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Spatial patterns of white stork (*Ciconia ciconia*) migratory phenology in the Iberian Peninsula

Oscar Gordo · Juan José Sanz · Jorge M. Lobo

Abstract In contrast 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 throughout some European countries but, to our knowledge, no one has related these patterns to some kind of explanatory variable which offers an ecologically-based explanation for the heterogeneous phenology observable among populations. Here, arrivals, 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 modeled by multiple regression. The best model for arrival dates accounted for 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 properly the blurred spatial pattern recorded for departure dates. Departure decisions are strongly influenced by social behavior in this species and depend on collective decisions influenced by peculiar local environmental conditions of each year rather than macrogeographical gradients. Environmental, geographical or spatial variables also did not capture 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.

Keywords Autumn departure · Length of stay · Modeling · Spain · Spring arrival

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Introduction

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 and Yohe 2003; Root et al. 2003). Among them, those focused on organisms' phenology has received much attention in recent years thanks to the demonstrated ability of the timing of natural events to ascertain the effects of climatic fluctuations (Sparks and Crick 1999; Sparks and Menzel 2002; Sparks and Smithers 2002). As opposed to this interest for phenological fluctuations during time, few studies have paid attention to the spatial aspect of phenology (e.g., Rötzer and Chmielewski 2001). In particular, birds has become one of the most employed bioindicators on climate change research (Sanz 2002; Crick 2004; Lehikoinen et al.

2004) thanks to their exhaustive monitoring both among investigators and amateurs (Whitfield 2001; Collison and Sparks 2003), which has allowed the compilation of large databases for any sort of biological parameter (Sparks and Crick 1999; Gibbons 2000; Svensson 2000; Collison and Sparks 2003; Crick et al. 2003). If we focus on bird migration, this previously mentioned difference between temporal and spatial phenological studies becomes even more disconcerting.

The description of the spatial bird colonisation 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., Middendorf 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 (Huin and Sparks 1998, 2000; Gordo et al. 2007). The situation is even worse for the Iberian Peninsula due to the absence of data when previously mentioned pan-European studies were carried out (Sliwinsky 1938), making any report on this issue absolutely novel (Pérez-Tris and Santos 2004; Gordo et al. 2007).

Arrival and departure of migratory birds seem such obvious phenomena that nobody has wasted time on an accurate and comprehensive description of its geographical patterns and, as consequence, this matter remains unexplored for most species in many areas. For example, recording the arrival date of a migratory bird is a very simple measurement. However, the necessity for a huge amount of data to cover an area with a dense network of observations is difficult to attain, especially if no volunteers are involved (Sparks and Crick 1999). At present, the easy and simple approach to recording the timing of bird migration by observation of arrival and departure dates remains equally valid as a century ago. Moreover, new and more powerful analytical tools (e.g., GIS software) allow investigators to offer more thorough responses using 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 for inclusion in a volunteer-based monitoring scheme. It is common (at least in some European countries), conspicuous (e.g., by using human buildings to breed), and unmistakable (anyone knows what a white stork is). Therefore, it is very easy to monitor with minimal potential biases (Tryjanowski et al. 2004, 2005a). There were some studies in the 20th century which described the geographical patterns of its migratory phenology (Sliwinsky 1938; Zabłocka 1959; Jespersen 1949; Panouse 1949; Grishchenko 1995). In the 1930s, Sliwinsky (1938) specifically stressed the complete

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 include Iberian populations. All previously cited studies focus 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 a gap in the knowledge about the environmental variables related to the spring and autumn migratory phenology of the white stork. Variability in timing of arrival and departure 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). As in the inter-individual variability for the same population, this fact could be potentially reflected in different reproduction success for each population (Lázaro et al. 1986; Nowakowski 2003; Tryjanowski et al. 2005b). This gains interest in a species that showed strong fluctuations in their numbers during the last century with serious implications for its conservation status (Bernis 1981; Dallinga and 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 in order to offer an explanation with an ecological perspective of the observed variability in phenology among populations.

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. These volunteers have been 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 its use of man-made structures for construction of its large and conspicuous nests (Lázaro et al. 1986; Tryjanowski et al. 2004; Molina and 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 and Del Moral 2005), and generally occurring in humanized habitats, such as cattle pastures, crops and farmland.

Hence, we are absolutely confident in the accuracy of records since it is difficult to miss the presence of the species once it has arrived or its absence once it has departed. Furthermore, its morphology and habits are sufficiently different from 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 from the breeding population of a certain site was sighted. The departure date was the last day that an individual was observed in a certain locality. Both dates were transformed into a Julian day scale (1 = 1 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 for this variable (see Fig. 1 for more details).

Before our analyses, we corrected the data of these three dependent variables to prevent effects of long-term temporal trends (Gordo and Sanz 2006), which can potentially bias the comparison between UTM cells 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 100 km^2 UTM square was calculated for the arrival, departure and length of the stay. 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. 1).

Explanatory variables for phenological modelling

A set of 31 explanatory variables was used to model migratory phenology of the studied species (see Table 1). These variables were classified into four groups: spatial, environmental, geographical, and biological. In the case of the environmental group, seven topographic and ten climatic variables were extracted for each of the 100 km^2 UTM Iberian squares ($n = 6,063$) 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 each 1 km^2 included in each 100 km^2 UTM cell 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, 1975a, b; Fernández-Cruz 2005) we expect later arrivals and earlier departures for those localities furthest away. 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 where the species occurred (see Fig. 2). All 100 km^2 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 arrival and departure dates. They can help us to distinguish 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 and Del Moral 2005). Population density can affect phenology in two ways. Firstly, denser populations could increase the chances for observers to detect early individuals (Sparks et al. 2001; Tryjanowski and Sparks 2001), although it is unlikely there is such a bias due to the conspicuousness of this species (Tryjanowski et al. 2005a). Secondly, in denser areas, earlier arrival would be profitable for individuals since first arrived white storks could maintain nest-site fidelity and save energy employed for its construction (Dallinga and 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 in order to estimate if the total number of days that white storks remain on their breeding grounds are related to arrivals, departures or both. We expect that the length of the stay would be longer because arrivals would be earlier and departures later.

Finally, spatial variables were used simply in order 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 and Legendre 1998). The nine terms of TSA can also help to incorporate the effects caused by other historical, biotic or environmental variables not otherwise taken into consideration (Legendre and 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 departure dates observed between localities could be different wintering and passage areas among white stork populations. This fact is particularly important for this species since a growing number of individuals remain in Spain and North Africa during the wintering period (Van den Bosche 2002; Molina and 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 and 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. 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. Firstly, 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

Fig. 1 Maps of arrival dates (**a**), departure dates (**b**) and lengths of stays (**c**) of white storks (*Ciconia ciconia*) in Spain. Median values for each UTM cell 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 UTM cells of the breeding area (Martí and Del Moral 2003). *Scale colour bar* and values for tables and histograms in Julian day (1 = 1 January) for arrival and departures, and the number of days for stays. Details about the number of records, localities, UTM cells, mean, standard deviation (SD) and the histogram of the distribution of these observations are given for each variable

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. Then, 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 in this complete model, backward removing all non-significant variables in order to determine potential relevant non-considered variables spatially structured. The predicted scores of the complete 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 with data just for the period 1944–1980. The presence of a few wintering individuals has been reported in some cases for many decades (e.g., Duclós 1956; Cruz-Valero 1964). However, these anecdotal records became regular since the 1980s (Tortosa et al. 1995; Molina and Del Moral 2005), although it is impossible to determine the precise year when numbers of wintering individuals began to increase, because the first censuses of wintering white storks in Spain were not conducted until the 1990s (e.g., Tortosa 1992; Gómez-Tejedor and De Lope 1993; Máñez et al. 1994; SEO/BirdLife 1996). The sharp advancement noticed by Gordo and Sanz (2006) in arrival dates since the beginning of the 1980s points towards this decade as the time when migratory behavior of white storks started to shift. Therefore, data used as control in repeated models included only records up to the year 1980.

Explanatory variables are always unavoidably correlated due to their existing 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 variable, a hierarchical partitioning procedure was implemented (Birks 1996; MacNally 2000; MacNally
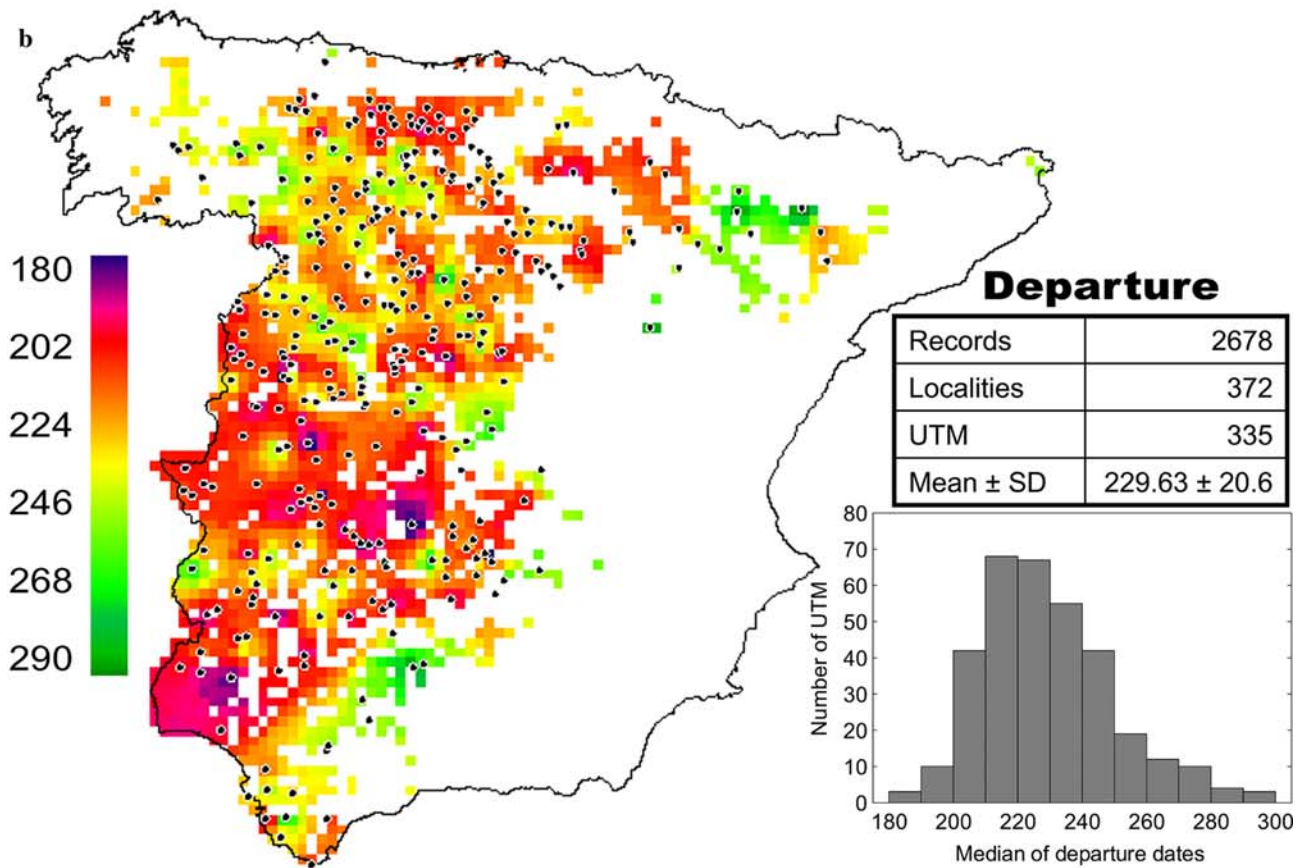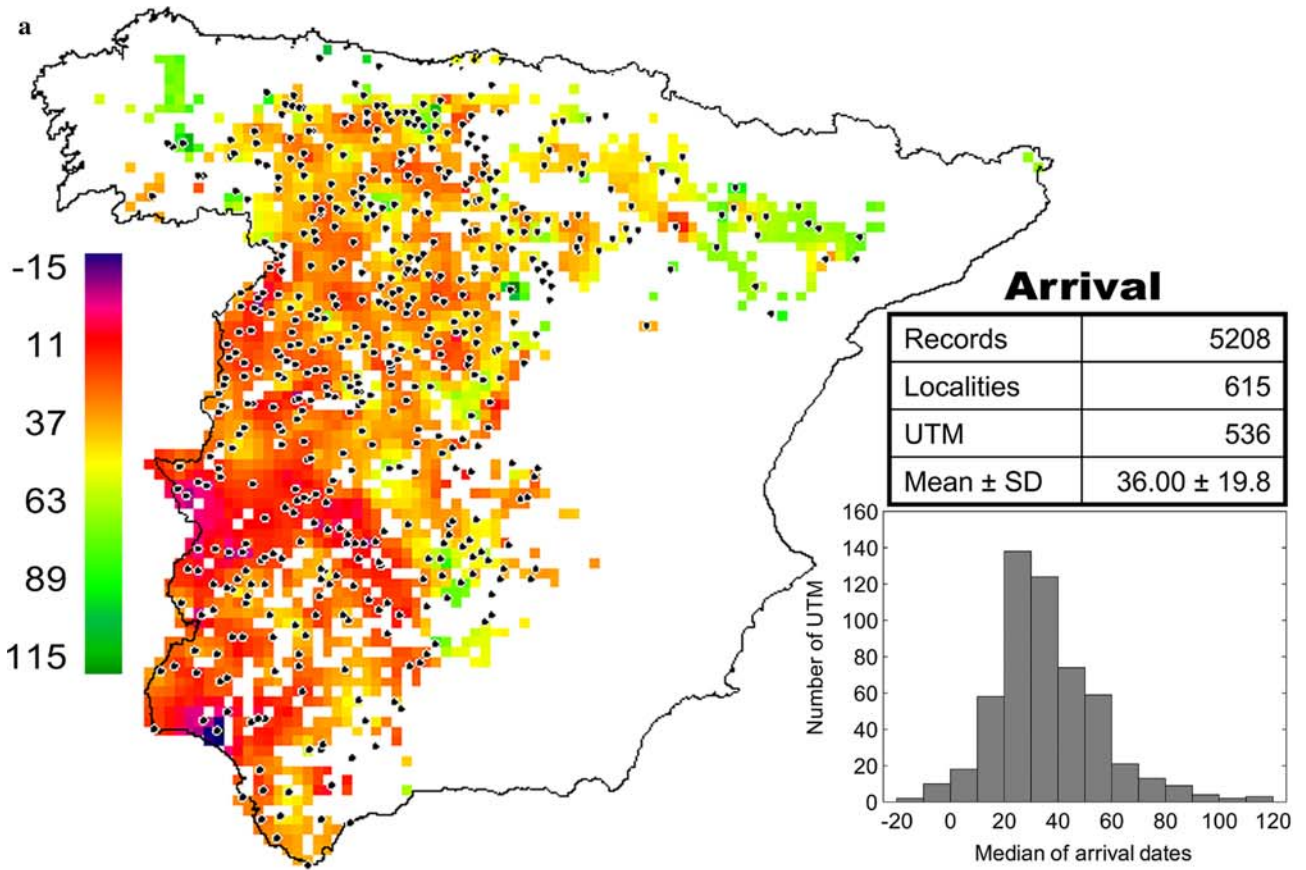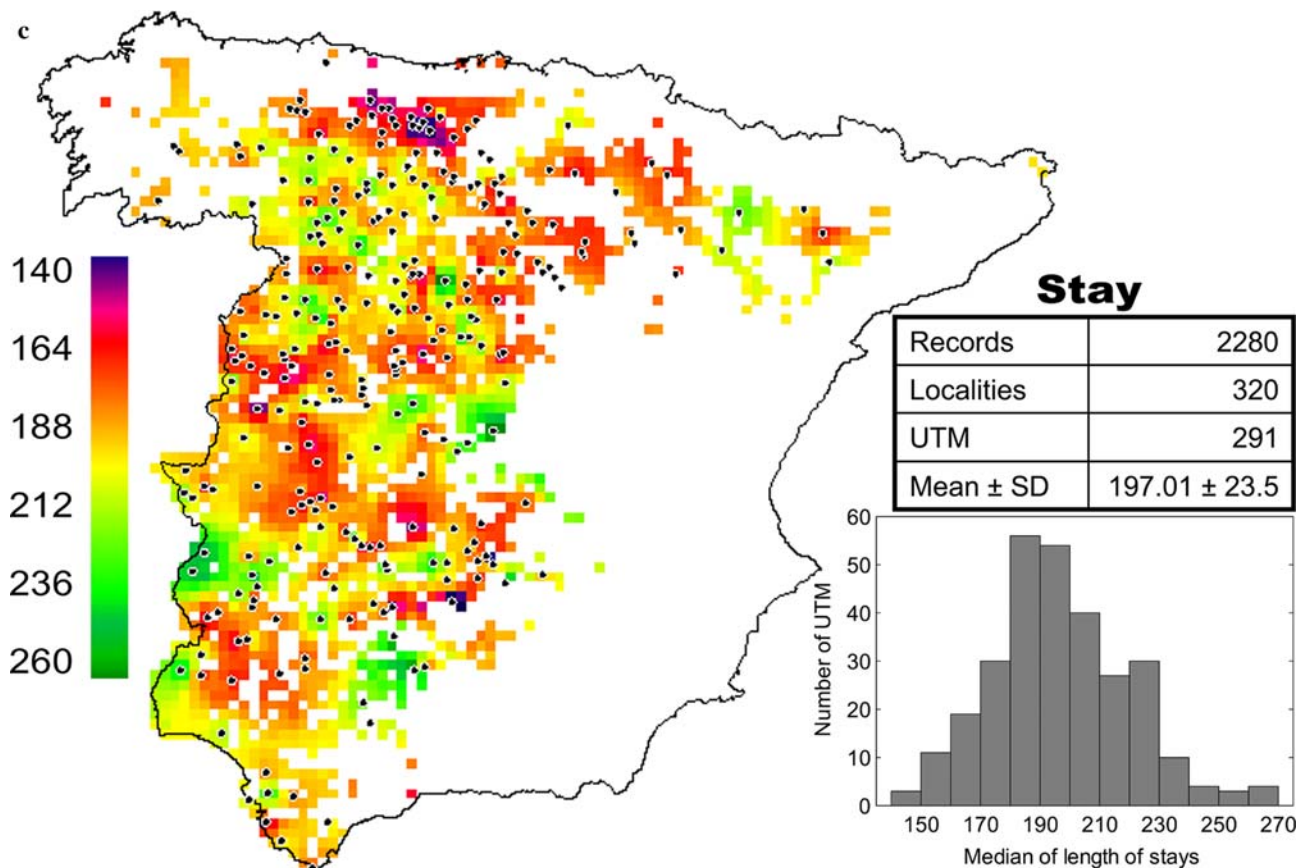
Fig. 1 continued

2002). The 2^k possible functions among k significant explanatory variables were calculated, thus 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 and Ord 1981; Legendre and Legendre 1998; Keitt et al. 2002). These analyses were conducted with GS+ (Gamma Design Software 2002).

To determine the existence of differences in the natal origin among individuals recovered during winter, two ANOVA were performed with the latitude and longitude where individuals were born as dependent variables and the wintering region (Spain, North Africa or sub-Saharan Africa) where they were recovered as categorical predictor.

Results

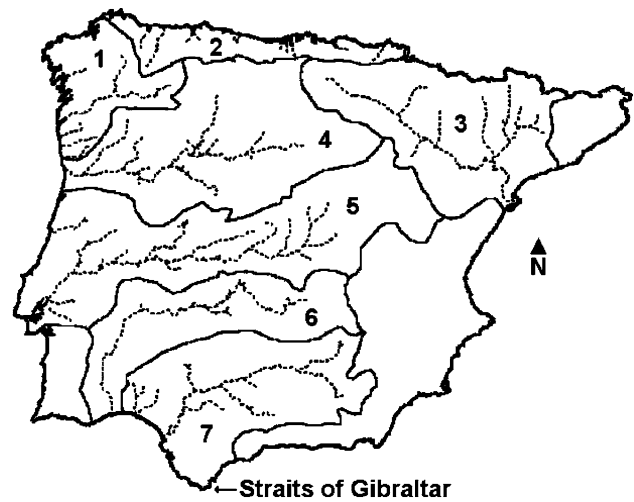### Spatial patterns and factors related to arrival dates

A visual inspection of the spatial variation in arrival dates does not detect an obvious pattern (Fig. 1a). A region of earlier arrivals appears in the south western corner of Spain in contrast 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 to late dates. Overall, the extreme dates for the spring arrival distribution of the Iberian white stork populations are between the last week of December and mid-April, which considerably extends those reported in the literature (Bernis 1959), probably as result of our broad spatio-temporal dataset. Similar 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 2). Signs of latitude and longitude in the spatial model indicated that white storks arrive later to northern and eastern localities, as shown in

Table 1 List of variables used in analyses. For each one, the acronym, complete description and units (in brackets) are given

Variables	Description
Spatial	
LAT	Latitude (m)
LONG	Longitude (m)
Environmental	
MEA	Mean altitude (m)
MIA	Minimum altitude (m)
MXA	Maximum altitude (m)
AR	Altitude range (m)
SLP	Slope (deg)
ASP	Aspect (deg)
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
Geographical	
DIR	Distance to the closest main Iberian river (km)
DSG	Distance to the Straits of Gibraltar (km)
CAN	Cantabrian
DUE	Duero
EBR	Ebro
GDN	Guadiana
GDQ	Guadalquivir
MIÑ	Miño
TAJ	Tajo
Biological	
ARR	Arrival date (Julian day)
DEP	Depature date (Julian day)
NNEST25	Number of occupied nests in a 25-km radius area around each UTM

Fig. 2 Map of the Iberian Peninsula with territory divided into the main Iberian basins where the Spanish populations of the white stork breed. *Solid lines* delimit basins and *broken lines* are main rivers. Codes for the basins: *1* Miño, *2* Cantabrian, *3* Ebro, *4* Duero, *5* Tajo, *6* Guadiana, *7* Guadalquivir

located in the northernmost parts of the white stork distribution in Spain. The quadratic function with distance to the Straits of Gibraltar of the geographic model also pointed towards later arrivals to those localities far away from Gibraltar. On the other hand, the biological model significantly included the number of nests in the surrounding area. The higher the number of nests the earlier white storks arrive (Fig. 3). When analyses were repeated with data for the period 1944–1980, the parameters estimates of explanatory variables (not shown) and the explanatory capacity of models were almost identical (Table 2).

The final complete model included five variables and had slightly more explanatory capacity (Table 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. 4), the complete model could be slightly improved when the spatial variables were included. This fact 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. 5a) help us to visualize better the underlying gradients in arrival dates which are difficult to see in the picture resulting from original observations (Fig. 1a). White storks arrive first to the south-western corner of Spain, especially across the Guadiana basin. Then, most of the breeding grounds are colonized in only 1 month. Finally, later populations reach the northern margin and the Ebro basin around mid-March according to our model.

Fig. 1a. Environmental and geographical models showed almost the same explanatory capacity (Table 2). The relationships of arrivals and the involved variables in both models agree with the previous pattern. The positive relationship with summer rainfall and the aridity index point towards earlier arrivals to those drier and more arid regions. These regions are in southern Spain. However, included basins in the geographical model (Cantabrian and Ebro basins; see Fig. 2) showed later arrivals. They are

Table 2 Best models obtained for spring arrivals

Model type	Variables	B	Adj R^2	Pure Adj R^2	Control model
Spatial	LONG	14.171	0.260	0.091	0.264
	LAT	4.218			
	LONG^2 × LAT	9.007			
	LAT × LONG^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	NNEST25	–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			
	NNEST25	–0.014			
Complete + spatial terms	LONG	10.631	0.337		0.326
	LONG^2	6.652			
	LAT	–6.181			
	LONG × LAT	–11.920			
	EBR	9.361			
	SUR	13.505			
	NNEST25	–0.011			

The variables included in each model, their estimated parameters (b), the adjusted coefficient of determination (Adj R^2), the relative importance (pure Adj R^2), and the explanatory capacity of the same models with data for 1944–1980 period (control model) are shown for each type of variable (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

## Spatial patterns and factors related to departure dates

The picture obtained from departure dates did not show any obvious spatial gradient (Fig. 1b). Earlier dates occur in some sites located in the extreme south-west of Spain and near the centre of the distribution. However, 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 also extends previously reported dates (Bernis 1959) due to the longer temporal and broader spatial range of our data set.

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 the 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 those more arid sites later. The biological model included both the population density and the median arrival date in the same UTM square (Adjusted $R^2 = 0.047$; $F_{2,321} = 8.96$; $P < 0.001$). White storks depart later from those sites with low nest density and later arrivals. When these analyses were repeated with data for the period 1944–1980, the parameters estimates of explanatory variables and the explanatory capacity remained equally low (values of the adjusted coefficient 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 did not add any significant term when they were included together with these variables. This fact emphasizes the nonexistence of spatial gradients in departure dates. The control model was slightly better (Adjusted $R^2 = 0.071$). Predicted scores (Fig. 5b) point towards earlier departures in the extreme south-west of Spain, in contrast to later ones in all eastern populations. However, in spite of the significance of the model, the biological reliability of this pattern should be taken into
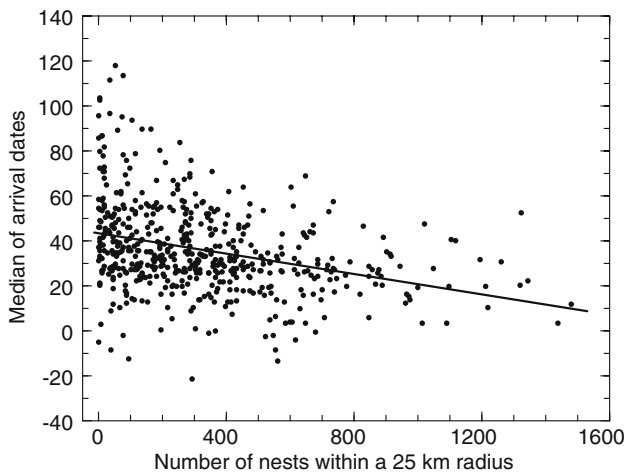
Fig. 3 Scatterplot of the median arrival date against the number of occupied nests within a 25-km radius area around each UTM cell. *Solid line* is the best linear fitted model

account with care, due to the extremely low explanatory capacity of the models. Neither residuals from the final models nor residuals for each type of variable models showed spatial autocorrelation at any lag distance (Fig. 4).

Spatial patterns and factors related to the length of the stay

There is no spatial clear pattern in the length of stay (Fig. 1c), as in departure dates. Short and long stays appeared in a complicated patchiness throughout Spain according to interpolated median values. The shortest stays were recorded in the Cantabrian basin, whereas the longest occurred in several localities from central 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 the observed variability. The spatial 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 longer in those localities with less precipitation during the summer. The geographical model also included 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 the Straits of Gibraltar. Hence, the spatial, environmental and geographical models showed low explanatory capacities and had the same interpretation: white storks from southern populations stay for a longer period. In spite of the strong
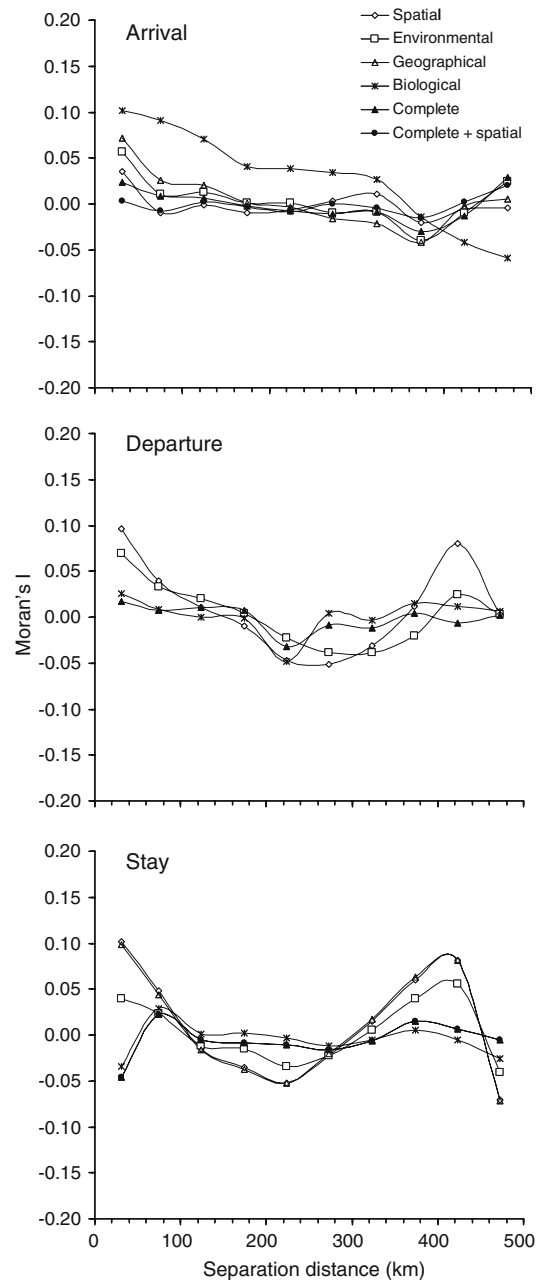
Fig. 4 Spatial autocorrelation of residuals from spatial, environmental, biological and complete models accomplished for arrivals, departures and stays. Isotropic correlogram represents the variation in the scores of Moran's I spatial autocorrelation statistic with the increasing in the separation distance between 100 km^2 UTM cells (in km), using a lag distance of 50 km and an active lag of 500 km

significance of previous models, the low explanatory capacity again diminishes 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
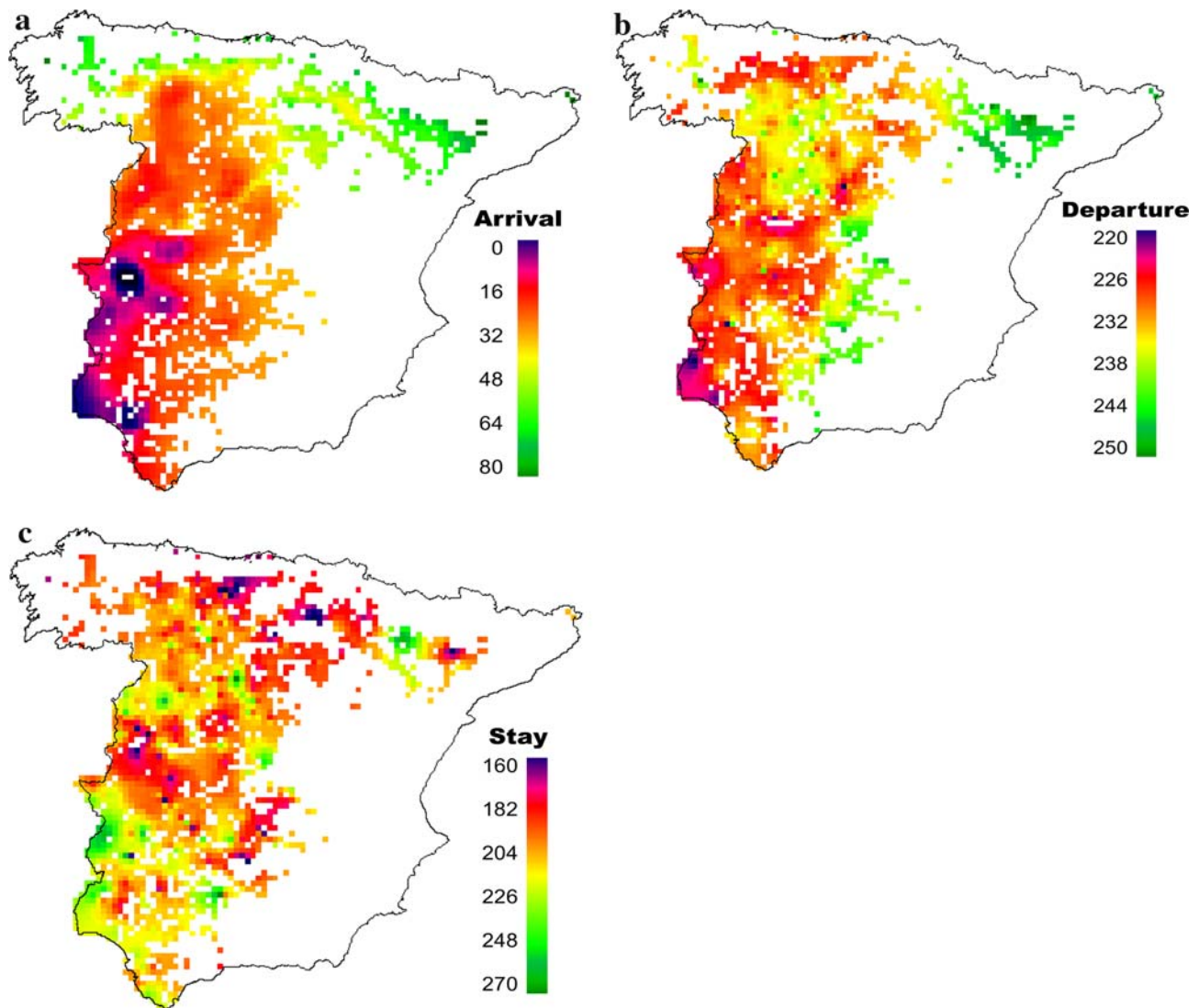
Fig. 5 Maps of predicted arrival dates (**a**), departure dates (**b**) and length of stays (**c**) according to the best complete models. *Scale colour bar* in Julian day (1 = 1 January) for arrival and departure, and number of days for stay

$R^2 = 0.842$; $F_{2,288} = 773.3$; $P < 0.001$), 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 that previously described (Adjusted $R^2 = 0.844$; $F_{3,287} = 522.9$; $P < 0.001$). The overwhelming explanatory capacity of this model was related to 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, summer rainfall 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 was 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 with the rest, did not show spatial autocorrelation for their residuals (Fig. 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 were

no differences in the natal latitude among recovery regions ($F_{2,120} = 1.06$; $P = 0.350$). However, individuals recovered during winter 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 migratory phenology of the white stork were able to capture only partially the enormous variability observed among localities (see Fig. 1a). However, some gradients arise from data which point towards certain spatial structure of arrivals in relation to 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 the pre-nuptial migratory period (i.e., winter climate variables in Table 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. 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 as able to resist adverse cold climatic conditions as the white stork (Mata et al. 2001). The occurrence of wintering individuals in the Iberian Peninsula (Duclós 1956; Cruz-Valero 1964; Tortosa 1992; Gómez-Tejedor and De Lope 1993; Máñez et al. 1994; Tortosa et al. 1995, SEO/Birdlife 1996; Marchamalo 2002; Vergara et al. 2004; Molina and Del Moral 2005) suggests that this species is also not constrained by low winter temperatures here. Therefore, due to its extremely early return, colonization patterns of the white stork are independent of the progression of the spring through Iberia.

During the last two decades, a growing number of wintering individuals have been recorded in the Iberian Peninsula (Gómez-Tejedor and De Lope 1993; Máñez et al. 1994; Tortosa et al. 1995; SEO/BirdLife 1996; Marchamalo 2002; Vergara et al. 2004; Molina and Del Moral 2005). These individuals could seriously affect measurements of the arrival and departure dates because these dates are sensitive to any ''aberrant'' migratory behavior (e.g., sick individuals). This influence has already been noticed for the temporal trends in migratory phenology of this species (Gordo and Sanz 2006). 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 closer 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 white stork arrivals. When analyses were repeated with data recorded between 1944 and 1980, the effect of predictor variables and the explanatory capacity of models 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 such 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 were born in easternmost Spanish populations, i.e. those with the latest arrivals (see Fig. 1a), which would be contrary to our prediction. In conclusion, neither the presence of wintering individuals nor differences in selected wintering quarters are the origin of the weak spatial patterns for white stork arrivals and, especially, departures and stays.

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, first eggs are laid about mid-March (Cramp and Simmons 1977; Bernis 1981), 2 months 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 long-distance migrant bird species. Since the white stork is a single-brooded species, an earlier arrival does not increase the chances for second and third clutches as in other migratory species (e.g., barn swallow *Hirundo rustica*; Møller 2002). However, Tryjanowski et al. (2004) showed for a Polish population that an early return can have benefits for individuals through higher breeding success. This association is mediated by the date at which laying begins. However, it is difficult to imagine how this can affect reproduction in Spanish white storks since the period between arrival and laying dates notably exceeds that recorded for eastern European populations (about 15 days; Tryjanowski et al. 2004). Furthermore, the guaranteed food supplies from rubbish dumps throughout the breeding season would diminish the importance of an early return (Tortosa et al. 2002, 2003; Massemin-Challet et al. 2006). These strong differences force us to stress more caution when results for the better studied eastern European populations are extrapolated to the Iberian populations, because both groups are probably under different ecological pressures as a result of the environmental peculiarities of their breeding, wintering and passage areas (Bernis 1959).

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

A third alternative hypothesis could be suggested for the relationship between arrivals and population density. Those areas with a higher density of breeding individuals could simply coincide with those ones with earlier migrant populations, because both variables are within 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 still revealed 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 from the arrival dates. 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 summer precipitation were the only climatic variables included in our models. Both variables are closely related to productivity during the summer, the most unfavorable 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 in Iberia at the height of winter, when water is not restricted thanks to the precipitations of the previous autumn (October–November), those that are falling during the winter (December–February) and those that will fall in the following spring (March–May). This very early arrival allows the white stork to finish its breeding season in early summer (June–July). The white stork thus avoids having the dry and harsh conditions of the end of the summer (August–September) during its reproductive period in spite of its long duration (more than 3 months; Bernis 1981). Moreover, by departing at this time individuals can reach Sahelian wintering quarters at the end of monsoon season and they can consequently profit from benign ecological conditions during October and November in that region. When the dry season in the Sahel becomes restrictive (December–January), the white stork returns to Iberia. Therefore, it is not surprising that rainfall also influences spatial phenological patterns in this species, as it does for many other biological parameters of its life-cycle (Maclean et al. 1973; Kanyamibwa et al. 1990, 1993; Carrascal et al. 1993; Mullié et al. 1995; Barbraud et al. 1999; Jovani and Tella 2004; Denac 2006b; 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, and (2) they profit the peak of productivity already available very early in the spring as a result of the especially marked seasonality in those more arid regions.

Environmental and geographical variables were unable to explain most of the variability observed between localities both in departure dates and length of stays. This was to be expected 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 only be attributed to the veritable absence of a strong spatial structure in both variables (see Fig. 1). However, the absence of strong relationships with one or some explanatory variables makes it extremely difficult or even impossible to offer ecological-based responses for the large differences observed in departure dates and lengths of stays among populations.

Regarding departure dates, one can argue that there are mixed records of Spanish and Central European individuals during the post-nuptial migration (August–September). If this is true, then the meaning of such data 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 2001; but see Barbraud et al. 1999; Vergara et al. 2004; Molina and Del Moral 2005), where Spanish storks do not bred. 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 very unlikely.

The absence of spatially structured factors with effects on departure dates could be due to: (1) the social behavior of white storks during the autumn migration, and (2) the questionable correspondence between departure dates and the real onset of the autumn migration for this species. During July and August, Spanish white storks show a growing gregariousness (Bernis 1959). Individuals from neighboring populations aggregate in large flocks (sometimes up to several thousands of individuals) in the best places for feeding (e.g., rubbish dumps) and roosting (e.g., salt-marshes) prior to the definitive departure towards the African wintering quarters (Fernández-Cruz 2005). These flocks would reduce their migration costs because they can locate lift in an easier way and the more active individuals will encourage others to finish their stay on the breeding grounds (Kosicki et al. 2004). Therefore, departure dates are probably, in most cases, recording the displacement of individuals from neighboring populations towards a meeting point and thus the beginning of flock formation prior to the real onset of the autumn migration. In conclusion, departures are strongly influenced by social behavior, which in turn depends 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 also be due to the questionable meaning of such phenological measurement at the population level. Firstly, arrival and departure dates are two extreme measures of the respective distributions of arrival and departure dates in a certain population. That the amplitude (and thus its extreme values) of such migratory distributions would be directly dependent on the population size is only to be expected. More numerous populations should show more diversity in their 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 on departure dates (i.e. higher partial R^2 in final model), which could be an invalid measurement for autumn migration in this species, as we have previously discussed.

Zusammenfassung

Räumliche Muster in der Zugphänologie des Weissstorches (*Ciconia coconia*) auf der iberischen Halbinsel

Im Gegensatz zur Beachtung, die zeitliche Trends in der Phänologie erfahren, sind räumliche Muster von Ankunft, Abzug oder Aufenthalt von Transsahara-Ziehern in den meisten ihrer europäischen Brutgebiete bis heute weitgehend unbekannt. Im Falle des Weißstorchs *Ciconia ciconia* zielten einige Arbeiten zwar auf die Beschreibung der räumlichen Zugmuster, aber unseres Wissens nach hat noch keiner diese Muster zu diversen Variablen in Bezug gesetzt, um eine Erklärung der räumlich heterogenen Phänologie, wie sie sich über verschiedene Populationen hinweg beobachten lässt, vor ökologischem Hintergrund zu liefern. In der vorliegenden Arbeit wurden Ankunft, Abzug und Aufenthalt dieser Vogelart, die für hunderte spanische Orte erfasst wurden, zu einer Reihe von die Umwelt betreffenden, geographischen, biologischen und räumlichen Wirkungsvariablen in Bezug gesetzt und mit Hilfe multipler Regression modelliert. Das beste Modell für Ankunftsdaten erklärte bis zu 34% der Datenvariabilität und wies in Richtung einer früheren Ankunft von Populationen aus dem Südwesten Spaniens und solchen mit höheren Populationsdichten. Letztere Beziehung ergibt sich vermutlich aus einem Wettbewerb, der Nistplatztreue zu entsprechen. Keine Variable hingegen konnte hingegen das unscharfe räumliche Muster gut erklären, das von den Abzugsdaten vorlag. Die Entscheidung abzuziehen ist bei dieser Vogelart stark von sozialen Verhaltensweisen geprägt und hängt von Kollektiventscheidungen ab, die eher von spezifischen lokalen Umweltbedingungen eines jeden Jahres beeinflusst sind, als von makrogeographischen Gradienten. Ebenso wenig waren die Umwelt betreffende, geographische oder räumliche Variablen in der Lage einen Großteil der Variabilität in der Aufenthaltsdauer der Populationen zu erklären. Dennoch war diese Variable stark an die Ankunfts- und Abflugsdaten der Populationen gekoppelt. Weißstörche verweilen länger in Gegenden mit früheren Ankunftsdaten und besonders in solchen mit späteren Abzugsdaten.

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