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Spatial and temporal migratory patterns of trans-Saharan birds in the Iberian Peninsula

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El doctorand

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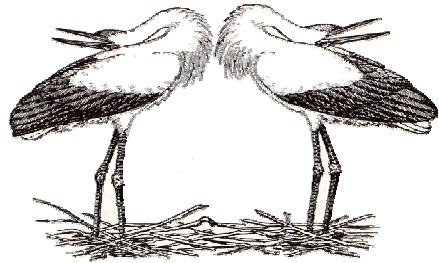
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Chapter 3

Spatial patterns of white stork migratory phenology in the Iberian Peninsula

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ABSTRACT

Oppositely to the attention attracted by temporal trends of phenology, the spatial patterns of arrivals, departures or stays of trans-Saharan birds are still nowadays largely unknown in most of their European breeding areas. In the case of the white stork *Ciconia ciconia*, some studies have attempted to describe its migratory patterns but, to our knowledge, no one has related these patterns to some kind of variable to offer an ecological-based explanation to the heterogeneous phenology observable among populations. Here, arrival, departures and stays of this species recorded in hundreds of Spanish localities were related to a set of environmental, geographical, biological and spatial predictors and modelled by multiple regression. The best model for arrival dates accounted up to 34% of variability of data and pointed towards an earlier arrival in those populations located in south-western Iberia and with higher population densities. This last relationship is probably due to the competition for nest-site fidelity maintenance. However, no variable was able to explain well the blurred spatial pattern recorded for departure dates. Departure decisions are strongly influenced by social behaviours in this species dependent on collective decisions influenced by peculiar local environmental conditions of each year rather than macrogeographic gradients. Environmental, geographical or spatial variables did not capture either much of the observed variability in the length of the stays among populations. However, this variable was strongly related to the arrival and departure dates of populations. White storks stay longer in localities with earlier arrivals and, especially, later departures.

INTRODUCTION

Phenology has received much attention in recent years thanks to its demonstrated ability to ascertain the effects of climatic fluctuations on organisms (Sparks & Crick, 1999; Sparks & Menzel, 2002; Sparks & Smithers, 2002). Particularly, birds has become one of the most employed bioindicators (Sanz, 2002; Crick, 2004; Lehikoinen *et al.*, 2004) thanks to its exhaustive monitoring both among investigators and amateurs (Whitfield, 2001; Collison & Sparks, 2003), which has allow the compilation of large databases for any sort of biological parameter (Sparks & Crick, 1999; Gibbons, 2000; Svensson, 2000; Collison & Sparks, 2003; Crick *et al.*, 2003). A growing number of studies have reported long-term temporal changes in several ecological parameters in accordance with the hypothetical effects of recent climate change (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003).

In opposition to this interest for its temporal fluctuations, few studies have paid attention to the spatial aspect of phenology (e.g. Rötzer & Chmielewski, 2002). When we focus on bird migration, this difference between time and space became even more disconcerting. The description of the spatial bird colonization patterns during spring migration was of great concern for some authors in the past century. This interest culminated in several studies for the commonest migratory species in some countries (e.g., Middendorff, 1855) or even for the whole European continent (e.g., Sliwinsky, 1938; Southern, 1938; Stresemann, 1948; De Smet, 1970). However, this topic was virtually forgotten in Western Europe during the last decades and only recently reassessed (e.g. Huin & Sparks, 1998, 2000). The situation is even worst for the Iberian Peninsula due to the absence of data when previously mentioned pan-European studies were carried out (Sliwinsky, 1938), making absolutely novel any report in this issue (Pérez-Tris & Santos, 2004).

Arrival and departure of migratory birds seem so obvious phenomena that nobody has wasted its time in an accurate and comprehensive description of its geographical patterns and as consequence this matter has remained unexplored until nowadays for most of species in many areas. To record, for example, the arrival date of a migrant bird is a very simple measurement.

However, the necessity of a huge number of data to cover an area with a dense network of observations is difficult to reach, especially if no volunteers are involved (Sparks & Crick, 1999). At present, the easy and simple approach to record the timing of bird migration by the observation of arrival and departure date remains equally valid as one century ago. Moreover, new and powerful analytical tools (e.g. GIS software) allow to investigators offer more thorough responses with this same kind of data.

The white stork (*Ciconia ciconia*) has been a classical study subject in bird migration. In the case of migratory phenology, this species shows many advantages to be included in a volunteer-based monitoring scheme. It is common (at least in some European countries), conspicuous (e.g. by using human building in lot of cases to bred their nests) and unmistakable (anyone knows how a white stork is). Therefore it is very easy to monitor with a minimal potential biases (Tryjanowski *et al.*, 2004; Tryjanowski *et al.*, 2005). There were some studies along the 20th century that described the geographical patterns of its migratory phenology (Sliwinsky, 1938; Zabłocka, 1959; Jespersen, 1949; Panouse, 1949; Grishchenko, 1995). Sliwinsky stressed specifically already in 1930s the absolute absence of data for the Spanish and Portuguese populations in spite of their numerical importance. This fact resulted in a partial picture of the migratory patterns for Europe because her maps did not included Iberian populations. All previously cited studies focussed on the description of spatial patterns of colonization and abandonment of breeding areas by white storks but suffer from an ecological-based explanation of these observed patterns since they did not relate phenology with any environmental variable. Therefore, there is still an empty space in the knowledge about the environmental variables related to the spring and autumn migratory phenology of the white stork. Variability in timing on arrival and departures due to the spatial configuration of territories affects in turn the calendar of the rest of life-cycle events such as laying and fledging dates (Slagsvold, 1977). Like in the inter-individual variability for the same population, this fact could be potentially reflected in a different reproduction success for each population (Lázaro *et al.*, 1986; Nowakowski, 2003; Tryjanowski *et al.*, 2005). This wins interest in a

species that showed strong fluctuations along the last century in their numbers with serious implications for its conservation status (Bernis, 1981; Dallinga & Schoenmakers, 1987; Bairlein, 1991).

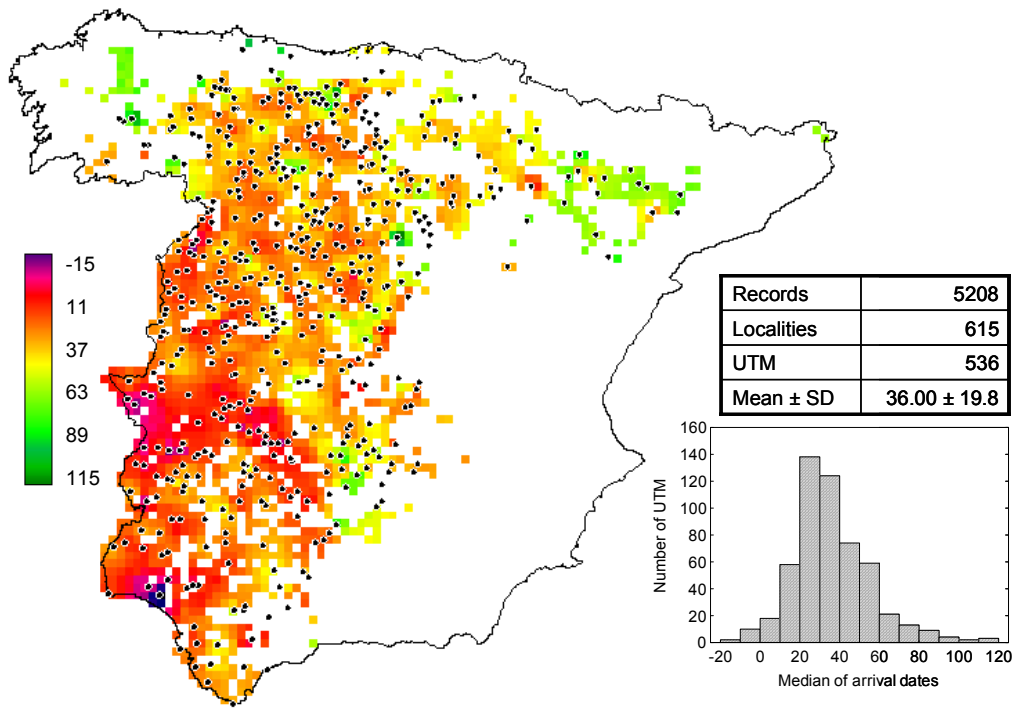
The aim of this study is to describe the geographical patterns of colonization during the spring, the abandonment during the autumn, and the variability in the length of the stay of the white stork populations from Spain. Furthermore, we searched for the underlying environmental variables to these spatial patterns to offer an explanation under an evolutionary ecology perspective of the observed variability in phenology among populations.

MATERIAL AND METHODS

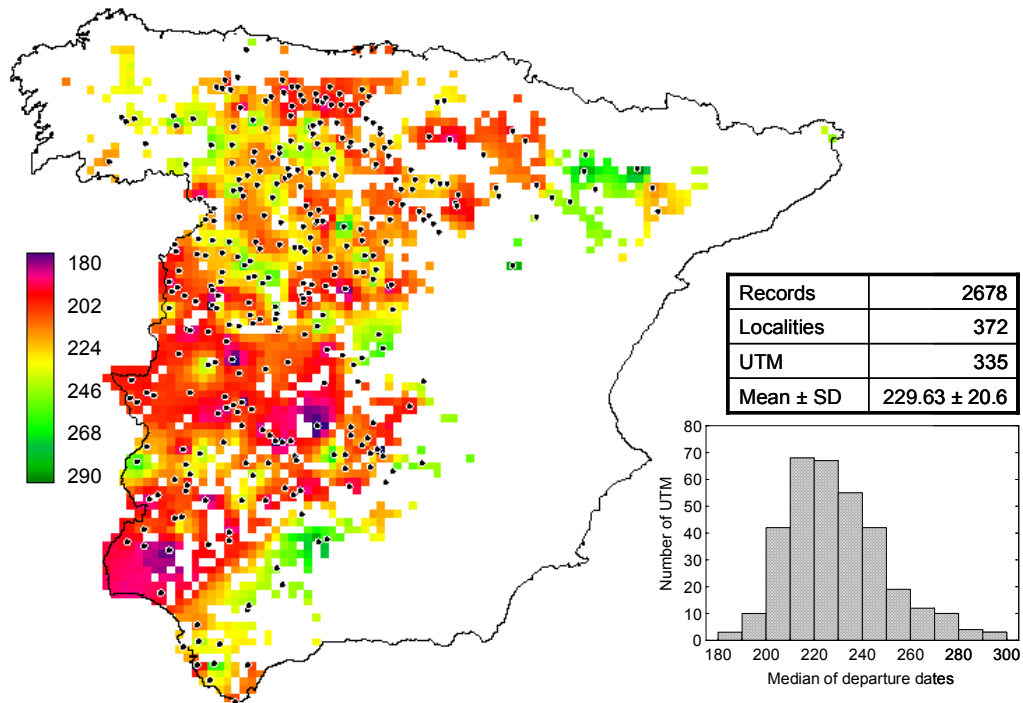
White stork phenological data

Migratory phenology data were obtained from the phenological database of the Spanish *Instituto Nacional de Meteorología*. This database results from a volunteer observer network created several decades before by the *Instituto Nacional de Meteorología*. These volunteers are recording since 1944 the arrival and departure dates of the white stork populations breeding in their home cities or towns in Spain. This species is especially appropriate for a long-term monitoring purpose based on volunteers thanks to use man-made structures for construction of its large and conspicuous nests (Lázaro *et al.*, 1986; Tryjanowski *et al.*, 2004; Molina & Del Moral, 2005). Furthermore, it is basically a gregarious species, commonly feeding in groups (Alonso *et al.*, 1994; Mullié *et al.*, 1995) and nesting colonially (Molina & Del Moral, 2005), and generally occurring in humanized habitats like cattle pastures, crops and farmlands. Hence, we are absolutely confident on the accuracy of records since it is difficult to skip over the presence of the species once it arrives or its absence once it departs. Furthermore, its morphology and habits are enough different to any other migratory species (e.g. black stork *Ciconia nigra*) to prevent any misidentification.

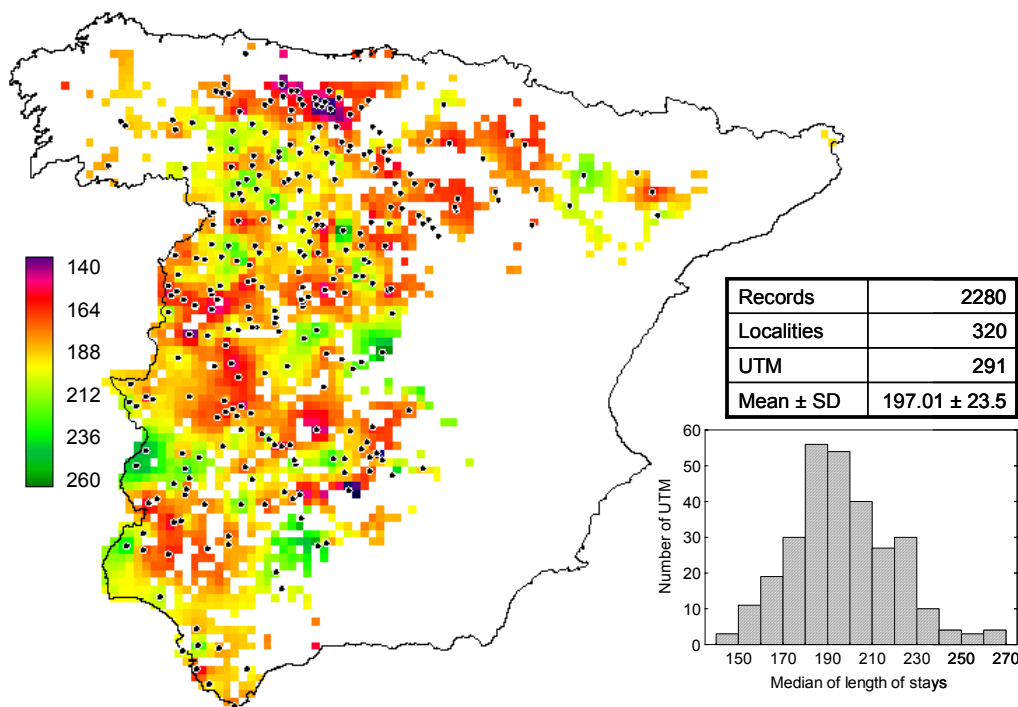
Three phenological variables were used. The arrival date was defined as the day when the first individual of the breeding population of a certain site was sighted. The departure date was the last day that an individual was observed in



a)



b)



c)

Figure 3.1 Maps of arrival dates (a), departure dates (b) and (c) lengths of the stays. Median values for each UTM were calculated by interpolation of data from available localities (black dots) to improve visual inspection of spatial phenological patterns. We have only represented values for those UTMs where the species breeds nowadays (Martí & Del Moral 2003). Scale colour bar in Julian day (1 = 1 January). Details about the number of records, localities, UTMs, mean, standard deviation (SD) and the histogram of the distribution of these observations are given for each variable.

a certain locality. Both dates were transformed in a Julian day scale (1 = first of January), taking into account leap-years and in these cases adding 1 day after 28 February. The length of the stay was defined as the number of days elapsed between the arrival and departure dates in the same locality and year when both records were available. The necessity of this coincidence is the reason for the scarcer number of records in this variable (see Fig. 3.1 for more details).

Previously to analyses, we corrected data of these three dependent variables to prevent effects of long-term temporal trends (Gordo & Sanz, 2006) which can potentially bias the comparison between UTMs with values recorded in different decades. To achieve this objective, we carried out a multiple regression analysis for each variable with the year and its quadratic term as predictor variables. Residuals from these models were used to correct original

data. Therefore, new corrected values for arrivals, departures and stays do not show temporal trends. Corrected dates were used hereinafter for all analyses.

The median value of all records included in the same UTM 100 km² square was calculated for the arrival, departure and length of the stay. As some volunteer observers reported data for near localities, the final number of available rows for calculations (i.e. different UTM cells) was fewer than the number of original localities since some localities were included in the same UTM (see Fig. 3.1).

Explanatory variables for phenological modelling

A set of 30 explanatory variables was used to model migratory phenology of the studied species (see Table 3.1). These variables were classified into four groups named: spatial, environmental, geographical, and biological. In the case of environmental group, seven topographic and ten climatic variables were extracted for each one of the 100 km² UTM Iberian squares (n=6063) using IDRISI 32 Geographic Information System (Clark Labs, 2001). Topographical variables were obtained from a Digital Elevation Model (Clark Labs, 2000). Mean, minimum and maximum altitude of all 100 pixels of 1 km² included in each 100 km² UTM were extracted and the altitudinal range in each cell calculated, together with the slope, aspect (the mean direction of the slope) and the diversity of aspects for each UTM cell. Climate were quantified through rainfall and mean temperatures during each one of the four seasons (spring, summer, autumn and winter), together with the annual temperature variation and an aridity index. The aridity index is expressed as:

$$AI = 1/(P/T + 10) \times 100$$

where *P* is the mean annual precipitation and *T* the mean annual temperature. All climatic variables were provided by the *Instituto Nacional de Meteorología*.

Two geographical variables were also calculated: the distance from each UTM cell to the Straits of Gibraltar and the distance to the closest main Iberian river. Since the Straits of Gibraltar is an obligate pass point for this soaring bird both during spring and autumn migration (Bernis, 1974; Bernis, 1975a,b; Fernández-Cruz, 2005) we expect later arrivals and earlier departures for those

Variables	Description
<i>Spatial</i>	
LAT	Latitude (m)
LONG	Longitude (m)
<i>Environmental</i>	
MEA	Mean altitude (m)
MIA	Minimum altitude (m)
MXA	Maximum altitude (m)
AR	Altitude range (m)
SLP	Slope (degrees)
ASP	Aspect (degrees)
DASP	Diversity of aspects
WIR	Winter rainfall (L)
SPR	Spring rainfall (L)
SUR	Summer rainfall (L)
AUR	Autumn rainfall (L)
WIMET	Winter mean temperature (°C)
SPMET	Spring mean temperature (°C)
SUMET	Summer mean temperature (°C)
AUMET	Autumn mean temperature (°C)
ATR	Annual temperature range (°C)
AI	Aridity index
<i>Geographical</i>	
DIR	Distance to rivers (km)
DSG	Distance to Straits of Gibraltar (km)
CSG	Cost from Straits of Gibraltar
CAN	Cantabrica
DUE	Duero
EBR	Ebro
GDN	Guadiana
GDQ	Guadalquivir
MIÑ	Miño
TAJ	Tajo
<i>Biological</i>	
ARR	Arrival date (Julian day)
DEP	Departure date (Julian day)
NNEST50	Number of occupied nests in the 50x50 km area around each UTM

Table 3.1 List of variables used in analyses. The acronym, complete description and units (in brackets) are given for each one.

far localities. Since it is a species closely related to the presence of rivers and water ponds (Lázaro *et al.*, 1986; Carrascal *et al.*, 1993) we also included the distance to the closest main river as a potential predictor.

Information on the major Iberian river basins was included in the model as categorical geographical predictors. We only included those basins were the



Figure 3.2 Map of the Iberian Peninsula with territory divided into basins of the main Iberian rivers. Solid lines delimit basins and broken lines are main rivers. Codes for the basins: 1-Miño, 2-Cantabrica, 3-Ebro, 4-Duero, 5-Tajo, 6-Guadiana, 7-Guadalquivir.

species occurred (see Fig. 3.2). All UTM squares were attributed to each basin according to a 0-1 code. Basins are a natural partitioning of the territory and they could be associated to regional differences in phenological dates.

Biological type variables were: population density and arrivals and departures dates. They can help us to discern between the imposed effects of the previously mentioned variables and the effects of some self-specific biological characteristics of the white stork. Population density was assessed by the number of occupied nests in the 25 km radius area surrounding each UTM cell. Data about the precise location of all nests in Spain were obtained from the white stork national census carried out in 2004 by SEO/Birdlife (Molina & Del Moral, 2005). Population density can affect phenology in two ways. Firstly, denser populations could increase chances for observers to detect early individuals (Sparks *et al.*, 2001; Tryjanowski & Sparks, 2001), although the conspicuousness of this species makes difficult such type of bias (Tryjanowski *et al.*, 2005). Secondly, in denser areas earlier arrival would be profitable for individuals since first arrived storks could maintain nest-site fidelity and save energy employed for its construction (Dallinga & Schoenmakers, 1987; Tryjanowski *et al.*, 2004; Vergara *et al.*, 2006). In the case of departures, arrival

dates were used to determine the influence of previous migratory phenology in this phase (Jespersen, 1949; Kosicki *et al.*, 2004). In the case of the length of stay, both arrivals and departures dates were included to estimate if the total number of days that white storks remain in their breeding grounds are related to early arrivals, later departures or both. We expect that the stays would be longer such as arrivals would be earlier and departures later.

Finally, spatial variables were simply used to assess the existence of spatial gradients. They were defined as the central latitude and longitude of each UTM cell and included in the analysis as a third degree polynomial (Trend Surface Analysis or TSA; see Legendre & Legendre, 1998). The nine terms of TSA can also aid to incorporate the effects caused by other historical, biotic or environmental variables not otherwise taken into consideration (Legendre & Legendre, 1998). Latitude and longitude were standardized (mean=0 and standard deviation=1) as topographical, climatic and geographical variables, in order to eliminate measurement scale effects of these variables.

Another hypothetical origin for heterogeneousness in arrival and departures dates observed among localities could be different wintering and pass areas among white stork populations. This fact is particularly important for this species since a growing number of individuals remain all years in Spain and North Africa during wintering period (Van den Bosche, 2002; Molina & Del Moral, 2005). Unfortunately, there is not a precise knowledge of the wintering area for each Spanish population and thus an explanatory variable with this kind of information could not be included in models. To check this hypothesis we gathered ringing data for Spanish individuals recovered during October and November. These months are considered the wintering period for Spanish populations of the white stork (SEO/Birdlife, 1996; Molina & Del Moral, 2005). Recoveries were classified in three regions: Spain, North Africa and sub-Saharan Africa.

Statistical analyses

To summarize the relationship between phenological and explanatory variables, General Regression Models (GRM) procedures implemented in STATISTICA (StatSoft, 2001) were performed. Since the unimportant deviations

from a perfectly normal distribution exhibited by all three dependent variables (see Fig. 3.1) do not have a sizable effect on the F statistic (StatSoft, 2001), regression analyses were accomplished with original non-transformed data.

Analyses were carried out into three steps. First, we explored the relationship between the dependent (i.e., arrival, departure or stay) and each explanatory variable one-by-one selecting the linear, quadratic or cubic function whose terms were statistically significant ($P < 0.05$). Secondly, only those explanatory variables with significant relationships in the previous step were submitted to a backward stepwise procedure group-by-group in order to examine the explanatory capacity of each type of variables. TSA performed with spatial variables assessed simply the spatial structure of data, while associations with environmental, geographical or biological variables help us to offer an ecological-based interpretation of these spatial patterns. After, all significant explanatory variables previously obtained in the environmental, geographical and biological models were subjected jointly to another backward stepwise procedure to obtain a complete model for white stork phenological variables. Finally, the nine terms of the third degree polynomial of central latitude and central longitude (i.e. spatial variables) were also incorporated to this complete model, backward removing all non-significant variables in order to determine potential relevant non-considered variables spatially structured. The predicted scores of this final model were mapped and examined.

To determine if the growing number of wintering individuals affect spatial patterns obtained by previous models, we repeated all previous models only with data for the period 1944 to 1980. The presence of a few wintering individuals has been reported in some cases since many decades ago (e.g. Duclós, 1956; Cruz-Valero, 1964). However, these anecdotic records became regular since 1980s (Tortosa *et al.*, 1995; Molina & Del Moral, 2005), although it is impossible to determine the precise year when numbers of wintering individuals began to increase because the first censuses were conducted in 1990s (e.g. Tortosa, 1992; Gómez-Tejedor & De Lope, 1993; Máñez *et al.*, 1994; SEO/BirdLife, 1996). The sharp advancement noticed by Gordo & Sanz (2006) in arrival dates since the beginning of the 1980s points towards also

those years. Therefore, data used as control in repeated models included only records until 1980.

Explanatory variables are always unavoidably correlated due to be immersed in a common spatial scenario (i.e. Spain). This fact hinders the estimation of their true relevance. To determine the relative importance of each type of explanatory variables a hierarchical partitioning procedure was implemented (Birks, 1996; MacNally, 2000; MacNally, 2002), so the 2^k possible functions among k significant explanatory variables was calculated estimating the importance of each one as the average effect of including this variable in all possible models built with the remaining ones.

To examine if residuals of arrivals, departures and stays models are still spatially structured, Moran's I autocorrelation coefficient with a Bonferroni-corrected significance level (Sawada, 1999) was calculated against ten classes separated by a lag distance of 50 km (from 50 to 500 km). Residuals from regression analyses with each type of explanatory variables were also checked for autocorrelation. If residuals are spatially autocorrelated, one or several important spatially structured explanatory variables can be left out (Cliff & Ord, 1981; Legendre & Legendre, 1998; Keitt *et al.*, 2002). These analyses were conducted with GS+ (Gamma Design Software, 2002).

To determine the existence of differences on the natal origin among individuals recovered during winter two ANOVAs were performed with the latitude and longitude where individuals were born as dependent variables and the wintering region as categorical predictor.

RESULTS

Spatial patterns and factors related to arrival dates

A visual inspection of the spatial variation in arrival dates does not allow detecting an obvious pattern (Fig. 3.1a). A region of earlier arrivals appears in the south western corner of Spain in opposition to the northern and eastern marginal populations where the latest dates were recorded. However, areas in between do not show a clear gradient from early towards late values. In overall, the extreme dates for the spring arrivals distribution of the white stork are

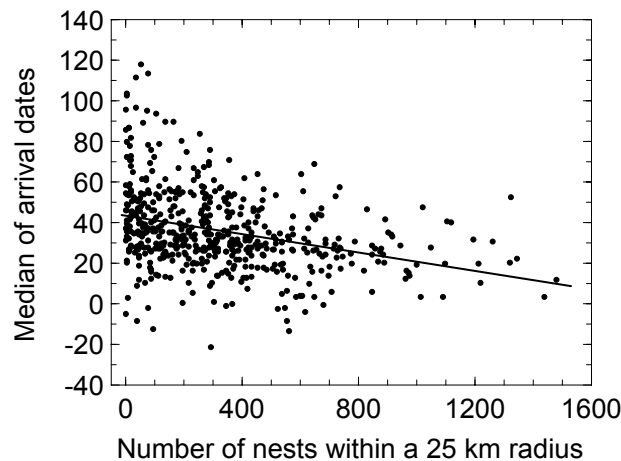


Figure 3.3 Scatterplot of the median arrival date against the number of occupied nests within a 25 km radius for each UTM. Solid line is the best linear fitted model.

between the last week of December and mid-April, which enlarged notably those reported in literature (Bernis, 1959) probably as result of our broad spatio-temporal dataset. Similarly to reported dates for Algeria (Jespersen, 1949), distribution of the arrival dates was slightly right skewed.

Trend surface analysis (TSA) performed with the spatial variables demonstrated the existence of weak but significant spatial gradients (Table 3.2). Signs of latitude and longitude in the spatial model indicated that white storks arrive later to northern and eastern localities, as showed the Fig. 3.1a. Environmental and geographic models showed almost the same explanatory capacity (Table 3.2). The relationships of arrivals and the involved variables in both models agree with the previous general pattern. The positive relationship with summer rainfall and aridity index pointed towards earlier arrivals to those drier and more arid regions. These regions are in southern Spain. However, both included basins in the geographic model (Cantabrian and Ebro basins; see Fig. 3.2) showed later arrivals. They are located in northernmost parts of the white stork distribution in Spain. The quadratic function with distance to the Straits of Gibraltar of the geographic model pointed also towards later arrivals to those localities far away from Gibraltar. On the other hand, the biological model included significantly the number of nests. Those localities with higher number of nests in the surrounding areas were also those with earlier arrivals (Fig. 3.3).

Model type	Variables	<i>b</i>	Adj R^2	Pure Adj R^2	Control Model
Spatial	LONG	14.171	0.260	0.091	0.264
	LAT	4.218			
	LONG ² xLAT	9.007			
	LATxLONG ²	-6.903			
Environmental	AR	4.090	0.247	0.079	0.231
	SUR	20.065			
	AI	10.044			
Geographical	CAN	26.384	0.231	0.062	0.189
	EBR	12.100			
	DSG	8.672			
	DSG ²	2.893			
Biological	NNEST50	-0.022	0.108	0.042	0.112
Complete	AR	3.222	0.300		0.293
	EBR	9.526			
	SUR	6.147			
	AI	14.781			
	NNEST50	-0.014			
Complete + spatial terms	LONG	10.631	0.337		0.326
	LONG ²	6.652			
	LAT	-6.181			
	LONGxLAT	-11.920			
	EBR	9.361			
	SUR	13.505			
	NNEST50	-0.011			

Table 3.2 Best models obtained for the spring arrivals. The variables included in each model, their respective parameters (*b*), the adjusted coefficient of determination (Adj R^2), relative importance (Pure Adj R^2), and the explanatory capacity of the same models with data for 1944-1980 period (control model) are showed for each type of variables (spatial, environmental, geographical and biological), the complete model and the complete model with spatial terms. All models were significant at $P < 0.0001$ and included only significant variables at $P < 0.05$. See Table 1 for the acronyms of the explanatory variables.

When models were repeated with data for the period 1944-1980, the explanatory capacity was almost identical (Table 3.2).

The final complete model included five variables and had a bit more of explanatory capacity (Table 3.2). Among these variables summer rainfall and the number of nests were the most relevant (partial R^2 for both variables = 0.225). Although the residuals of each model did not show significant autocorrelation scores at any lag distance (Fig. 3.4), the complete model could be slightly improved when the spatial variables were included. This stresses the probable existence of some remaining variability unable to be explained by the

employed explanatory variables. The mapped scores obtained from the final model (Fig. 3.5a) help us to visualize better the underlying gradients in arrival dates which are difficult to percept in the picture resulting from original observations (Fig. 3.1a). White storks arrive first to the south-western corner of Spain, especially across the Guadiana basin. After, most of the breeding grounds are colonized in only one month. Finally, later populations reach the northern margin and the Ebro basin around mid-March according to our model.

Spatial patterns and factors related to departure dates

The picture obtained from departure dates did not show any obvious spatial gradient (Fig. 3.1b). Earlier dates occur in some sites located in the south-western extreme of Spain and near the centre of the distribution (purple colours). However, the last individuals are sighted in the Ebro valley, some localities from the Northern Plateau and the south-eastern fringe of the Iberian distribution. Therefore, rough data did not offer evident patterns since early and late departures are not clearly segregated in the space. According to our dataset, departures begin in mid-July and continue until the end of September. This period enlarges also previously reported dates due to the longer temporal and broader spatial range of our data set (Bernis, 1959).

The absence of clear patterns after a visual inspection of rough data was confirmed through the extremely poor model performance of TSA as well as the other types of employed variables. In TSA, only a significant gradient to later departures appeared in eastern localities (Adjusted $R^2 = 0.012$; $F_{1,333} = 5.10$; $P = 0.025$). In the case of geographical group, no explanatory variable was significant related to departures and thus no model could be constructed. In the case of environmental variables, the model included only the aridity index (Adjusted $R^2 = 0.015$; $F_{1,333} = 6.21$; $P = 0.013$). White storks leave later those more arid sites. The biological model included both the population density and the median arrival date in the same UTM (Adjusted $R^2 = 0.047$; $F_{2,321} = 8.96$; $P < 0.001$). White storks depart later in those sites with low density and later arrivals. When these models were repeated with data for the period 1944-1980, the explanatory capacity was almost identical (values of the adjusted coefficient

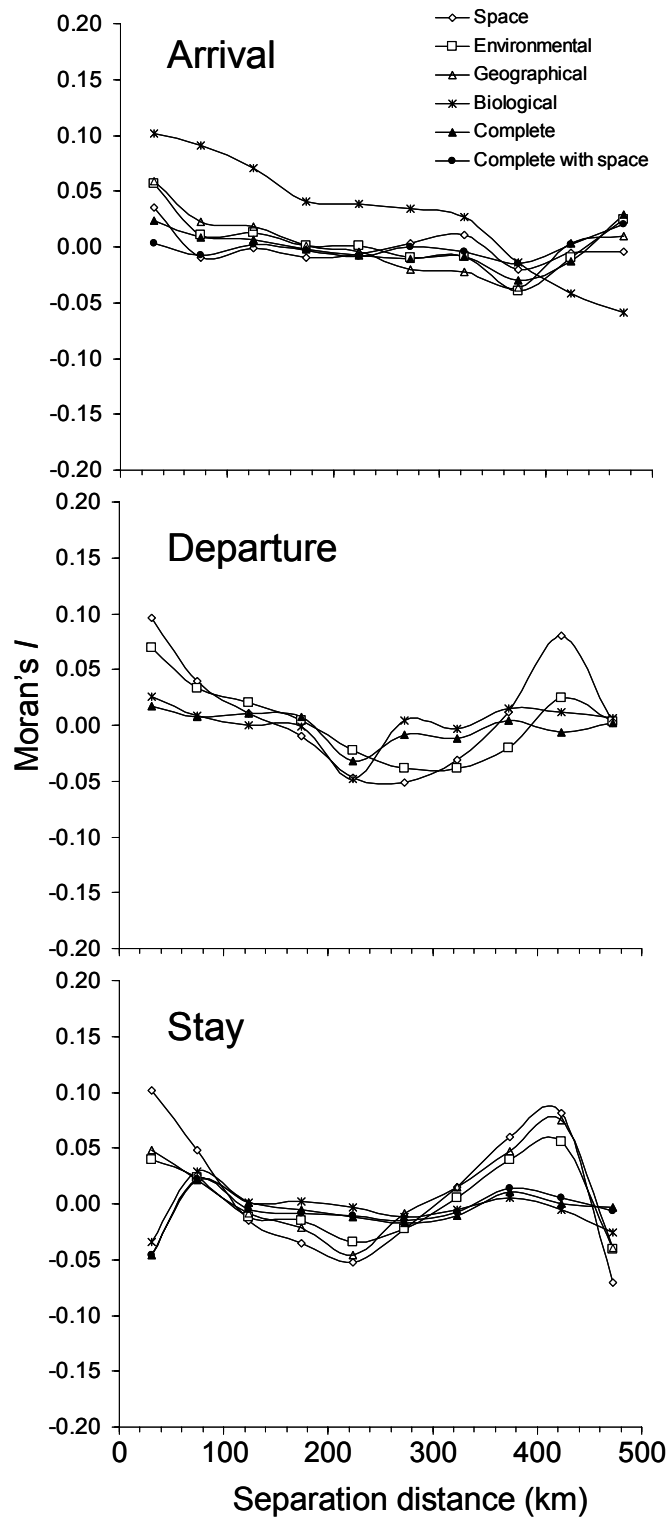


Figure 3.4 Spatial autocorrelation of residuals from spatial, environmental, biological and final complete models accomplished for arrivals, departures and stays. Isotropic correlogram represents the variation in the scores of Moran's I spatial autocorrelation statistic with the increasing in the separation distance between 10x10 km UTM cells (in km), using a lag distance of 50 km and an active lag of 500 km.

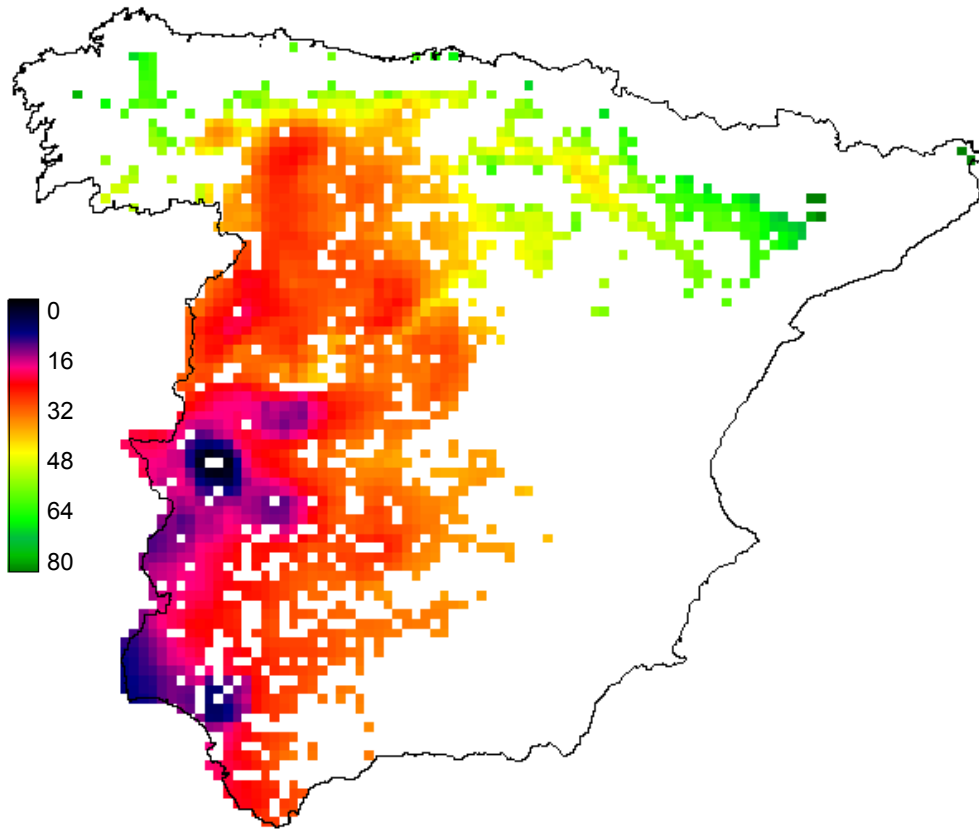
of determination were: spatial = 0.056; environmental = 0.019; biological = 0.048).

When all the former variables were submitted together in a complete model, only the arrival date and the aridity index remained (Adjusted R^2 = 0.061; $F_{2,321}$ = 11.49; P < 0.001). Spatial terms do not add any significant term when they were included together with these variables. This fact emphasizes the inexistence of spatial gradients in dates of departure. The control model was slightly better (Adjusted R^2 = 0.071). Predicted scores (Fig. 3.5b) points towards earlier departures in the south-western extreme of Spain, in opposition to later ones in all eastern populations. However, in spite of the significance of the model, the biological reliability of this pattern should be carefully taken into account due to the extremely low explanatory capacity. Neither residuals from the final models nor residuals for each type of variable models showed spatial autocorrelation at any lag distance (Fig. 3.4).

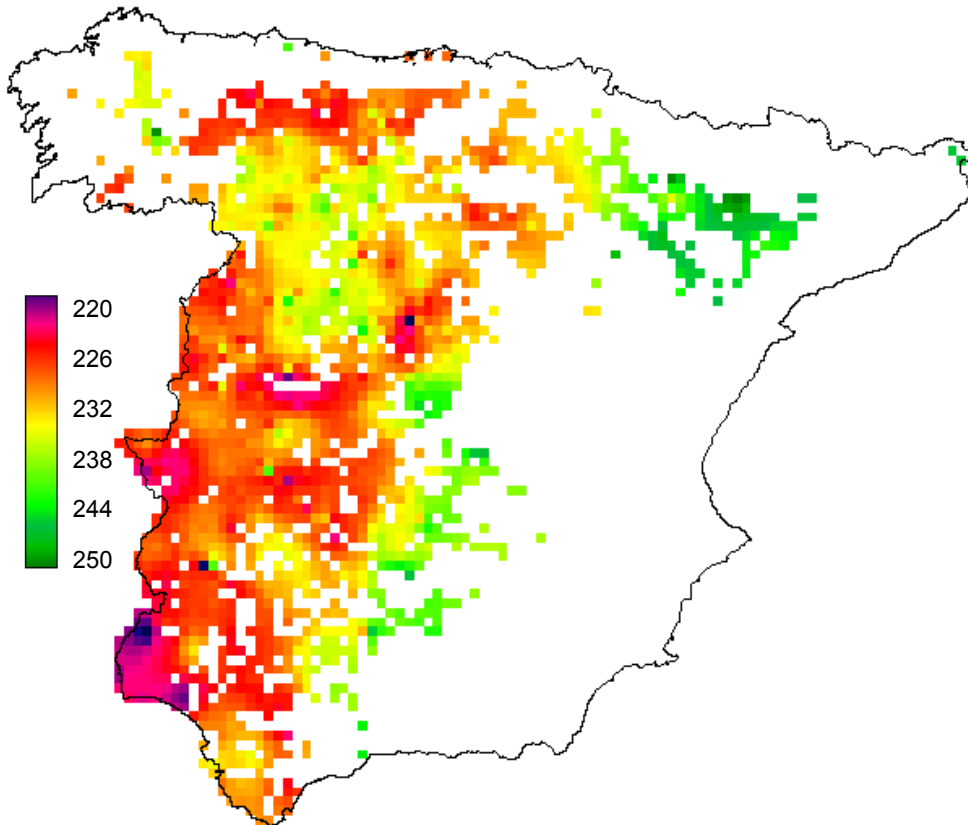
Spatial patterns and factors related to the length of the stay

There is not any spatial clear pattern (Fig. 3.1c), as in departure dates. Short and long stays appeared in a complicated patchiness according to interpolated median values. The shortest stays were recorded in the Cantabrian basin, whereas the longest occurred in several localities from the centre and southern Spain. The distribution of median values for stays was close to normality ranging from 5 to 8 months. Therefore, there were large differences in the length of the stay among localities.

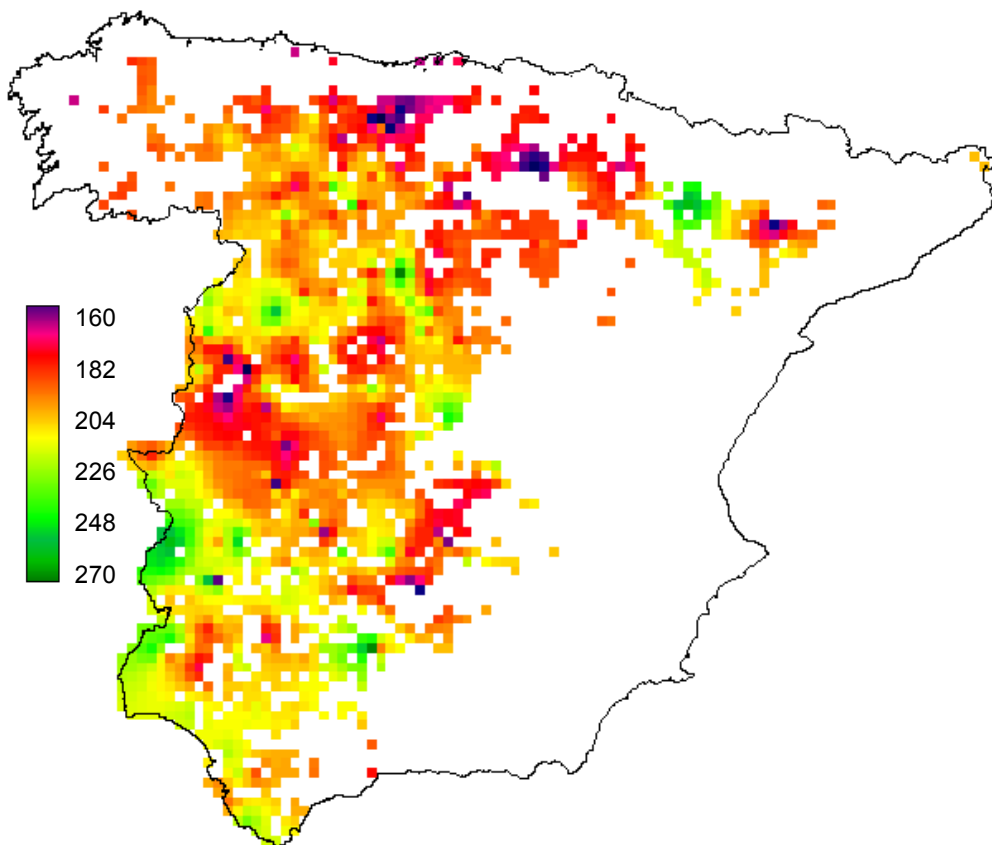
Spatial, environmental or geographical variables were unable to explain most of this observed variability. Final TSA model included only latitude (Adjusted R^2 = 0.061; $F_{1,289}$ = 19.75; P < 0.001). There was a slight gradient towards shorter stays in northern areas. Stays were better modelled by environmental variables (Adjusted R^2 = 0.104; $F_{1,289}$ = 34.63; P < 0.001). This model only included summer rainfall. White storks remain more time in those localities with less precipitation during the summer. The geographical model included also only one variable (Adjusted R^2 = 0.062; $F_{1,289}$ = 20.20; P < 0.001). White storks stayed less time in those localities far away from Straits of Gibraltar. The spatial, environmental and geographic models showed moderate



a)



b)



c)

Figure 3.5 Geographical representation of predicted scores for 10x10 km UTM cells from the best final complete models of (a) arrival dates, (b) departure dates and (c) length of the stays. Scale colour bar in Julian day (1 = 1 January).

explanatory capacities and had the same interpretation: white storks from southern populations stay for a longer period. However, in spite of significance of these models, the low explanatory capacity diminishes again the biological reliability of this pattern.

In contrast to arrivals and departures, the biological model for this variable did not include the number of nests. However, the relationships with median arrival and departure dates were extremely strong (Adjusted $R^2 = 0.842$; $F_{2,288} = 773.3$; $P < 0.001$), especially with the last one (partial adjusted $R^2 = 0.491$). Longer stays are related to earlier arrivals and especially to later departures.

The final complete model was almost identical to the previously described (Adjusted $R^2 = 0.844$; $F_{3,287} = 522.9$; $P < 0.001$). The overwhelming

explanatory capacity of this model was related with the relevance of the migratory phenological variables. Summer rainfall was also included, although its importance in this final model was negligible. When spatial terms were included, this environmental variable was substituted by latitude. In any case, the explanatory capacity remained equal (Adjusted $R^2 = 0.846$; $F_{3,287} = 524.5$; $P < 0.001$). The overwhelming dominance of arrival and departure phenology in the final models was expected according to the pure adjusted R^2 for each group of variables (spatial = 0.008, environmental = 0.025, geographical = 0.011, biological = 0.766). There were a slight decrease in the explanatory capacity in all control models (values of the adjusted coefficient of determination were: spatial = 0.055; environmental = 0.075; geographical = 0.040; biological = 0.827; complete model = 0.827; complete model with space = 0.827).

These final models, as the rest, did not show spatial autocorrelation for their residuals (Fig. 3.4).

Natal origin of wintering recoveries

A total of 123 wintering recoveries were found for Spanish individuals ringed between 1957 and 2002 (24 in Spain, 44 in North Africa and 55 in sub-Saharan Africa). There was no differences in the natal latitude among recovery regions ($F_{2,120} = 1.06$; $P = 0.350$). However, wintering individuals in Spain belong to more eastern populations than those recovered in North Africa and sub-Saharan Africa ($F_{2,120} = 10.263$; $P < 0.001$).

DISCUSSION

Models for spring migration of the white stork were able to capture only partially the enormous variability observed among localities (see Fig. 3.1a). However, some gradients arise from data which points towards certain spatial structure of arrivals in relation with some of the extrinsic (environmental and geographical) and intrinsic (biological) variables used in our analyses. Among environmental variables, climate was revealed as the most important predictor, although its predictive capacity was moderate and better related to prevailing conditions during the summer. A greater effect of climate during pre-nuptial migratory period (i.e. winter climate variables in Table 3.2) was a priori

expected, especially in this species because arrivals for the overwhelming majority of the Iberian populations are at the height of winter (see Fig. 3.1a; Cavanilles, 1802; Bernis, 1959), when low temperatures may be restrictive for migrants. However, hardness of Mediterranean winter climate is not enough (especially in southern Spain) for a large bird able to resist adverse cold climatic conditions as the white stork (Mata *et al.*, 2001). The occurrence of wintering individuals all years in the Iberian Peninsula (Duclós, 1956; Cruz-Valero, 1964; Tortosa, 1992; Gómez-Tejedor & De Lope, 1993; Máñez *et al.*, 1994; Tortosa *et al.*, 1995, SEO/Birdlife, 1996; Marchamalo, 2002; Vergara *et al.*, 2004; Molina & Del Moral, 2005) suggests also that this species is not constrained by winter low temperatures here. Therefore, colonization patterns of the white stork are independent of the progression of the spring course through Iberia due to its extremely early return.

During the last two decades a growing number of wintering individuals has been recorded in the Iberian Peninsula (Gómez-Tejedor & De Lope, 1993; Máñez *et al.*, 1994; Tortosa *et al.*, 1995; SEO/BirdLife, 1996; Marchamalo, 2002; Vergara *et al.*, 2004; Molina & Del Moral, 2005). These individuals could seriously affect measurements as the arrival and departure dates because they are sensitive to any “aberrant” migratory behaviour (e.g. sick individuals). This influence has been noticed already for the temporal trends in migratory phenology of this species (Gordo & Sanz 2006). These wintering individuals can erroneously produce earlier or later records for arrivals and departures, respectively, in those areas close to their wintering places. Alternatively, wintering individuals in Spain are close to their breeding sites and thus can potentially advance its phenological calendar as a whole (Kosicki *et al.*, 2004; Massemin-Challet *et al.*, 2006). However, our study demonstrates that the existence of wintering individuals is not the reason for the relatively weak spatial patterns observed in the white stork arrivals. Explanatory capacity and the effect of predictor variables for the same models performed with data recorded between 1944 and 1980 were almost identical. Therefore, the existence of increasing numbers of wintering individuals in recent years does not affect observable differences among populations at a macroscale as Spain. On the

other hand, the hypothetical link between populations with earlier arrivals (or later departures) and preferred wintering areas in Spain or North Africa was not supported by ringing recoveries for the period 1957-2002. Moreover, wintering individuals in Spain belonged to more eastern populations, i.e. those with the latest arrivals (see Fig. 3.1a), which would be contrary to predictions. In conclusion, nor the presence of wintering individuals neither differences in wintering selected quarters are the origin of the weak spatial patterns for white stork arrivals (and departures).

Another phenomenon that could help to understand the absence of strong spatial patterns linked to environmental gradients during the spring migration is the long period between the arrival and the start of breeding. In the Iberian Peninsula, firsts eggs are laid about mid-March (Cramp & Simmons, 1977; Bernis, 1981), two month later than the arrival of the first individuals. Therefore, the crucial period between spring arrival and beginning of the reproduction is much longer than in most of migratory bird species. Since the white stork is a single-brooded species, an earlier arrival does not increase chances for second and third clutches as in other migrants (e.g., barn swallow *Hirundo rustica*; Møller, 2002). However, Tryjanowski *et al.*, (2004) showed for an eastern population that an early return have benefits for individuals throughout higher breeding success. This association is mediate by the date at which laying begins. However, it is difficult to imagine how can be affected reproduction in Spanish white storks since the period between the arrival and laying exceeds notably that recorded for eastern populations (about 15 days; Tryjanowski *et al.*, 2004). Furthermore, the guaranteed food supplies through all the breeding seasons by rubbish dumps would diminish the importance of an early return (Tortosa *et al.*, 2002; Tortosa *et al.*, 2003; Masseurin-Challet *et al.*, 2006) These strong differences force us to stress more caution when results for the better studied eastern populations are extrapolated to the Iberian populations because both groups probably are under different evolutionary pressures as result of the environmental peculiarities of their breeding, wintering and pass areas (Bernis, 1959).

In denser populations, earlier individuals could also have higher breeding success due to the competition for nest occupancy (Dallinga & Schoenmakers, 1987; Sasváry *et al.*, 1999; Tryjanowski *et al.*, 2004; Sæther *et al.*, 2006; Vergara & Aguirre, 2006; Vergara *et al.* 2006; but see Wuczyński, 2005). Earlier individuals avoid the costs of nest construction by reutilization of best placed old nests within the colony. Time and energy saved in construction of such enormous nests could be invested in reproduction enhancing fitness of earlier individuals. In fact, nest-site fidelity is very high in Iberian populations (about 80 %) and it is related to lower breeding failure, which demonstrates the importance of nest reutilization for individuals' fitness. Moreover, in a context with a density regulation influenced by social factors such as defence of best breeding territories, aggressive intraspecific interactions, or limited access to food resources (Tryjanowski & Kuźniak, 2002; Massemin-Challet *et al.*, 2006; Sæther *et al.*, 2006) earlier individuals would be also benefited. This hypothesis is fully in agreement with the strong negative association found in the present study between arrival dates and population density (see Fig. 3.3). However, this denso-dependency may be reflecting a potential bias in records (Sparks *et al.*, 2001; Tryjanowski & Sparks, 2002). Since the characteristics of this species make difficult to skip over its arrival (or departure) date (Tryjanowski *et al.*, 2004; Tryjanowski *et al.*, 2005; Sæther *et al.*, 2006), we think that early arrivals are not a sampling artefact due to increased chances of observers to detect early individuals in those more populated areas.

A third alternative hypothesis could be even suggested for the relationship between arrivals and population density. Those areas with higher density of breeding individuals could simply coincide with those ones with earlier migrant populations because both variables are immersed in the same spatial matrix (i.e. the Iberian Peninsula) which imposes common environmental gradients. Regressing residuals from the trend surface analysis of the arrival dates against population density revealed still a strong negative association between them ($r = -0.191$; $t_{536} = -4.509$; $P < 0.001$). Therefore, those more populated areas receive earlier individuals even if the spatial pattern due to environmental and geographical factors is removed. We conclude that

competition for nest-site fidelity maintenance and other social mechanisms for density regulation are the best candidates to explain this relationship.

Interestingly, the aridity index and the precipitation in summer were the only climatic variables included in models. Both variables are closely related to the productivity during the summer, the most unfavourable and limiting season under a Mediterranean climate. The influence of these variables concurs with the well-coupled life cycle of the white stork with the wet seasons of the breeding and the wintering areas, at least in the case of the Iberian populations (Bernis, 1959). The white stork arrives to Iberia at the height of the winter, when water is not restrictive thanks to precipitations of the previous autumn, those that are falling during the winter and those that will fall in the next spring. This very early arrival allows white storks to finish its breeding season in early summer (June-July). The white stork thus avoids dry and harsh conditions at the end of the summer (August-September) during the reproductive period in spite of its long duration (more than 3 months; Bernis, 1981). Moreover, departing at this time individuals can reach Sahelian wintering quarters at the end of monsoon season and they can consequently profit benign ecological conditions during October and November in that region. When dry season in the Sahel became restrictive (December-January), the white stork returns to Iberia again. Therefore, it is not surprising that rainfall influences also spatial phenological patterns in this species, as it does in many other biological parameters of its life-cycle (Maclean *et al.*, 1973; Kanyamibwa *et al.*, 1990; Carrascal *et al.*, 1993; Kanyamibwa *et al.*, 1993; Mullié *et al.*, 1995; Barbraud *et al.*, 1999; Jovani & Tella, 2004; Sæther *et al.*, 2006). In conclusion, an early arrival to those more arid regions in Spain during the summer benefits individuals doubly because: 1) they avoid poor environmental conditions during this season which can compromise individual survival by advancing all life-cycle (i.e. arrival, breeding, laying and fledging), and 2) they profit the peak of productivity available already very early in the spring as result of the especially marked seasonality in those more arid regions.

Environmental and geographical variables were unable to explain most of the variability observed among localities both in departure dates and length of

stays. This was expectable since there were no strong spatial gradients, as the trend surface analyses revealed. Due to the reliability of recorded dates and the low effect of wintering individuals (i.e. equal adjusted R^2 in control models), we conclude that poor model performance can be only attributed to the veritable absence of a strong spatial structure in both variables (see Fig. 3.1). However, the absence of strong relationships with one or some explanatory variables makes extremely difficult or even impossible to offer ecological-based responses for large differences observed in departures dates and lengths of stays among populations.

In departure dates, one can argue that there are mixed records of Spanish and Central European individuals during the post-nuptial migration (August-September). If it is true, then the meaning of such date would be seriously questionable. We think that this possibility is improbable in our study. Individuals from Central Europe migrate southwards mainly through the Mediterranean coast (Bairlein, 1981; Papi *et al.*, 1997; Fiedler, 2002; but see Barbraud *et al.* 1999; Vergara *et al.*, 2004; Molina & Del Moral, 2005), where Spanish storks do not breed. Moreover, these populations represent a small fraction of the western European population group (approximate ratio between Spanish and Central European white storks 20:1; Van den Bosche, 2002). Therefore, the probability of confusion between Iberian and non-Iberian individuals is still scarcer.

The absence of spatially structured factors with effects on departure dates could be due to: 1) the social behaviour of white storks during the autumn migration, and 2) the questionable correspondence between departure dates and the real onset of the autumn migration. During July and August, Spanish white storks show a growing gregariousness (Bernis, 1959). Individuals from close populations aggregate in large flocks (sometimes up to several thousands of individuals) in those best places for feed (e.g. rubbish dumps) and roost (e.g. salt-marshes) prior to the definitive departure towards African wintering quarters (Fernández-Cruz, 2005). These flocks would reduce migration cost because locate lift in an easier way and more active individuals encourage others to finish its stay in breeding grounds (Kosicki *et al.*, 2004). Therefore, departure

dates are probably recording in most cases the displacement of individuals towards a meeting point of near populations and thus the beginning of flock formation prior to the real onset of the autumn migration. In conclusion, departures are strongly influenced by social behaviours, which in turn depend on collective decisions influenced by peculiar local environmental conditions of each year rather than macrogeographic gradients.

The absence of clear spatial patterns in the length of the stays could be also due to the questionable meaning of such phenological measurement at population level. Firstly, arrival and departure dates are two extreme measures of the respective distributions of arrival and departure dates in a certain population. Anyone can expect that the amplitude (and thus its extreme values) of such migratory distributions would be directly dependent on the population size. More numerous populations should show more diversity in its arrival and departure dates and thus should increase the time window employed by the whole population, i.e. larger stays. However, the length of the stay was the only phenological variable non-related to the population density. Therefore, results do not support this hypothesis. Secondly, stays rely more strongly in departure dates (higher partial R^2 in final models), which could be an invalid measurement for autumn migration in this species as we have previously discussed.

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RESUM

Patrons espacials de la fenologia migratòria de la cigonya blanca a la Península Ibèrica

A diferència de l'interès suscitat per les tendències temporals de la fenologia, els patrons espacials de les arribades, emigracions i estades de les aus transsaharianes és encara desconegut per a molts dels seus territoris de nidificació europeus. En el cas de la cigonya blanca *Ciconia ciconia*, alguns estudis han

intentat descriure els seus patrons migratoris però, pel que sabem, cap d'ells ha relacionat aquests patrons a alguna mena de variable per tal d'oferir una explicació amb fonament ecològic per a l'heterogeneïtat observable en la fenologia entre poblacions. En el present estudi, arribades, emigracions i estades d'aquesta espècie enregistrades a centenars de localitats espanyoles es van relacionar amb un conjunt de predictors ambientals, geogràfics, biològics i espacials, i es van fer models de regressió múltiple. El millor model per a les arribades va explicar fins el 34 % de la variabilitat de les dades i va indicar que les cigonyes arriben abans a les poblacions del sud-oest de la península amb majors densitats de població. Aquesta última relació es probablement deguda a la competència per ocupar el mateix niu. Per contra, cap variable va ser capaç d'explicar els patrons observats per a les dates d'emigració. La decisió d'emigrar està molt influenciada per comportaments socials, que depenen de decisions col·lectives influenciades per les condicions particulars que hi ha nivell local cada any més que no pas per gradients macrogeogràfics. Les variables ambientals, geogràfiques o espacials tampoc van ser capaces de capturar gaire de la variabilitat observada en la durada de les estades entre poblacions. En canvi, aquesta variable es va relacionar molt fortament amb les dates d'arribada i emigració de la població. Les cigonyes romanen més temps en localitats amb arribades més primerenques i especialment amb emigració més tardana.