with the solitary habitats of both species, might account at least in part for their lower levels of spatial autocorrelation. Further research is needed to determine the effects of scale and resolution on the measure of spatial autocorrelation. A breeding distribution might show a clustered pattern on a large-scale map but a scattered pattern on a small-scale map, and vice versa. This possibility could be tested by enlarging the study area to include neighboring regions, or even the whole Iberian Peninsula, and examining its effects of such enlargement on the levels of spatial autocorrelation. The effects of map resolution could be tested by analyzing the data at different grid sizes, for example, in a 20 Km X 20 Km or 5 Km X 5 Km grid. In this regard, Chou (1991) has shown that Moran’s I increases systematically with the level of resolution but that when derived from maps of a lower resolution level it discriminates spatial patterns
more effectively than when derived from maps of a higher resolution level. This implies that, in map pattern analysis based on spatial autocorrelation, finely resolved data do not necessarily provide more accurate information than more crudely resolved data.

**Modelling Avian Distributions in Terms of Spatial and Environmental Factors**

In this section, Study Model III is used to predict the distributional patterns exhibited by the species over the study area, i.e., their breeding occurrences and their absences.

*Pernis apivorus* Linnaeus 1758

Climate plays an important role in the breeding distribution of this species, particularly moisture variables $\text{EXPREC}$ and $\text{EVTPOT}$. The negative correlation between the breeding probability and these two variables (Table 7) suggests that neither arid nor extremely moist environments are suitable for *Pernis apivorus*. The tendency to avoid arid zones is further supported by the significant ($P < 0.10$), positive correlation found for $\text{REGHUM}$, a variable which measures aridity. After $\text{EXPREC}$ and $\text{EVTPOT}$, $H_{\text{veg}}$ (vegetation diversity; Fig. 17b) was also a powerful explanatory factor.

The European Honey-Buzzard seems to prefer forest zones located in moderately wet areas. This would explain well its distributional pattern within the study area (Fig. 21a), being absent from the Mediterranean district, where forests are scarce and climate too dry, and from the
Cantabrian basin, where suitable vegetation is present but climate is very humid (annual rainfall exceeding 1,600 mm).

The aversion of the Honey-buzzard to arid climates might be due to excessive soil dryness during the summer which makes it difficult for this species to maintain its specialized diet—honey and hymenopterous larvae and adults, which it extracts by digging in the ground (De Juana, 1980). This is consistent with the high negative correlation with EVTPOT, a variable which represents the maximum amount of water vapor that can be lost by the ground due to evaporation.

It remains unclear the biological reasons for the absence of the European Honey-Buzzard from the Cantabrian Basin district, where summers are not dry and suitable habitats seem to exist. A similar pattern is exhibited by the distribution of *Pernis apivorus* in neighboring France, where it does not occur at all in the Mediterranean districts and becomes very sporadic in the humid regions of Normandy, Maine and Picardy (Yeatman, 1976). A possible explanation would be that excessive wetness in temperate areas restricts the abundance and distribution of many insects (Andreawartha and Birch, 1954).

*Falco subbuteo* Linnaeus 1758

Neighborhood effects are by far the most important factor accounting for the spatial distribution of *Falco subbuteo* in the study area (Table 8).
CULT and $H_{veg}$, two variables aimed at representing the structure of the vegetation, also play an important role.

The correlation with the diversity of the vegetation as well as with farmland is indicative of a preference of *Falco subbuteo* within the study area for diverse landscapes, where woodlands and open country alternate. This type of habitat corresponds to landscapes of central and especially southern Navarre. These are precisely the areas where this species most commonly occurs. This species becomes, however, rare in the southern tip of the study area and is conspicuously absent from the northern third (Fig. 26a). Absence from southern Navarre may be explained by the scarcity of woodland areas that, with the exception of a few patches of Aleppo pine woods and riparian vegetation, is characteristic of that region. Although forests become denser in the northern parts of the study area, there are nonetheless some areas of open woodland which should be suitable habitats for *Falco subbuteo*. This species is also reportedly absent in the French Pyrenees (Yeatman, 1976). However, there are records of this species at elevations well above 1,500 m in central Spain (Garzón, 1974) and the Atlas Mountains in Morocco (De Juana, 1980).

It is also puzzling that the Eurasian Hobby is lacking from the Cantabrian district where elevations are very modest and habitats seem to be adequate. It is, then, not so obvious why the Eurasian Hobby is almost completely absent from the Pyrenean and Cantabrian districts, especially in
the light of the fact that this species occurs in zones at higher latitudes where similar conditions prevail. A possible explanation would be the humid climate of the Cantabrian district and the cool temperatures of the Pyrenean sector might not favor the abundance of large insects (dragonflies, bumblebees, etc.), a major component in the diet of *Falco subbuteo*. In the neighboring Basque region where suitable habitat areas of open woodland exist but where humidity is also high, this species is reportedly rare (Álvarez et al., 1985).

**Pterocles orientalis** (Linnaeus) 1758

Cultivated land (CULT), summer mean temperature (HTEMP) and last frost of spring (SFROST) are the most important factors in accounting for the breeding distribution of this species over the study area (Table 9). The strong association observed for CULT (Fig. 6) came as no surprise since this is a steppe species with a definite inclination for open country in arid and stony terrain. This type of landscape is precisely found in areas of southern Navarre, such as the semi-desert Bardenas district in the SE. Since the Black-bellied Sandgrouse adapts very well to agricultural landscapes (Elósegui, 1985), the Mediterranean dry farming fields of southern Navarre also constitute suitable habitats.

This proclivity to occupy Mediterranean landscapes is in concordance with the positive association found for HTEMP (mean summer temperatures). The Mediterranean zones of the study area have the highest
summer temperatures and the earliest termination of spring frosts in
Navarre. According to Voous (1960) the July isotherm of 24° C constitutes
the northern boundary of the world breeding distribution of this species. In
the study area, the northern limit to its breeding distribution corresponds to
the July isotherm of 21° C. The thermic regimes prevailing in northern
Navarre, where summer temperatures range between 14° C and 20° C and
where spring frosts may take place as late as June, apparently exceed the
ecological tolerances of this species.

_Melanocorypha calandra_ (Linnaeus) 1766

Neighborhood effects (SWF), cultivated land (CULT), distance to rivers
(HDR350) and continentality (CONT) were the most important factors in
explaining the breeding distribution of the Calandra Lark in Navarre (Table
10). CULT was the most significant variable among the environmental
factors. The distribution of this species follows closely that of the flat
agricultural and steppe landscapes characteristic of the Ribera district.

The weaker but positive correlation with continentality also suggests a
preference of the Calandra Lark for warm, Mediterranean environments since
the Ribera district exhibits the highest values of the continentality index in
the study area. The absence of this species in central and northern Navarre
is explained by habitat and climate change from south to north, i.e., the
increasing scarcity of open-space habitats and a climate which becomes less
continental (cooler summers and milder winters) and progressively wetter.
Voous (1960) equates the northern boundary of the world distribution of the Calandra Lark with the July isotherm of 22° C. In the study area, its breeding distribution is contained below the July isotherm of 19°.

More difficult to interpret is the strong association found for HDR350, distance to rivers. Given the way in which HDR350 is numerically specified (see Methods section; Table 5), a positive correlation with it implies that the breeding probability for a particular species increases as one approaches a river. A negative association, on the other hand, would mean that the probability for a species to breed decreases as one approaches a river or stream. Therefore, the negative coefficient exhibited by HDR350 would seem to suggest a negative correlation between closeness to a river and the breeding probability of the species. From a biological perspective, this negative association could be reflecting the preference of *Melanocorypha calandra* for open spaces (steppes and flat arable terrain), avoiding riparian forests as breeding grounds.

*Lullula arborea* (Linnaeus) 1758

After SWF (neighborhood effects), PREC (annual precipitation) was the most important explanatory factor (Table 11), followed by $H_{\text{veg}}$ (vegetation diversity) and REGHUM (length of arid period). BIOCLIM, a measure of seasonal and altitudinal coldness, played only a secondary role.

The negative but strong association with annual precipitation indicates that the Wood Lark seems to avoid excessive humidity. On the other hand,
the positive correlation found for $H_{\text{veg}}$ suggests a preference for habitats of diverse vegetation. The negative correlation with REGHUM and BIOCLIM suggests that this species does not particularly favor arid and hot climates.

The ubiquity of *Lullula arborea* throughout central Navarre can be explained satisfactorily in terms of the sub-Mediterranean climate--moderately wet and not too hot--that this district enjoys and by its wide range of semi-open habitats, where zones of cultivated land alternate with grassland, scrubland and patches of woodland.

The infrequent occurrence of the Wood Lark in the *Ribera* district, Cantabrian Basin and parts of the Pyrenean region fits fairly well with the scheme just delineated. The Cantabrian district, where deciduous and coniferous forests alternate with grassland/scrubland, could theoretically offer plenty of suitable semi-open habitats but, at the same time, it may be unfavorably humid. The montane forests of the Pyrenean region may be too dense. The practically treeless and arid *Ribera* region does not offer many adequate biotopes for this species, and the few occurrences of the Wood Lark within this district (Fig. 33a) are linked to existing patches of Mediterranean pinewood and some riparian forests.

**Ficedula hypoleuca** (Pallas) 1764

Among environmental factors, vegetation structure ($H_{\text{veg}}$) appears to largely determine the distribution of the European Pied Flycatcher in the study area. Climatic factors are relegated to a secondary importance.
However, neighborhood effects play an even more critical role as denoted by the great margin by which SWF outperformed \( H_{veg} \) (Table 12).

The distribution of the European Pied Flycatcher in the study area (Fig. 36a) can be explained fairly well in terms of neighborhood effects and vegetation structure alone. The regular occurrence of this species in the Cantabrian district appears to be related to the availability of deciduous forests of beech and hydric oaks (see Appendix I for maps showing the distribution of the different forest types found in Navarre). In the sub-Mediterranean areas \textit{Ficedula hypoleuca} finds suitable habitats in the beech and mixed-oak forests of the western sierras. The reason for the absence of this bird from the semi-open landscapes of central Navarre may have to do with the make-up of the woodlands in this district, i.e., evergreen oaks (\textit{Quercus ilex} and \textit{Q. faginea}), along with some coniferous woods (Vouos, 1960).

The virtual absence from the Pyrenean sector is somewhat puzzling. The effective model predicts as suitable breeding areas a number of geographic units in the NE sector where \textit{Ficedula hypoleuca} is actually absent (see Figure 50b). The Pyrenean district is densely forested and possesses a general climatic regime similar to that of the western sierras where the species breeds regularly. Although there are important masses of \textit{Fagus sylvatica} as well as many small woods of hydric oaks, there is only one breeding occurrence recorded for the species (Fig. 36a).
Conifers, many of which have been planted in reforestation plans, are the dominant vegetation of this sector, and perhaps they inhibit the expansion of Ficedula hypoleuca into the Pyrenean district. It would be interesting to see the effect of a systematic use of nesting boxes in the coniferous forests of this district.

Sitta europaea Linnaeus 1758

$H_{veg}$ (vegetation diversity) was the most important factor in modelling the breeding distribution of the Eurasian Nuthatch in Navarre. CONT (continentality index), BIOCLIM (seasonal and altitudinal coldness) and REGHUM (length of arid period) played a secondary role (Table 13). The negative correlation with these three variables suggests the aversion of the Eurasian Nuthatch to warm and arid climates. The high positive association with vegetation diversity indicates the high dependence of Sitta europaea on forested areas.

These environmental conditions are found in the cool, humid forests of the Pyrenean region, northwestern sierras and also in the humid woods of the Cantabrian Basin. These areas are those parts of the study area with low continentality indices, oceanic to sub-Mediterranean climates and Eurosiberian bioclimatic zones. The absence of the species can be understood primarily in terms the scarcity of suitable habitats in central and southern Navarre. Secondarily, its absence must have to do with the
continental climate and aridity of the Mediterranean bioclimatic zones of southern Navarre.

*Serinus citrinella* (Pallas) 1764

The breeding distribution of the Citril Finch in the study area is most closely related to neighborhood effects (SWF), and also correlated with vegetation ($H_{veg}$) and altitude (ALT; see Table 14). Its breeding range coincides with the high-elevation, heavily vegetated, zones of the study area. They correspond to the Pyrenean sierras in the northeast, the Basque-Cantabrian sierras to the northwest and the mountains of the Cantabrian Basin of more modest elevations (Fig. 2). An isolated nucleus occurs in the pre-Pyrenean sierras the south of the Pyrenees (see Fig. 2), where vegetation is prominent and elevation reaches almost 1,500 meters. The absence of the species in approximately two thirds of the study area can be explained by the scarcity of woodlands and a decrease in elevation from north to south.

One issue calls for further consideration. If indeed the Citril Finch appears linked to montane forests, the precise biotopes and the elevation range where it occurs differ from the usual ones in other regions of its breeding range in the southwestern Palearctic (see Appendix II), i.e., coniferous forests at elevations above 2,000 m.
Elósegui (1985) reports that in the Basque-Cantabrian sierras, western Pyrenean sierras and in the mountains of the Cantabrian Basin, the Citril Finch appears associated with beech forests adjacent to alpine meadows, generally at altitudes above 1,000 meters. Since beech (*Fagus sylvatica*) forests are a predominant constituent of the Navarrese woodlands within the range of this species, it seems to have adapted to this habitat as it is the only one available in numerous potential breeding areas. This habitat shift has also been reported for this species in the neighboring regions of La Rioja and Basque Country (De Juana, 1980; Alvarez et al., 1985). In contrast, the populations occurring in the eastern Pyrenean sierras are found in fir and pine forests, at elevations of up to 2,000 meters as elevations increase from west to east. It remains unclear as to why the species is not more common in the pine forests of this same sector where altitude and habitat seem to be adequate. Figure 51b shows that the model does predict the breeding occurrence of the species in some of the empty grid cells in the Pyrenean district.

The low altitude at which some of the observations were made is also surprising, especially for a species which is not usually found below 1,200 m. There are occurrences mentioned (Elósegui, 1984) at elevations as low as 700 meters in the Cantabrian district. Álvarez et al. (1985) report observations at similar elevations the Basque region to the west of the study area.
Pyrrhula pyrrhula (Linnaeus) 1758

Vegetation diversity ($H_{\text{veg}}$) and July mean temperature (HTEMP) are the main environmental factors governing the breeding distribution of the Eurasian Bullfinch in the study area. Humidity was also important but on a secondary level (Table 15). Thus, in the study area, Pyrrhula pyrrhula avoids aridity and zones with hotter summers. This simple scheme explains well its distribution pattern in Navarre.

Pyrrhula pyrrhula occurs throughout the northern half of the study area, precisely where most of the suitable habitats—deciduous and coniferous forests—are available, and where humid to sub-Mediterranean climates with mild summers and abundant rainfall prevail. The distribution map predicted by the model (Fig. 52) only shows four grid cells in which apparently suitable habitats exist but where the species has not been observed. The absence from the southern half of the study area is readily explained in terms of the scarcity of humid forests and of high summer temperatures. Reportedly, the southern boundary of the breeding world distribution of the Eurasian Bullfinch is the July isotherm of 21° C (Voous, 1960). The vast majority of breeding occurrences in Navarre are below the July isotherm of 22° C.

All species considered

The analysis reported in this study shows that the breeding distributions of nine avian species strongly correspond with environmental
factors on a regional scale and often with a spatial weighting function (SWF) representing neighborhood effects. Significant associations most frequently found were between the species' breeding distributions and the spatial term, SWF, and twelve environmental factors (Fig. 53).

The spatial term, SWF, was the leading or co-leading explanatory variable in the effective models corresponding to five species (*Falco subbuteo, Melanocorypha calandra, Lullula arborea, Ficedula hypoleuca* and *Serinus citrinella*), implying that the occurrence of individuals of the same species in neighboring localities was a powerful predictor. SWF exhibited a very low profile for *Pernis apivorus, Pterocles orientalis, Sitta europaea* and *Pyrrhula pyrrhula*. The poor performance of this variable in the case of *Pernis apivorus* is consistent with the fact that its Moran's I coefficient was the lowest (Table 6) among the nine species, suggesting a low degree of spatial autocorrelation. However, the irrelevant role of this factor for *Pterocles orientalis, Sitta europaea* and *Pyrrhula pyrrhula* was surprising since these species exhibited very high Moran's I coefficients (Table 6), indicating a high degree of spatial autocorrelation.

The incorporation of the spatial term (Model II compared to Model I) was accompanied by a highly significant (P < 0.005) improvement of the avian distribution models for three species (*Falco subbuteo, Melanocorypha calandra* and *Lullula arborea*), a more modest (P < 0.1) improvement for two species (*Ficedula hypoleuca* and *Serinus citrinella*) and no significant
Figure 53. Number of significant associations between breeding distributions and explanatory variables for the effective models. Variable abbreviations are SFRS = SFROST, HTMP = HTEMP, CNT = CONT, BCL = BIOCLIM, EVT = EVTPOT, EXPR = EXPREC, RH = REGHUM, PRC = PREC and HDR = HDR350. The number of species is designated by basic type of distributional pattern exhibited in the study area, namely, Eurosiberian or Mediterranean.
improvement for the rest (*Pernis apivorus, Pterocles orientalis, Sitta europaea* and *Pyrrhula pyrrhula*) Table 16. This improvement for the majority of species did not translate into a dramatic increase in the overall forecasting accuracy of the models; PCE values generated by the study models without the spatial term (Model I) were already relatively high. Inclusion of the spatial term, however, did produce a significant increase in the sensitivity of most models, i.e., their ability to correctly predict a breeding occurrence. This increase was most dramatic at high cutpoint values, where sensitivity tends to be the lowest. For example, in the case of *Falco subbuteo*, its sensitivity increased from 16% to 51% for a cutpoint = 0.8. That the model correctly classified 51% of breeding occurrences at such a high cutpoint underscores the importance of the spatial term in the model.

Variables reflecting vegetation structure (H_veg and CULT; see Table 5), were important predictors of the avian distributions (see Fig. 53). Vegetation diversity was the best predictor for *Sitta europaea*; was as good a predictor as climate for *Pterocles orientalis* and *Pyrrhula pyrrhula* and was the second best predictor, after the spatial term (SWF), for *Falco subbuteo*, *Melanocorypha calandra, Ficedula hypoleuca* and *Serinus citrinella*. H_veg was associated more often with Eurosiberian species and CULT with the Mediterranean ones (Fig. 53). This reflects the different habitat requirements of each group of species, open spaces in the case of the
Mediterranean species and forests or semi-open forests in the case of those exhibiting northerly distribution patterns.

The addition of non-climatic factors particularly improved the performance of Study Model I for species which prefer humid-forest habitats (S. europaea, S. citrinella and P. pyrrhula), except in the case of F. hypoleuca. However, with the exception of F. subbuteo, inclusion of non-climatic parameters did not improve significantly the performance of Study Model I for species which prefer semi-open forests (P. apivorus and L. arborea) or open-habitats (P. orientalis and M. calandra). This finding suggests a relative heavier weight of habitat factors in determining the distributions of forest species than those of semi-open or open habitat species. As discussed in the previous paragraph, vegetation diversity and cultivated land within each geographic unit were primary predictors among habitat factors. Since humid forests are specifically restricted to the temperate zones of the study area, habitat factors become powerful indicators of both favorable areas and of moist climate. Therefore, explanations in terms of changes in vegetation are sufficient to accurately account for distributional patterns of species closely linked to forest habitats. Since semi-open forests and open habitats spread over wider areas, climate plays a more relevant role in the definition of the distributions of species which prefer these types of habitats.
The relatively high levels of forecasting accuracy generated by the climatic models (only included parameters were climatic variables; see Tables 7-15) would seem to indicate a close relation between climate and species distributions. Bustamante et al. (1988) found that climatic factors were significant in describing the patterns of breeding avifauna of eastern Navarre. However, the high level of forecasting accuracy observed for the climatic models may be inflated because of (1) the considerable correlation which exists among many of the climatic parameters and (2) the high correlation which exists between climate and vegetation.

When the performance of the climatic parameters specified in the effective models is compared to that of habitat variables, it would appear that they only play a secondary role in predicting the breeding distributions. Climatic factors were significant predictors ($\alpha = 0.05$) for six species. Of those, only in two instances ($P. apivorus$ and $L. arborea$) were climatic characteristics better predictors than habitat variables. In four cases climatic factors were either less significant than habitat variables ($M. calandra$ and $S. europaea$) or comparably good predictors ($P. orientalis$ and $P. pyrrhula$).

Climatic parameters which were significant can be classified as two basic types: thermic and hydric. Significant thermic variables were July mean temperature (HTEMP), continentality (CONT) and thermicity index or bioclimatic zonation (BIOCLIM). These variables seem to be in connection with the thermic regime during the breeding season --i.e., the spring-summer
period. Important hydric factors were potential evapotranspiration (EVTPOT), humidity regimes (REGHUM, length of arid period) and annual surplus of precipitation (EXPREC). These three variables are in connection with the moisture balance.

The biological reasons for the association between environment and spatial distributions are usually very complex. The reproductive cycle is a hazardous and costly process and therefore, breeding distribution patterns can be interpreted in terms of energetic constrains of reproduction in relation to survival (Blondel, 1990). Constraints on reproductive success are exerted both upon the adults and the young. While the parents have to balance maintenance needs with care of the young, the young in the nest are subject to direct climatic stress.

In temperate zones the critical season for survival is winter, when direct energetic costs of thermoregulation are maximum (Aschoff, 1981; Root, 1988a, 1988b) and food supply minimum. However, during the breeding season, when environmental conditions are much less harsh (particularly near the boundary with Mediterranean areas), i.e., direct energetic costs are minimized and food supply maximized, avian distributions should be affected by climate in indirect ways. Environmental factors, climate and habitat, are likely to interact with biotic constrains to determine breeding distributions by affecting the efficiency of foraging and reproduction rather than by causing direct death or total reproductive failure.
(Brown and Gibson, 1983). This implies that the ecological tolerances during the reproductive cycle of many avian species in temperate areas may be narrower in connection with habitat than in relation to climate. Habitats must provide the right elements for mating, nesting, foraging, etc, independent of their climatic characteristics, i.e., they must ensure that maintenance needs and thus the time needed for foraging are minimized and that when the young are hatched food is more plentiful (Elkins, 1988).

The critical season for survival in Mediterranean areas is not winter but summer which is dry and hot, and when food becomes scarcer than in temperate zones. High temperatures before the end of the breeding season constitute a limiting factor causing hyperthermia and problems of water balance for the young in the nest (Blondel, 1990). Low temperatures may be also a limiting factor at the beginning of the breeding season: low spring temperatures and/or late snows and frosts may delay breeding so much by its impact on food availability, that reproductive success is minimal (Elkins, 1988). The cost of reproduction in Mediterranean areas is especially high for the adults because they have to endure severe summer heat and dryness after great breeding effort. The findings in this study about the greater importance of habitat factors for the avian distributions analyzed are in harmony with the generally accepted idea that at least in the temperate zones, species breeding ranges seem to be more restricted by habitat than by any other factor (e.g., MacArthur, 1972). Organisms, particularly animal
species, do not possess an unlimited capacity to adjust to abrupt habitat changes, particularly at a demanding time such as the breeding season. Those breeding distributions which showed the closest association with climate corresponded to the three species which find in Navarre part of their northern (Black-bellied Sandgrouse and Calandra Lark) or southern (Eurasian Bullfinch) Palearctic distribution boundary (see Appendix I). This "boundary effect" implies that along the "edges" of these species distributions climate exerts a limiting effect not only by its possible influence on food supply, but more directly in connection with the species' physiological tolerances. Summer heat and aridity in the Mediterranean areas must exceed the ecological tolerance of the Eurasian Bullfinch. Coldness and humidity must preclude the presence of the Black-bellied Sandgrouse and Calandra Lark from the sub-Cantabrian zone. Although the Cantabrian zone is warmer than the sub-Cantabrian one, its wetness (particularly during spring) must exceed the ecological tolerance of these two species.

The Eurasian Hobby, European Pied Flycatcher, Eurasian Nuthatch and Citril Finch showed in general a stronger correlation with habitat factors. These species breed in a wider variety of climatic types (see Appendix II) than the previous three. This implies that although climate controls directly where the boundaries of a biogeographic distribution are, within the overall breeding range of a species, i.e., where climatic conditions are within permitted ecological tolerance of the species, habitat is the most important
determinant of species occurrence/absence. Their absence from the Mediterranean zones of the study area can be interpreted then in terms of the lack of appropriate habitats.

The European Honey-Buzzard and the Wood Lark constituted special cases in that in spite of exhibiting a broad climatic tolerance (they occur from boreal to Mediterranean climates; see Appendix II), they were more closely associated with climatic characteristics than with habitat factors in the study area. The specialized diet (i.e., honey, bees, wasps) of the European Honey-Buzzard may account for this circumstance. The absence of this migratory species from the wetter and more arid districts of the study area must be closely related, respectively, with food availability upon its arrival to the study area in late spring (Elósegui, 1985), and during the summer. The wide variety of habitats (grassland and heather with a meager presence of trees; woodland edges and clearings; fields bordered with hedges or protective trees; sparse oak woods; olive groves and orchards; see Appendix II) occupied by the Wood Lark may be related to the high correlation with climatic factors exhibited by its distribution in Navarre. This is reflected in its "sub-Mediterranean" distribution pattern, spreading over a wide central belt of territory, partially penetrating into both northern and southern Navarre. Thus, climatic factors were more effective than habitat factors in elucidating this species' distribution.
The evidence provided by this study can only be circumstantial. The explanatory models are based on the association between observed patterns and location attributes and explain the avian distributions only in that sense. In spite of its limitations, the correlative evidence presented here provides valuable information about what further research needs to be done in order to obtain more direct evidence showing how environmental factors limit the species distributions in relation to the ecology, physiology and behavior of the species. For example, data from this and similar studies could be used not only to judge which species should be examined physiologically and which species should be examined ecologically, but also to determine which environmental factors should be primarily investigated.
VI. CONCLUSION

This study describes how the breeding distributions of nine avian species in the region of Navarre (in Northern Spain) can be explained in terms of their environmental and spatial characteristics. A key feature of this investigation was to assess how well avian distributions could be accounted for in terms of climatic and habitat factors at the regional scale.

A second objective of this research was to illustrate the role of a GIS modelling strategy in assisting ecologists and biogeographers in displaying and analyzing distributional data. Inductive modelling, using spatial autocorrelation statistics and logistic regression analysis allowed the development and testing of hypotheses about spatially-varying relationships between different environmental variables. While the modelling strategy itself was described using avian distributions, it could equally treat higher taxonomic units and other kinds of organisms.

A spatial term representing neighborhood effects was the most important predictor in the models of five species distributions, and the inclusion of this spatial term improved the logistic regression models of those five species by increasing their sensitivity, i.e., their ability to correctly predict a breeding occurrence. The improvement of the models was reflected in a major increase in the sensitivity for two of the species distributions, though was less significant for another three.
Although patterns of association between the breeding distributions and environmental variables are complex and species specific, some common trends emerged. (1) Among the environmental factors, habitat structure was the most important determinant of the breeding distributions. Although climatic models --i.e., including only climatic parameters-- generated high levels of forecasting accuracy. (2) Climatic variables tended to be less significant than habitat variables in models in which both types of variables were specified.

The use of GIS, spatial autocorrelation statistics and logistic regression proved to be a valid approach to address the analysis of biogeographic distributions, as shown by the significant value of the models in predicting the avian distributions analyzed. Predictive modelling of this kind can be a useful addition to the current range of methodologies available to biogeographers and modelers of spatial data.
APPENDIX I. ENVIRONMENTAL CHARACTERIZATION OF NAVARRE

Geology and Physiography

Geologically, the study area constitutes a complex in which two major
morphotectonic regions can be distinguished, an alpine region, including
northern Navarre (originated as Iberia and France collided during the
Pyrenean phase of the Alpine orogeny, i.e., Eocene-lower Miocene), and a
neogenic region, corresponding to southern Navarre (formed during a
distension period, following the Alpine orogeny, which resulted in the
formation of a rift valley (Melendez-Hevia and Melendez-Hevia, 1978). The
geological structure of the study area conditions a marked orographic
contrast between the northern and southern parts of the study area. This
contrast can be seen in Fig. 2. Most of the northern half of the study area
lies above 600 m, whereas elevations in the south are for the most part
below 400 m. (MA & GN, 1986).

The Ribera region is characterized by flat terrain, only crossed by
gentle hills and sierras. The rugged Montaña district includes three
morphological zones (MA & GN, 1986):

1. The Pyrenean Zone to the northeast is formed by the western most
extension of the Pyrenees Mountains and associated pre-Pyrenean sierras.
Its axis, along which the highest elevations (up to 2,438 m) of the study
area are found, runs east-west in progressive degradation of the elevations
in that same direction.

186
2. The Basque-Cantabrian Zone includes the western half of the Montaña sector and is formed by the eastern fringes of the Basque-Cantabrian Mountains. Elevations are lower than those in the Pyrenean Zone.

3. The Cantabrian Basin lies in the northern tip of the Montaña district. This district includes the Cantabrian Watershed Mountains and lowland areas at elevations which approach sea level. Closeness to the ocean determines a relief characterized by narrow and steep valleys.

Climate

The climate of the study area is characterized by a north-to-south gradient of decreasing moisture and increasing temperatures. Northern Navarre has a temperate climate with mild winters, cool summers, high air humidity, abundant cloudiness, and frequent, evenly-distributed, rainfall. Frosts are rare due to oceanic influence. Southern Navarre has a continental climate, i.e., characterized by a sharp seasonal contrast of temperatures with severe winters and dry, warm, summers (Font-Tullot, 1983a,b; MA & GN, 1986).

The geographic variety of the study area and the combination of the temperate and Mediterranean climates over wide areas originate a considerable meso-climatic variation (Elias-Castillo and Ruiz-Beltrán, 1986; Elósegui, 1985; see Fig. 3).
The Candabrian climatic region is the wettest area of Navarre, with no arid period, mild temperatures year round and a short cold season. To the south, the rugged relief of the sub-Cantabrian region has both a cooling and a drying effect. Based on precipitation and temperatures, the sub-Cantabrian region can be subdivided into three zones: eastern or Pyrenean, western and central. The Pyrenean zone has a an alpine-like climate tempered by the effects of the ocean --i.e., very humid and with a long cold season. A similar climate, but drier, prevails in the western zone. In the central zone, the tempering effects of the ocean are felt more effectively due to its lower elevations, producing a more benign climate than those prevailing in both the western and Pyrenean zones.

With characteristics intermediate between a Mediterranean and a temperate climate, the sub-Mediterranean climatic region spreads over a central belt of territory along the southern edge of the Montaña district. Its climate is sub-humid, characterized by cooler temperatures and precipitation considerably higher (650-1,200 mm/yr) than those of the genuinely Mediterranean areas in the Ebro Valley.

In the Ribera district, climate becomes typically Mediterranean with an arid period of up to five months, hot summers, and cool winters. The northern portion of this area is slightly cooler and moister (500 to 650 mm/yr) than its southern portion, where precipitation never exceeds 500 mm.
Vegetation

In most of the Ribera district the potential vegetation would predominantly be evergreen, sclerophyllous forests (*Quercus ilex* ilex, *Q. i. rotundifolia*) with Mediterranean dry scrub (*Q. coccifera*) restricted to drier areas. In contrast, broad-leaf deciduous forests would be the typical vegetation of the Montaña district. Hydric-oak forests (*Q. pyrenaica*, *Q. pubescens*, *Q. robur*, *Q. petraea*, *Q. mas*) would occur in low-elevation, humid areas of the Cantabrian and sub-Cantabrian regions whereas higher elevations would support beech forests (*Fagus sylvatica*). Some aciculated formations (*Pinus sylvestris*, *P. uncinata*) would characterize high elevations of the Pyrenean district. Mesic-oak forests (*Q. faginea*) would occur naturally in the transitional sub-Mediterranean region between the temperate and Mediterranean zones. Riparian forests with abundant poplar, elm, alder, hazel, willow, etc, would occur along rivers both in the Montaña and in the Ribera districts.

Anthropogenic changes in the physiognomy of the vegetation of the study area are most dramatically evidenced by the reduction of the woodland range, much of which has been degraded to scrub or even to low heath or open grassland. Only about one third of the territory is covered today by forests (Elósegui, 1985). In addition, the composition of remaining forests has been impacted by reforestation programs introducing exotic species such as the Monterey Pine (*Pinus insignis*).
Forests are concentrated in the mountainous and relatively inaccessible portions of northern Navarre whereas farming predominates in the southern half. A description of the major vegetation types found in Navarre is provided below (MA & GN, 1986; Elósegui, 1985; Rivas-Martínez, 1987).

Fields and crops

Cultivated land (Fig. 6) represents about two 2/5 of the territory and occupies what once was forest and steppe ecosystems. Adjoining cereal fields of, mainly, wheat and barley represent 2/3 of the cultivated land with the rest corresponding to orchards, vineyards, olive and almond groves (MA & GN, 1986).

The Grassland

Natural prairies and meadows concentrate in northern Navarre (Fig 5a). Sub-alpine pastures, characterized by the abundance of Nardus stricta, occur in the Pyrenean areas. Mediterranean, montane pastures on sub-Mediterranean areas are characterized by the abundance of Festuca scoparia, while in the genuinely Mediterranean Ribera district are the pastures of Suaeda brevifolia, Agropyron glaucum, Atriplex halimus, etc.

The Scrubland

Scrubland (Fig. 5b) occurs in marginal habitats throughout the region’s ecosystems. The following types can be distinguished from north to south:
1. **Humid scrubland** occurs in degraded beech and hydric-oak forests of the Cantabrian and sub-Cantabrian zones and is characterized by the dominance of *Pteridium aquilinum*, *Erica sp.*, *Daboecia cantabrica* and *Ulex europaeus*.

2. **Sub-humid scrubland** is found in degraded pine and mesic-oak forests of central Navarre. *Buxus sempervirens* is the dominant species.

3. **Mediterranean scrub** occurs over degraded sclerophyllous-oak woodland areas of southern Navarre and characterized by the abundance of *Quercus coccifera* and *Rhamnus lycioides*. This dry scrub is often degraded to dwarf shrubs and herbs (rosemary, thyme, sub-shrubby flax, lavenders, sage, etc). Saltwort and other halophile shrubs are characteristic of endorreic depressions in the arid steppe zones of the *Ribera* district, whereas reeds and tamarix are typical of fluvial areas, pools and irrigation ditches.

**Woodlands**

Forests in the study area are dominated by beech (*Fagus sylvatica*). Beech forests alone represent almost 40% of the woodland of Navarre; the Navarrese region includes 1/3 of the range of this species in Spain (MA & GN, 1983). These forests cover the slopes of the Cantabrian Mountains and Basque-Cantabrian Mountains, but their importance decreases toward the Pyrenean district (Fig. 54a), where deforestation has been particularly significant.
Figure 54. Distribution of beech forests (A) and of coniferous forests (B) in the study area. Scots pine (*Pinus sylvestris*) is the dominant conifer in northern Navarre, whereas Aleppo pine (*P. halepensis*) is typical of the Mediterranean pinewood to the south.
Most of the conifers found in Navarre (Fig. 54b), with the exception of *Abies alba*, *Pinus uncinata*, *P. sylvestris*, *P. halepensis* and *Taxus baccata*, correspond to exotic species (*Pseudotsuga menziesii, Picea abies, Larix sp., Chamaecyparis lawsonia, Pinus insignis, P. laricio, Cupressus sp.*) introduced in reforestation programs. In the Pyrenean district deforestation has been followed by the spontaneous expansion of Scots pine (*Pinus sylvestris*).

Remnant forests of *P. montana* (var *uncinata*) are found in the eastern fringes of the Navarrese Pyrenees and some formations of Aleppo pine (*P. halepensis*) in southern Navarre.

Mixed coniferous/deciduous forests concentrate in the northeastern portion of Navarre (see Fig. 55a). To the northeast of the Pyrenean district beech forests are found in association with fir (*Abies pectinata*) and Scots pine (*Pinus sylvestris*), and to a lesser extent with hydric and mesic oaks. To the southeast are found mixed formations of Scots pine and xeric oaks.

Figure 55b shows the distribution of other deciduous species which usually form small, mixed forests such as beech/chestnut (*Castanea sativa*) and hydric-oaks/chestnut. Other deciduous species scattered in Navarre include, ash (*Fraxinus sp.*), mountain-ash (*Sorbus sp.*), birch (*Betula alba*), elm (*Ulmus sp.*), English walnut (*Juglans regia*), basswood (*Tilia platyphyllos*), hawthorne (*Craeagus sp.*), maple (*Acer sp.*) and holly (*Ilex aquifolium*). Only narrow stripes of the original riparian, broad-leaved, forests are left
Figure 55. Distribution of the mixed coniferous-deciduous forests (A) and broad-leaved deciduous (other than beech and oak) forests (B) in the study area. Beech/fir forests are particularly significant to the northeast. Scots pine/Holm oak forests are found to the southern portion of the Pyrenean district.
along some river courses. Alder (Alnus sp.), locust (Robinia sp.) and hazel (Corylus avellana) are characteristic of the Riparian forests of northern Navarre, whereas poplar (Populus alba and P. nigra), in association with willows, elms, etc, are typical of those of southern Navarre.

The temperate-Mediterranean transition existing in Navarre from north to south determines a hydric-mesic-xeric gradient of oak species (MA & GN, 1986). Hydric oak (Quercus robur, Q. petraea and Q. mas) forests correspond to small woods which exhibit a patchy distribution. Their main distributional areas are the Cantabrian, sub-Cantabrian regions and low valleys of the Pyrenean district (Fig. 56a). Sub-hydric oaks (Q. pubescens and Q. pyrenaica) are found in sub-Cantabrian and sub-Mediterranean areas.

Mesic oaks (Q. faginea) forests occur in sub-Mediterranean areas of central Navarre (Fig. 56b), compressed between the hydric oaks to the north and the xeric oaks to the south (Fig. 57a). Deforestation in the southern portion of Navarre has reduced the once extensive Mediterranean oak woodland. Small woods of Mediterranean oaks (Quercus ilex ilex and Q. i. rotundifolia) are found in the Ribera district and some Basque-Cantabrian areas. Paradoxically, their larger forests occur today in the Basque-Cantabrian sierras, Pyrenean valleys and central basins, i.e., the northern boundary of their potential range. Mixed hydric/mesic and mesic/xeric oak forests originate along contact areas between the different types of oaks (Fig. 57b).
Figure 56. Distribution of hydric (A) and mesic (B; *Quercus faginea*) oaks in the study area. The most northerly occurrences correspond to forests of *Q. robur* and *Q. petraea*, whereas the most southerly ones correspond to forests of *Q. pubescens* and *Q. pyrenaica*. 
Figure 57. Distribution of evergreen Mediterranean oaks (A; *Quercus ilex* *ilex* and *Q. i. rotundifolia*) and mixed oak forests (B) over the study area.
This appendix provides basic information about present world distribution, habitat requirements, diet and migratory/sedentary character of each species to help in the interpretation of the biological implications derived from the analytical sections. Descriptions below are based on Voous (1960) and Sibley and Monroe (1990). Notes on the species' distribution in the study area are based on Elósegui (1985), and information on their Iberian distribution were extracted from De Juana (1980). For English names I followed Clements (1991).

*Pernis apivorus* Linnaeus 1758. European Honey-Buzzard.

**Distribution:** west Palearctic, in boreal, temperate, Mediterranean and steppe climatic zones. It occurs in western and central Eurasia from south British, southern and northeastern Scandinavia, across northwestern and central Russia to southwestern Siberia and Mediterranean region (including Corsica), Turkey, Iran and Transcaucasia. In Iberia it is found in the mountains of northern and central Spain. Due to its elusive character, the breeding range described for *Pernis apivorus* in the study area may be incomplete. **Habitat:** wooded regions with open patches of meadow and grassland. **Food:** predominantly honey and the larvae, and adult insects, of wasps and bumble bees. **Movement:** migratory.
Falco subbuteo Linnaeus 1758. Eurasian Hobby.

Distribution: trans-Palaearctic and Oriental distribution, in boreal, temperate, Mediterranean, steppe, desert, and even tropical winter-dry climates. It is practically absent from Scandinavia and the British Isles and not abundant in the Mediterranean Basin. In Iberia, this species is more common in the northern regions than in the Mediterranean areas. The Eurasian Hobby is abundant in central and southern Navarre but it is absent from the Pyrenean sierras and Cantabrian district. Habitat: regions of open forest in mountainous country; cultivated land with growth of some trees; steppes with scattered and isolated patches of trees; and also in riparian forests. Food: large insects, small birds and, accidentally, small mammals and reptiles. Movement: migratory.

Pterocles orientalis (Linnaeus) 1758. Black-bellied Sandgrouse.

Distribution: the Black-bellied Sandgrouse has a reduced distribution within the Palaearctic, divided into two components: (1) an Asian contingent spreading from Anatolia and northern Caspian Sea to Pakistan and Turkestan, and (2) an Ibero-Berber population in the southwest palaearctic found in the Iberian Peninsula, Canary Islands and northern Africa. In Iberia this species occurs almost everywhere except in the humid regions of northern Spain. Its distribution over the study area exhibits a Mediterranean
character --present in the south and sporadic in central Navarre-- and forms part of the northern boundary of its European distribution. **Habitat:** arid, stony, streches, fields. **Food:** Seeds. **Movement:** Sedentary.

*Melanocorypha calandra* (Linnaeus) 1766. Calandra Lark.

**Distribution:** southwest palearctic, in Mediterranean and steppe climatic zones. It is found in northern Africa, Iberian Peninsula, southern France, central and southern Italy, Balkans, Balearic Islands, Sardinia, Sicily and Cyprus. It also occurs in Turkey, Near East, Iraq, Iran, northern Afghanistan, southern Russia, eastern Transcaspia and western Turkestan. The bulk of the European population of this species concentrates in the Iberian Peninsula where it is common except in the humid regions of northern Spain. Within the study area *Melanocorypha calandra*, with an estimated population of several thousand, exhibits a typically Mediterranean distribution, occurring in the *Ribera* district and barely penetrating into central Navarre. **Habitat:** dry open country, lowland grassy steppes with high vegetation; loamy sage brush steppes and flat arable terrain, cereal fields or areas where vineyards and cereal fields alternate. **Food:** mainly vegetable; small seeds and fresh grass shoots, also insects, such as grasshoppers. **Movement:** sedentary.
**Lullula arborea** (Linnaeus) 1758. Wood Lark.

**Distribution.** west palearctic, in boreal, temperate, Mediterranean and in steppe climatic zones. The Wood Lark is found from the southern British Isles, southern Scandinavia and central Russia to northwestern Africa, northern Mediterranean region, Turkey, Near East, west and southern Russia (Black Sea, Crimea, Caucasus and Transcaucasus) and western Transcaspia. Throughout its breeding range this species is reportedly sporadic and in Europe it is seemingly experiencing a retreat southward (Yeatman, 1976). In Iberia, *Lullula arborea* is found almost ubiquitously, with the exceptions of the most arid, as well as the wettest, areas of Spain to the southeast and north, respectively. Replicating this distributional pattern in Navarre, the Wood Lark occurs throughout a wide central belt of the study area, barely penetrating into the Ribera and Cantabrian districts. **Habitat:** dry, grass and heather, sandy areas with a meager and scattered presence of trees; woodland edges and clearings of forests bordering with scrubland; agricultural fields bordered with hedges and protective trees; sparse oak woods; olive groves and orchards. **Food:** mainly ground insects; also small seeds. **Movement:** sedentary.

**Ficedula hypoleuca** (Pallas) 1764. European Pied Flycatcher.

**Distribution:** west palearctic, in boreal, temperate, and Mediterranean climatic zones. From the British Isles (not in Ireland) and Scandinavia across
Russia to southwestern Siberia, and south in Europe to western and northern France, northern Italy, (former) Yugoslavia and Bulgaria; locally in the Iberian Peninsula and northern Africa. The remarkable disintegration exhibited by the western part of the breeding range is likely to be the consequence of the gradual destruction of old deciduous woodland range and with it suitable habitats. Reportedly, there has been an expansion of its breeding range in central Europe since the turn of the century, establishing itself in parks, man-planted pinewood and cultivated areas with clumps of trees. The distribution of the European Pied Flycatcher in Iberia has an Atlantic-montane character and is purely relictual, with sporadic occurrences in the mountains of northern and central Spain. In Navarre, the European Pied Flycatcher breeds in the Cantabrian Basin, Basque-Cantabrian Mountains and, very sporadically in the Pyrenean valleys. **Habitat:** well developed deciduous forests with abundance of old trees but also open forests; both beech and oak woods and other broad-leaved species. **Food:** small insects, including numerous small caterpillars. **Movement:** migratory.

*Sitta europaea* Linnaeus 1758. Eurasian Nuthatch.

**Distribution:** trans-Palearctic and Oriental, in boreal, temperate, savanna, and tropical winter-dry climatic zones and mountain regions. In Europe this species reaches southern Sweden and Norway but it is missing in Ireland, Scotland and the Mediterranean islands except Sicily. The status
of the Eurasian Nuthatch in the Iberian Peninsula is not known too well. Voous (1960) attributes a general distribution to this species, however it seems to be absent from a wide zone in southern and eastern Spain. This seems to be confirmed by the distribution pattern exhibited by the species in the study area as well as in the neighboring regions of La Rioja and Basque Country and in Catalonia on the NE corner of the Iberian Peninsula (De Juana, 1980; Alvarez et al., 1985; Muntaner et al., 1983). In all these regions, *Sitta europaea* appears conspicuously concentrated in the humid and mountainous areas, avoiding the Mediterranean sectors. In the study area, the Eurasian Nuthatch breeds throughout the northern part but it is noticeably absent from most of central Navarre as well as from the Ribera district. **Habitat:** a large variety of wooded regions, with predilection for closed and mature broad-leaved deciduous forests, particularly of beech and oaks. It is also found in mixed forests of different deciduous species and also in mixed coniferous/deciduous (fir/beech) woods but it becomes much less abundant in forests of evergreen oaks and Scotch pine. **Food:** insects, spiders, nuts, seeds and fruits. **Movement:** sedentary.

*Serinus citrinella* (Pallas) 1764. Citril Finch.

**Distribution:** disintegratedly in the southwest Palearctic, in boreal mountain zones of central and southern Europe. It is found in the Iberian Peninsula, Balearic Islands, central and eastern France, Switzerland, southern
Germany, west Austria, northern Italy, Corsica and Sardinia. The Citril Finch is the only avian species endemic to the mountains of Europe. Its patchy distributional pattern is like that of a relic. In the Iberian Peninsula, it is discontinuously distributed with isolated populations in montane zones of northern Spain and some sierras of central Spain. The breeding distribution of *Serinus citrinella* within the study area is restricted to montane zones of the northern part. **Habitat:** open rocky areas with light subalpine woods of spruce and larch; montane pine forests, dry scrub and sunny forest edges near the timber line. Usually at elevations above 1,200 meters. **Food:** seeds of spruce and fir; also small seeds of medium-sized plants. **Movement:** sedentary.

*Pyrrhula pyrrhula* (Linnaeus) 1758. Eurasian Bullfinch.

**Distribution:** trans-palearctic, in boreal and temperate climatic zones and mountain regions. This species is common in central and northern Europe but becomes rare in the Mediterranean regions. It occurs from Scandinavia to southern France, Italy, Balkans, Azores Archipelago and the Iberian Peninsula, where it is restricted to a narrow strip that extends from the eastern Pyrenees to northern Portugal. The Eurasian Bullfinch is widely distributed in the northern half of the study area. The Navarrese populations of Bullfinches, as the rest of the Iberian contingent of this species, constitute the distinct subspecies *Pyrrhula iberiae*. **Habitat:** mainly
coniferous forests with a rich understory of dense young trees; dark taiga of spruce and fir or mixed riparian forests of birch and poplar. Toward more temperate regions, the Bullfinch occurs in subalpine coniferous and mixed forests, montane beech and fir woods. Also, in western Europe only, it occupies mixed broad-leaved forests, garden with hedges and parks, provided there is a rich undergrowth of bushes, young spruce, or other dense young conifers. Whereas in central Europe the Bullfinch is a common bird in plain areas, in the Mediterranean regions it becomes a species eminently montane. **Food:** exclusively vegetable; buds and seeds of small plants. **Movement:** sedentary.
APPENDIX III. CHARACTERIZATION OF THE NAVARRESE AVIFAUNA

The breeding avifauna of the study area is constituted by 183 species which were observed during the period of 1982-1984. In addition, thirteen more species are mentioned by Elósegui (1985) whose breeding status could not be confirmed for the same period, and therefore will not be considered here as part of the Navarrese breeding avifauna.

Systematically the 183 breeding species are distributed by orders as shown in Table 18. The number of passeriformes (101) stands out when compared to that of non-passeriformes orders (82). This represents a ratio of passeriformes to non-passeriformes of 0.81, very different from 0.67 which is the value for the same ratio reported for the rest of Europe (Voous, 1960). This situation is probably related to the scarcity of aquatic biotopes, resulting in an extreme rarity, for example, of anseriformes and charadriiformes. The number of falconiformes (20) is considerably high however when compared to the rest of Europe (De Juana, 1980).

Table 19 contains a comparison of the relative proportions of the different families within the order passeriformes. Muscicapidae (Old World flycatchers, warblers, kinglets and gnatcatchers) predominate by a great margin over the rest of the families. Fringillidae (finches, serins, linnets, siskins and crossbills), alaudidae (larks), corvidae (crows, jays and magpies), Motacillidae (wagtails and pipits), emberizidae (buntings) and paridae ( tits) reach a relative importance.
Table 18. Composition of the Navarrese breeding avifauna by orders.

<table>
<thead>
<tr>
<th>ORDER</th>
<th>NUMBER OF SPECIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Podicipediformes</td>
<td>2</td>
</tr>
<tr>
<td>Ciconiiformes</td>
<td>6</td>
</tr>
<tr>
<td>Anseriformes</td>
<td>4</td>
</tr>
<tr>
<td>Falconiformes</td>
<td>20</td>
</tr>
<tr>
<td>Galliformes</td>
<td>6</td>
</tr>
<tr>
<td>Gruiformes</td>
<td>7</td>
</tr>
<tr>
<td>Charadriiformes</td>
<td>7</td>
</tr>
<tr>
<td>Columbiformes</td>
<td>7</td>
</tr>
<tr>
<td>Cuculiformes</td>
<td>2</td>
</tr>
<tr>
<td>Strigiformes</td>
<td>6</td>
</tr>
<tr>
<td>Camprimulgiformes</td>
<td>2</td>
</tr>
<tr>
<td>Apodiformes</td>
<td>2</td>
</tr>
<tr>
<td>Coraciiformes</td>
<td>4</td>
</tr>
<tr>
<td>Piciformes</td>
<td>7</td>
</tr>
<tr>
<td>Passeriformes</td>
<td>96</td>
</tr>
</tbody>
</table>

Table 19. Composition by families of the order passeriformes in the study area.

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>NUMBER OF SPECIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hirundinidae</td>
<td>4</td>
</tr>
<tr>
<td>Alaudidae</td>
<td>7</td>
</tr>
<tr>
<td>Motacillidae</td>
<td>6</td>
</tr>
<tr>
<td>Laniidae</td>
<td>3</td>
</tr>
<tr>
<td>Oriolidae</td>
<td>1</td>
</tr>
<tr>
<td>Sturnidae</td>
<td>2</td>
</tr>
<tr>
<td>Corvidae</td>
<td>7</td>
</tr>
<tr>
<td>Cinclidae</td>
<td>1</td>
</tr>
<tr>
<td>Troglodytidae</td>
<td>1</td>
</tr>
<tr>
<td>Prunellidae</td>
<td>2</td>
</tr>
<tr>
<td>Muscicapidae</td>
<td>37</td>
</tr>
<tr>
<td>Aegithalidae</td>
<td>1</td>
</tr>
<tr>
<td>Paridae</td>
<td>5</td>
</tr>
<tr>
<td>Sittidae</td>
<td>2</td>
</tr>
<tr>
<td>Certhiidae</td>
<td>2</td>
</tr>
<tr>
<td>Remizidae</td>
<td>1</td>
</tr>
<tr>
<td>Ploceidae</td>
<td>4</td>
</tr>
<tr>
<td>Fringillidae</td>
<td>9</td>
</tr>
<tr>
<td>Emberizidae</td>
<td>6</td>
</tr>
</tbody>
</table>
Species size and composition vary along the north-to-south gradient that climate and vegetation define in the study area. In northern Navarre, particularly in the Cantabrian Basin, large-size as well as raptor species are rare and the ratio of passeriformes to non-passeriformes is very high. The number of medium-size and large-size species increases toward the south of the study area, where the ratio of passeriformes to non-passeriformes decreases.

The ornithological significance of the Navarrese avifauna can be appraised by considering its different faunal elements. As a first approximation, the typology proposed by Voous (1960) for the European avifauna can be used. The meaning of this classification varies from one species to another. Sometimes the avifaunal type evokes the biogeographic history of the species, while very often it is merely a description of the present world distribution. Nonetheless, when taken as whole, Voous' avifaunal types offer an idea about which geographical and/or historical factors may have been involved in the formation of a particular region's avifauna -- evolution centers, invasion routes, hypothetical refugia during glaciation or dry periods, etc (De Juana, 1980).

Of the 23 avifaunal types proposed by Voous (1960), only 15 are found in Navarre. Brief descriptions taken from Voous (1960) for each of each of them as well as their respective proportions among the 183 breeding species in the study area are provided in Table 20. The high proportion of
Table 20. Description and relative importance of Voous' avifaunal types (Voous, 1960) with representation in the Navarrese breeding avifauna.

<table>
<thead>
<tr>
<th>FAUNAL TYPE</th>
<th>%</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palearctic</td>
<td>32</td>
<td>Belonging to the fauna of the cold, temperate, and subtropical regions of the northern half of the Old World.</td>
</tr>
<tr>
<td>European</td>
<td>11</td>
<td>Belonging to the fauna of the temperate and Mediterranean regions of Europe. This fauna must have extended after the latest glacial period from the Mediterranean northward into Europe.</td>
</tr>
<tr>
<td>European-Turkestanian</td>
<td>11</td>
<td>Belonging to the fauna of the temperate and Mediterranean regions of Europe and southwest Asia. This fauna must have survived the latest glacial period not only in the Mediterranean region, but also much farther east, probably far into Turkestan.</td>
</tr>
<tr>
<td>Mediterranean</td>
<td>11</td>
<td>Belonging to the fauna of the Mediterranean region.</td>
</tr>
<tr>
<td>Holarctic</td>
<td>8</td>
<td>Belonging to the fauna of the cold, temperate, and subtropical regions of the Northern Hemisphere.</td>
</tr>
<tr>
<td>Of the Old World</td>
<td>6</td>
<td>Belonging to the fauna of the great land-masses of Eurasia and Africa combined.</td>
</tr>
<tr>
<td>Turkestanian-Mediterranean</td>
<td>5</td>
<td>Belonging to the fauna of the summer-warm and summer-dry regions of southern Europe and southwest Asia, including the warm, low-lying steppes.</td>
</tr>
<tr>
<td>Indian-African</td>
<td>4</td>
<td>Belonging to a fauna which is now largely discontinuous geographically, but which in the late Tertiary and Pleistocene must have extended continuously from southern Asia to northern and central Africa.</td>
</tr>
<tr>
<td>Cosmopolitan</td>
<td>3</td>
<td>Having a wide distribution in all or all but one continents that the faunal origin can no longer be deduced from the present distribution.</td>
</tr>
</tbody>
</table>

(continued on next page...)

213
<table>
<thead>
<tr>
<th>FAUNAL TYPE</th>
<th>%</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paleomontane</td>
<td>3</td>
<td>Belonging to the fauna of the alpine of snow zones of the high mountains of the palearctic realm.</td>
</tr>
<tr>
<td>Paleo-xeromontane</td>
<td>3</td>
<td>Belonging to the fauna of the arid slopes of the low mountains of the southern palearctic realm; some paleo-xeromontane elements have, after the latest glacial period, spread into the dry, sunny slopes of the high mountains.</td>
</tr>
<tr>
<td>Paleoxeric</td>
<td>2</td>
<td>Belonging to the fauna of the steppes and deserts of the southern palearctic realm.</td>
</tr>
<tr>
<td>Ethiopian</td>
<td>0.5</td>
<td>Belonging to the fauna of Africa south of the Sahara.</td>
</tr>
<tr>
<td>Sarmatic</td>
<td>0.5</td>
<td>Belonging to the coastal fauna that in the late Tertiary and Pleistocene inhabited the shallow, brackish or salt Sarmatic inland sea. This sea formed a continuation of the eastern Mediterranean Sea, stretching to the north to the Black Sea and possibly covering the present Hungarian Plain; eastwards it extended to Caspian and Aral seas, covering the present Kara Kum and Kyzyl deserts.</td>
</tr>
</tbody>
</table>
palearctic species indicates the similarity between the Navarrese breeding avifauna and that of the rest of the palearctic (see also the considerable proportion of «Holarctic» species). The avifauna of the study area also has some species only characteristic of western Eurasia («European»); a good number of species which are found widespread at low and medium latitudes toward the interior of Asia («European-Turkestanian» and «Turkestanian-Mediterranean»); some are exclusive of the Mediterranean world («Mediterranean»), and the rest are of variable biogeographic origin and meaning (De Juana, 1980).

When the avifaunal types found in Navarre are compared with Europe as a whole, the absence of some types is apparent. Boreal species of the «Arctic» (42 species in Europe over a total of 407), «Siberian» (21 species), «Siberian-Canadian» (6 species) or «North Atlantic» (5 marine species) faunal types are completely missing. This is perhaps the reason for the overall higher proportion of «Palearctic» and even «Holarctic» species in relation to the rest of Europe. The proportions of «European-Turkestanian» and «Mediterranean» species are also higher than in the rest of Europe.
LITERATURE CITED


