GEOGRAPHICAL VARIATION IN THE DENSITY OF THE WHITE STORK Ciconia ciconia IN SPAIN: INFLUENCE OF HABITAT STRUCTURE AND CLIMATE

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Abstract
The spatial variation in the density of white storks Ciconia ciconia in Spain is analysed with respect to landscape and meteorological variables. The density of breeding pairs in 1985 was negatively correlated with surface cover of woodlands and shrublands, and positively correlated with the area of dry or wet grasslands, reflecting food availability and foraging preferences of the storks. Average minimum temperature in April-May (the first few days after hatching) was also negatively correlated with stork density, and the reproductive success in a colony at El Tietar (Avila) was inversely correlated with the number of days with precipitation in May. The negative influence of minimum temperature and precipitation on breeding density appears to be linked with the mortality of recently born nestlings. Practical recommendations are made for the conservation of the Spanish population of white storks through incentive use of pastures, meadows and 'dehesas' for cattle grazing. Reintroduction efforts must be direct towards zones having large areas of these habitats, and mild weather.

Key words: Spain, white stork, distribution, habitat, climate.

INTRODUCTION
For endangered species occupying large home ranges, a knowledge of the ecological factors affecting distribution and abundance on a wide spatial scale is needed to understand population dynamics. Such knowledge has been used to define management recommendations in order to preserve or increase populations (see papers in Verner et al., 1986).

Studies on the white stork Ciconia ciconia in Spain since 1960 indicate a wide distribution and high population level in the southwest of the Iberian peninsula (Bernis, 1981; Chozas, 1986; Lázaro et al., 1986).

METHODS
Zoogeographical analysis
The data for this work come from three principal sources: abundance and distribution of the white stork in Spain (Lázaro et al., 1986); meteorological data from the principal Spanish observatories (Elias & Ruiz, 1977), and agrarian information from the Ministerio de Agricultura (1978).

The stork census data are grouped by ‘comarca’ (agricultural region; \( x = 1897 \text{ km}^2 \), \( n = 151 \)), and density is calculated and expressed in pairs/100 km². The weather variables refer to those prevailing during

Nevertheless, annual censuses have documented a clear decline in numbers (Chozas, 1986). Two factors appear to be most important in explaining this population decline: habitat destruction and change in agricultural practices (Chozas et al., 1989). However, there is little quantitative information on habitat selection by this species except that reported by Pinowska and Pinowski (1989) for Poland. Similarly, the effect of climate on the distribution of white storks remains unknown (but see Hennemann, 1985, and Root, 1988). Reproductive success is negatively affected by low temperatures and/or high precipitation, especially during the first few days after hatching, when the thermoregulation capacity of the chicks is very limited (O’Connor, 1984; Järvinen, 1989). It is expected that geographical areas with colder and wet springs would support lower population densities than warmer areas. Therefore, a quantitative analysis of the geographical distribution of stork abundance in relation to structural and climatic variables could shed light on the factors implicated in the variation in density of this species (Caughley et al., 1988; Wiens, 1984).

In this paper we attempt to generate a biogeographical model to determine which environmental conditions affect the distribution of the white stork in Spain and to identify optimal habitats. This model is tested using a sample of spatial units not included in generating the model, to check the validity of its predictions related to management practices (conservation and reintroduction).
the most critical part of the breeding period (April-May) when hatching takes place (Bernis, 1981) and the young chicks have to survive cold conditions: average (TA) and minimum (TM) temperatures, precipitation (mm, P) and number of days with precipitation (NDP).

Although the climatological data do not include the census year (1984), it is considered that they provide a good representation of the climatological conditions of each agricultural region since they are the averages of a minimum of 10 years between 1950 and 1975. Besides, the white stork is a long-lived trans-Saharan migrant that shows a high degree of philopatry (Creutz, 1985), so that the variation in its abundance in large geographical regions should follow general meteorological patterns and not between-year changes on a short-term basis (Wiens, 1984). Only those agricultural regions where white storks were present during the year of the census were included in the analysis.

The habitat variables (expressed as percent cover within each ‘comarca’) are dry arable and waste land, irrigated crops, wet and dry grasslands (hay meadow and permanent pasture respectively), scrubland, ‘dehesa’ (grassland with scattered trees) and woodland. A Principal Component Analysis was applied to this set of habitat variables to obtain independent factors describing geographical variation in the landscape (Nie et al., 1975; Bhattacharyya, 1981). These new multivariate components and meteorological variables were used in a stepwise multiple regression analysis to predict white stork abundance in agricultural regions.

In order to check the validity and generality of the regression model, we randomly chose 50% of the agricultural regions to carry out a multiple regression. This randomization-regression process was repeated 30 times (Díaz & Carrascal, 1991). The 30 regression equations obtained were subsequently used to predict the abundance of white storks in the regions not used in building the model. If the regression model has general validity the observed and predicted values of density should be significantly correlated.

### RESULTS

The structural variables considered were reduced to three independent components by means of a Principal Components Analysis (Table 1). The first component (PC1) describes the structural complexity of the landscape: woodland and scrubland vs arable and waste lands. The second component (PC2) contrasts dehesa landscape with arable land, while the third (PC3) contrasts open grassland with areas dedicated to crops. These three components together explain 71.2% of the original variance.

Nest density in the areas where white storks were present was negatively correlated with the first component (r = 0.38, n = 151, p < 0.001). This relationship shows a negative correlation with woodland and scrub areas, rather than a positive relationship with arable or waste fields (the simple correlation between nest density and percentage of arable + waste land was not significant: r = -0.08, p > 0.1). This is in agreement with the observed behaviour of white stork, which tends to

### Annual variation of reproductive success

A colony of white storks in Central Spain (El Tiétar, Avila) provided a good series of annual data on reproductive success (Muñoz-Pulido et al., 1989). This colony is illustrative of the climate and landscape predominant in the main area of distribution where the species is most abundant: a temperate area of ‘dehesas’. Reproductive success was calculated as the number of fledged young per breeding pair. The same meteorological variables (May data) utilized in the zoogeographical analysis were obtained for El Tiétar from the archives of the Confederación Hidrogeografía del Tajo.

Multiple regression analysis was used to determine those meteorological variables which significantly explained temporal variation in the reproductive success.

All variables were transformed (logarithmic, square root or arcsin) before the application of appropriate statistical tests (Sokal & Rohlf, 1981).

![Fig. 1. Nest density variation in factor space (Factor 1 vs Factor 2). Surface has been smoothed with a moving average (mean of five points). Density of nests increases as structural complexity decreases (Factor 1) and the area of ‘dehesas’ and pasture increases (Factor 2).](image-url)
Table 2. Results of the stepwise multiple regression analysis for density of nests
(Partial correlation coefficient \((r_p)\) and explained variance are given; \(n = 151\) areas)

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
<th>(r_p)</th>
<th>Explained variance (%)</th>
<th>Accumulated variance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of nests</td>
<td>PC1</td>
<td>-0.390***</td>
<td>12.37</td>
<td>12.37</td>
</tr>
<tr>
<td></td>
<td>PC2</td>
<td>0.389***</td>
<td>11.33</td>
<td>23.70</td>
</tr>
<tr>
<td></td>
<td>PC3</td>
<td>0.362***</td>
<td>7.06</td>
<td>30.76</td>
</tr>
<tr>
<td></td>
<td>TM</td>
<td>0.307***</td>
<td>5.56</td>
<td>36.32</td>
</tr>
</tbody>
</table>

* Measured as \(100 \times b \times r\), where \(b\) = standardized multiple regression coefficient, and \(r\) = simple correlation coefficient (see Alerstam, 1978).

The relationships between nest density and the second and third components were positive \((r = 0.36, p < 0.001\) and \(r = 0.21, p = 0.01\), respectively), showing a direct association between the presence of storks and the proportion of dry or wet grassland. Figure 1 shows the pattern of variation of nest density in the plane spanned by the first and second components.

The stepwise regression analysis between nest density (dependent variable) and the three landscape components and the meteorological variables showed that the three components and the minimum temperature in April-May were significantly associated with density of nests (Table 2). This regression model explained 36.3% of the original variance in stork density across the geographical distribution in Spain.

Estimate of the predictive power of the regression model

The 30 stepwise regression analyses, carried out on a random geographical subsample of nests, showed that PC2 was always significant while PC1 and PC3 and TM were nearly always significant (Table 3). Other meteorological variables entering the model were the average temperature for April and May (TA) and total precipitation (P), but their irregular presence in the regressions indicates that they did not make a significant contribution in explaining the geographical variation of stork density. The average figure for the percentage of variance explained by these 30 regression models was 39% (SD = 6%), all models being significant \((p < 0.05)\).

The nest densities observed in the 76 'comarcas' which were not used in constructing the model showed significant correlation with the values predicted by all 30 regression models, i.e. when predicted values were plotted against observed values, the slope \((b)\) and \(y\) axis intercept \((a)\) did not differ significantly from 1 and 0 respectively (Table 3).

Reproductive success

The reproductive success of white stork in the colony of El Tiétar was inversely correlated with the number of days with precipitation in May \((r = -0.81, n = 8, p = 0.016;\ Fig. 2)\), i.e. the greater the number of days with rain, snow or hail during the first few days after hatching, the lower the fledging success.

DISCUSSION

The results of this work demonstrate that, apart from other factors of direct human influences (hunting, pesticides, destruction of nests, electric wires), the physical structure of the landscape and climate play important roles in determining the pattern of abundance of the white stork in Spain.

The extent of flooded meadow and pasture is a key determinant of the abundance of this species. The same pattern was obtained on a local scale in some other

Table 3. Number of stepwise regression equations which significantly \((p < 0.05)\) include any principal component \((1, 2, 3)\) and original weather variables predicting the density of breeding pairs in 50% of the randomly chosen agricultural regions

<table>
<thead>
<tr>
<th>Initial set of variables</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>TA</th>
<th>TM</th>
<th>P</th>
<th>NDP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of equations</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%</td>
<td>29</td>
<td>30</td>
<td>27</td>
<td>1</td>
<td>27</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>97</td>
<td>100</td>
<td>90</td>
<td>3</td>
<td>90</td>
<td>3</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Average</td>
<td>0.0083</td>
<td>0.1657</td>
<td>0.7858</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.0890</td>
<td>0.7220</td>
<td>0.5049</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(H_0) Significance level</td>
<td></td>
<td></td>
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</tbody>
</table>
zones of the Iberian Peninsula (Alonso et al., 1991) and the European continent (Dallinga & Schoenmakers, 1989; Randik, 1989). This demonstrates that habitat selection in the white stork is geographically very constant, with implications for its population density (see, however, Van Horne, 1983). The existence of a habitat with adequate food thus constitutes the most important factor in the distribution of this species on a national scale (30.8% of the variance is explained by the landscape components) (Hildén, 1965; Wiens, 1989, for similar results with other species on a larger geographic scale).

In various parts of Europe one of the suggested causes of population decline of the white stork has been the drainage of damp meadows, and their substitution by monocultures (Kuzniak, 1985; Randik, 1989). The loss of adequate habitat has probably also been the main cause for its population reduction in Spain since the 1950s (Bernis, 1981). From a longer perspective, however, the present abundance of the white stork should be much higher than it was in the past, since the potential (predominantly forest) vegetation of the Iberian peninsula has been replaced by areas of extensive agriculture (Bellot, 1978) which provide better feeding environments (Alonso et al., 1991). Man is at present causing a decrease in the population levels of this anthropophilous species through modifications to the habitat, while previously he contributed to its increase.

**Practical recommendations**

The most obvious recommendation is to preserve and encourage the use of 'dehesas', dry permanent pastures and hay meadows for cattle. Since the beginning of the century, these lands have suffered a considerable reduction in surface area in favour of the creation of large monocultures. Therefore, grasslands must be preserved, avoiding drainage, urbanization or transformation into extensive croplands.

Efforts at reintroducing the species or protecting its breeding (attempted in several parts of Spain; Chozas et al., 1988) should be directed towards districts where there are still large areas of hay meadow and permanent pasture, and which have mild weather during the hatching period. These reintroduced populations should serve as nuclei to attract flocks of immature individuals, which would enlarge the size of the breeding colony. The results of these measures should be appraised over several years because of the longevity of the species and the prolonged period of sexual immaturity.

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White stork in Spain