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## Original article

# Geographic variation in onset of singing among populations of two migratory birds

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## ABSTRACT

Even though singing plays a major role in bird communication, environmental variables affecting the geographic patterns observed in the variation of singing onset within large areas have not previously been studied. The singing phenology of two long-distance migrants, the Cuckoo *Cuculus canorus* and the Nightingale *Luscinia megarhynchos*, recorded in thousands of sites throughout Spain, was related to a set of 51 explanatory variables by partial least squares regression. Observed variability in singing onset among localities follows spatial trends on an Iberian scale at  $10 \times 10$  km resolution, and was well modelled by some environmental variables. Of these variables, climate was the most influential. Males of both species sang earlier in warmer and drier sites. Males who were near the Straits of Gibraltar and in the southern Iberian basins, which are geographic gradients closely related with climate in the Iberian Peninsula, were also heard earlier. Most environmental variables affected the singing activity of both species equally, i.e., the same environmental gradients are linked to singing onset. However, the models' predictions indicated differences in the geographical pattern in singing onset between both species, mainly related to their rates of progression during spring migration through Spain. Local variables, such as land uses, vegetation productivity or species abundance, played a minor role on singing onset spatial patterns. Therefore, models' composition supports the hypothesis that singing onset is a good proxy of arrival dates in migratory species, since those variables related to indirect effects on singing onset phenology through migratory progression and arrival to the breeding grounds showed the highest influence.

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## 1. Introduction

Birdsong is one of the most important means of communication among birds. At the beginning of the breeding season, males sing to attract potential mates, as well as to establish and defend territories from competitors. The onset of spring

birdsong activity is highly dependent on environmental conditions and, in the case of migratory birds, necessarily on the arrival and establishment of males in their breeding grounds (Slagsvold, 1973, 1977). Since reproduction of migratory birds must be perfectly matched with the period of suitable ecological conditions in breeding grounds (Coppack and

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Both, 2002; Visser et al., 2004; Durant et al., 2007), migratory birds have a great urgency to reach their breeding grounds and attempt to breed as early as environmental conditions will permit (Perrins, 1970). Early breeding has demonstrated benefits in terms of increased reproductive success due to the acquisition of high-quality breeding territories (e.g., Vergara and Aguirre, 2006; Vergara et al., 2007), higher mating success (e.g., Møller, 1994), and higher survival of the offspring (e.g., Tryjanowski et al., 2004). Therefore, male migratory birds should start their singing activity just after their arrival to profit to the utmost breeding season. For shier and more elusive species, acoustic detection became the easiest way of detection and thus their singing onset, in most cases, is the first evidence of their annual arrival. Consequently, as singing is assumed to begin soon after arrival, spurred on by the urge to reproduce, the measure of singing onset is assumed to accurately reflect arrival date in most migratory species (Slagsvold, 1977; von Haartman and Söderholm-Tana, 1983; Huin and Sparks, 2000).

Singing onset has been used in several studies as a measure of spring migratory phenology. As far back as the nineteenth century, von Middendorff (1855) used singing onset of the Cuckoo *Cuculus canorus* to study its migratory progression through Russia. In fact, the popularity of the Cuckoo as the harbinger of spring in Europe probably led many other authors to follow in Middendorff's footsteps. Angot (1900; reviewed by Brestcher, 1935; Rendahl, 1965b) found that Cuckoos started singing later in regions from western and northern France and at high altitudes. Sliwinsky (1938) gathered data for thousands of European sites and drew the first sketch of the spring progression of the species through the whole continent. She showed that earlier singing onset takes place on the Atlantic coast of France and in the Danube plains of Hungary. From there, Cuckoos move approximately northward, although they are influenced by the complicated topography of central Europe. Nevertheless, Sliwinsky did not include data from Mediterranean regions (excepting the French Mediterranean coast) and her methodology was strongly constrained by the data modelling possibilities of her time (De Smet, 1967; von Haartman and Söderholm-Tana, 1983). Later studies for Sweden (Rendahl, 1965a), Belgium and the Netherlands (De Smet, 1967, 1970), Romania (Munteanu, 1982), Czechoslovakia (Beklová et al., 1983), Finland (von Haartman and Söderholm-Tana, 1983) or Britain (Huin and Sparks, 2000) also took advantage of the popularity of this species to compile huge amounts of first singing records. This allowed a more detailed description of the spatial variability in the singing onset in these regions.

Unfortunately, the previously reviewed picture for the Cuckoo is not representative of the available information about spatial patterns of migratory phenology for most bird species as well as for many regions of Europe. For instance, there is an absolute lack of studies in a very important passage and breeding area as the Mediterranean basin (but see Gordo et al., 2007a,b). In the particular case of the Cuckoo, the filling of this knowledge gap is of interest because the Iberian and North-African populations belong to the subspecies *C. c. bangsi*. Thus, the large amount of information available on other European populations may not be entirely applicable for the Spanish Cuckoo populations. In the case of other

popular spring singers, such type of studies has rarely been carried out (e.g., Stresemann, 1948; Munteanu and Maties, 1978; Grischtschenko and Serebryakov, 1996). Among them, nightingales (genus *Luscinia*) stand out by their singing activity, another popular phenological indicator of the spring. Surprisingly, there are almost no studies about spatial patterns of singing onset of nightingales. Huin and Sparks (2000) analysed the arrival of the Nightingale (*Luscinia megarhynchos*) to Britain, but the restricted distributional range of this species there made it difficult to determine a describable pattern. Nevertheless, Nightingales progressed through Britain following a southwestern–northeastern axis, while the Cuckoo follows a marked south–north axis in the same area. Such differences stress the necessity to determine to what extent spatial patterns found for the Cuckoo are representative for the rest of migrants (von Haartman and Söderholm-Tana, 1983).

Since Middendorff, all studies have focused on the description of geographical patterns rather than on an exhaustive search into the environmental factors governing them. Thus, the ecological-evolutionary mechanisms underlying the spatial variability in birds' singing onset remain to be determined. An accurate knowledge of the factors related to spatially migratory phenology would be critical to providing a better assessment of the potential hazards to migratory birds posed by current and future climate change (Møller et al., 2004).

Environmental features can affect singing onset indirectly via bird migratory progression through passage areas and arrival date to the breeding grounds, i.e. through spring migration timing. As it was pointed out, later singing onset is expected in the north and at sites of high elevation due to the delayed arrival of the first individuals. Furthermore, environment can affect singing onset directly, through stimulating singing activity once individuals have arrived at their breeding territories. Males should start singing activity just after their arrival, but their onset of singing also can be influenced by individual characteristics (e.g., Ilyna and Ivankina, 2001), population density (e.g., Olinkiewicz and Osiejuk, 2003), weather variability (e.g., Lengagne and Slater, 2002) and productivity or habitat type (e.g., Doutrelant et al., 1999). However, it still remains to be determined if these demonstrated direct effects, acting on a local population scale, are also important to the variability observed among localities from a large area.

The present study aims to estimate the main factors influencing spatial patterns of singing onset for two migratory species (the Cuckoo and the Nightingale) in Spain by means of a large number of potentially relevant explanatory variables. It also aims to discriminate the effects of those variables that have more opportunities to be effective at a local scale. The studied species are common and widespread in the Iberian Peninsula (Martí and Del Moral, 2003) and their song is easily detectable (Bernis, 1970; von Haartman and Söderholm-Tana, 1983; Tryjanowski et al., 2005). Such features are very important since they could seriously bias phenologic measurements (De Smet, 1967; Sparks et al., 2001; Tryjanowski et al., 2005). Furthermore, both species encounter similar ecological conditions during spring since they have similar migration dates (Nightingale is a bit later). These seem to be their only shared features, however, as the rest of their ecology and behaviour is completely different (Cramp, 1985,

1988). These characteristics make the two species ideal to test how a shared scenario (i.e., ecological conditions during the spring migration into Iberia) may impose convergent spatial patterns on singing onset, as compared to the specific preferences imposed by biological particularities of species and the local conditions of the regions in which they arrived.

## 2. Materials and methods

### 2.1. Bird phenological data

Singing phenology data for the Cuckoo and Nightingale were obtained from the phenological database of the Spanish *Intituto Nacional de Meteorología*. This database is the result of a volunteer observer network set up several decades ago by the *Intituto Nacional de Meteorología* to better understand the timing of seasons and improve agricultural practices, as has been done in other European countries (Leith, 1974). Up to the present day, these volunteers have been recording selected phenological events, using standard observation rules, applied to a list of common species of plants and animals (see Gordo and Sanz, 2006, for more details).

Singing onset phenology of both species was measured as the date when the first singing male is heard in each study locality and year. All available records from original registers from 1945 to 2004 were collected and computerized to obtain a total of 8621 data points from 898 localities (see Fig. 1). Dates were transformed to a Julian day scale (1 = first day of January), taking into account leap-years by adding 1 day after February 28.

Before analyses, potential bias was removed from long-term temporal trends on singing onset dates, which can hinder the comparison between UTM cells because of dates recorded in different decades. This analysis was performed only on the Cuckoo because it was the only species that showed temporal trends (Gordo and Sanz, 2006). For this purpose, a multiple regression analysis was carried out for singing onset dates using a quadratic function with the year as the explanatory variable. Residuals of these regressions were used as a measure of date of arrival independent of inter-annual variations. These corrected dates were used in all subsequent analyses of this species. Since the nightingale did not show any temporal trend (Gordo and Sanz, 2006), we employed directly raw data.

The median value of all records for the same UTM 100 km<sup>2</sup> cell was calculated in both species (Fig. 1). As some phenological stations are located in the same UTM cell, the final number of records available for calculations (i.e., different UTM cells) was fewer than the number of original localities (see Fig. 1). Median values for each UTM cell could have been biased due to a differing number of records (average number of records per UTM for the Cuckoo  $7.74 \pm 9.49$  SD, and for the Nightingale  $6.39 \pm 8.60$ ). This potentially biased effect in the sampling effort was tested for by means of Spearman correlations between median values and number of records in each UTM cell (Cuckoo:  $r_s = -0.005$ ,  $P = 0.89$ ; Nightingale:  $r_s = -0.042$ ,  $P = 0.38$ ). As median singing onset was not dependent on the number of records, all UTM cells with available records for both species were used.

### 2.2. Explanatory variables

A total of 51 explanatory variables divided into eight categories were used to model singing phenology of the studied species (see Table 1). Five topographic and ten climatic variables were extracted for each one of the 100 km<sup>2</sup> UTM Iberian squares ( $n = 6063$ ) using the Idrisi 32 Geographic Information System (Clark Labs, 2001a,b). Topographic variables were obtained from a Digital Elevation Model (Clark Labs, 2000). Mean altitude for all 100 pixels of 1 km<sup>2</sup> within each 100 km<sup>2</sup> UTM were used to calculate the mean altitude and the altitude range in each 100 km<sup>2</sup> UTM cell, together with the slope, aspect (the mean direction of the slope) and diversity of aspects for each cell. Delayed singing onset is expected in more mountainous UTM cells (Angot, 1900; Bernis, 1970; Huin and Sparks, 2000).

Climate variables were rainfall and mean temperature during each 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 Spanish *Intituto Nacional de Meteorología*. A negative relationship with temperature (i.e., higher temperatures lead to earlier singing onset) was expected, as shown by many previous studies (e.g., Slagsvold, 1977). Higher temperatures are related to earlier availability of suitable ecological conditions in spring for reproduction. However, fewer studies have tested the effects of precipitation or aridity. According to Gordo et al. (2007a,b) earlier singing onset can be expected in drier and more arid regions.

The three geographic variables were: the distance from each UTM cell to the Straits of Gibraltar; the distance to the nearest major Iberian river; and the cost of dispersion from the Straits of Gibraltar. Later singing onset was expected simply because of delayed arrival for Cuckoos and Nightingales in sites far from Gibraltar that are reached by means of a costly arrival route. Similarly, first-to-sing males were expected to be heard earlier near major rivers, since rivers are predicted to be natural migratory paths for spring colonization. Cost from the Straits of Gibraltar was calculated from a friction surface image (a variable reflecting impediment to, or ease of, movement) and the Costgrow algorithm module of the Idrisi 32 software (Eastman, 2001). The friction surface image was the product of altitude with distance-to-river variables. This takes into account the effect of altitude (low-lying vs. higher valleys) on the probable natural routes of dispersion along major Iberian rivers. Altitude and distance to rivers were standardized (mean = 1 and standard deviation = 0) before they were multiplied. Costgrow generates a cost surface measure of distance as the lowest cost in moving over a friction surface from an origin, in this case the Straits of Gibraltar pixel. Thus, this variable incorporates information on altitude, distance to rivers and distance to the Strait, representing the cost of dispersion from the Straits of Gibraltar along valleys used as migration routes.

Information on the major Iberian river basins (Fig. 2) was also included in the models as categorical predictors. A 0–1



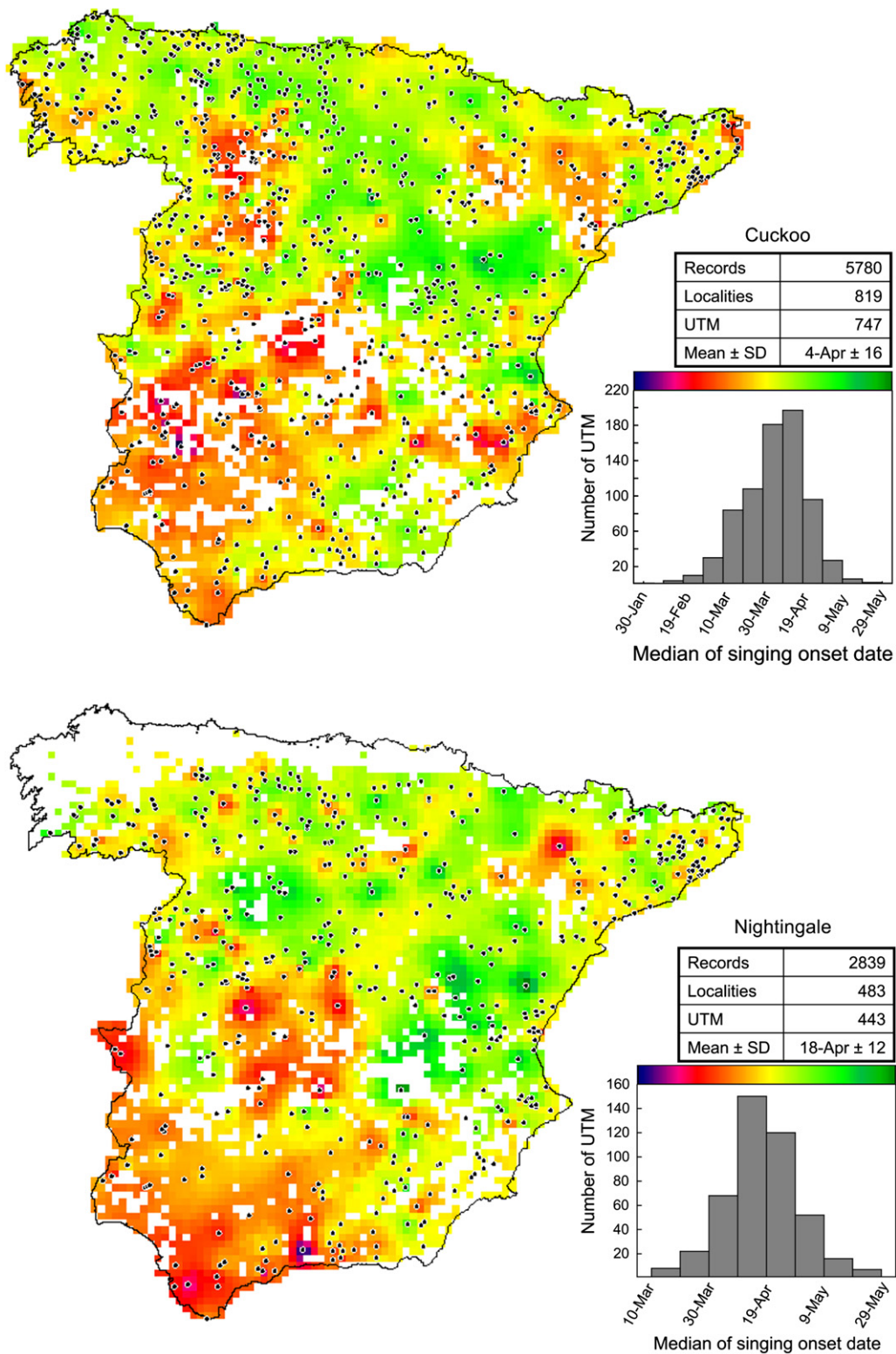


Fig. 1 – Interpolation map of singing onset dates for the Cuckoo and Nightingale. Values only for those UTM cells were the species breed, according to [Martí and Del Moral \(2003\)](#). Black dots represent localities of the Spanish phenological network with records. Details of number of records, localities, UTM cells, mean, standard deviation (SD) and a histogram of the distribution of these observations are given for each species. In the upper part of the histogram a colour bar gives the scale of dates for the map.

**Table 1 – List of variables used in analyses. The acronym, complete description and units (in brackets) are given for each**

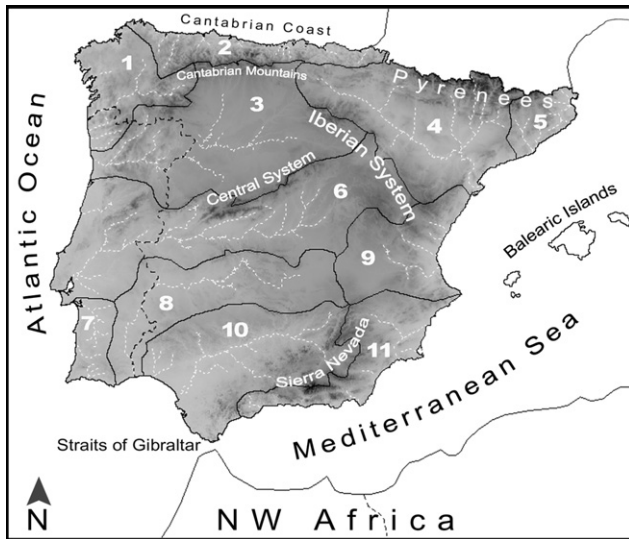
Variables	Description
<i>Spatial</i>	
LAT	Latitude (m)
LONG	Longitude (m)
<i>Topographic</i>	
MEA	Mean altitude (m)
AR	Altitude range (m)
SLP	Slope (degrees)
ASP	Aspect (degrees)
DASP	Diversity of aspects
<i>Climatic</i>	
WIR	Winter rainfall (L)
SPR	Spring rainfall (L)
SUR	Summer rainfall (L)
AUR	Autumn 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>Basins</i>	
CAN	Cantabrian
CAT	Catalana
DUE	Duero
EBR	Ebro
GDN	Guadiana
GDQ	Guadalquivir
MIÑ	Miño
SEG	Segura
TAJ	Tajo
TUR	Turia
<i>Geographic</i>	
DSG	Distance to Straits of Gibraltar (km)
DIR	Distance to rivers (km)
CSG	Cost from Straits of Gibraltar
<i>Abundance</i>	
P30	% of 10 × 10 km UTM where species is present in the 30 × 30 km area around it
<i>Vegetation productivity</i>	
WINDVI	Winter NDVI (January, February, March)
SPNDVI	Spring NDVI (April, May, June)
SUNDVI	Summer NDVI (July, August, September)
AUNDVI	Autumn NDVI (October, November, December)
<i>Land use</i>	
URB-IND	Urbanized land (% cover)
DRY-CROP	Non-irrigated arable crops (% cover)
IRR-CROP	Irrigated arable crops (% cover)
VINE	Vineyards (% cover)
FRUIT	Fruit trees (% cover)
OLIVE	Olive trees (% cover)
MOS-CROP	Mosaic of mixed crops (% cover)
CROP-NAT	Mosaic of crops and natural vegetation (% cover)
DEC-FOR	Deciduous forests (% cover)
CON-FOR	Coniferous forests (% cover)
MIX-FOR	Mixed deciduous and coniferous forests (% cover)
MOOR	Moorlands (% cover)
SCRUB	Scrublands (% cover)
TRANS-SF	Transition from scrubland to forest (% cover)
GRASS	Grasslands (% cover)
DIVSH	Heterogeneity of landscapes (Shannon diversity index)

code was assigned to all the UTM cells of each basin. The Cantabrian basin was excluded from the analysis for the Nightingale since this species does not exist there. Basins are a natural partitioning of territory and could be associated with regional differences in spring phenology, as previous studies have demonstrated (Gordo et al., 2007a,b).

Several variables better related to the local conditions than those previously shown were also considered. Firstly, a relative abundance index for both species was calculated for each 100 km<sup>2</sup> UTM cell from the Spanish bird breeding atlas (Martí and Del Moral, 2003) to differentiate core (with a supposed higher density of breeders) from marginal (lower density) distribution areas. Unfortunately, there are no measurements of absolute abundance for the whole of Spain, neither for the Cuckoo nor for the Nightingale. One may expect that population densities can affect singing behaviour locally (Sparks et al., 2001; Tryjanowski et al., 2005). The singing of a male can stimulate its neighbours (Olinkiewicz and Osiejuk, 2003), increasing overall singing activity in the given zone. This could result in earlier singing onset for core areas with a greater number of males, since increased singing activity should increase the opportunity for earlier recording. It was assumed that the main core areas have had consistently higher numbers of males throughout recent decades (Bernis, 1970). Presence/absence data from the Spanish breeding atlas (Martí and Del Moral, 2003) was used to count the number of 100 km<sup>2</sup> UTM cells with presences in the surrounding 30 × 30 km square (range from zero to nine). This value was divided by the number of available (i.e., terrestrial) UTM cells in the 30 × 30 km square to obtain the percentage of occupancy. This gives a perfectly comparable value of occupancy for UTM cells completely surrounded by terrestrial cells, and coastal and frontier cells surrounded by fewer than nine cells.

Vegetation productivity was also evaluated as a possible local explanatory variable. This variable could affect the energy input to the ecosystem and consequently the directly or indirectly dependent trophic levels, such as the abundance of available insects (the main food source for our studied species). Population density may thus be affected, and this in turn can affect singing activity (see above). On the other hand, the seasonal spatial pattern of vegetation productivity in the Iberian Peninsula could constrain the beginning of the reproductive season of birds. In the case of the Cuckoo, such constraint would be exercised by their host species (Palomino et al., 1998; but see Rose, 1982). Migrant birds have adjusted their life cycle to match their arrival as closely as possible to the availability of suitable ecological conditions in breeding grounds (Coppack and Both, 2002). Since ecological conditions in spring become suitable at different times in different areas (e.g. northern vs. southern sites, or valleys vs. alpine areas), the beginning of reproduction also differs in time (Slagsvold, 1976; Sanz, 1997; Fargallo, 2004). Therefore, one may expect that areas that become productive early in spring should be linked with early male singing activity.

Vegetation productivity was measured as the Normalized Vegetation Difference Index (NDVI). NDVI is the normalized difference between red (0.55–0.68 µm) and infrared (0.73–1.1 µm) reflectance, measured by the Advanced Very High Resolution Radiometer (AVHRR) sensor of NOAA polar orbiting satellites (Smith et al., 1997). NDVI is determined by the degree



**Fig. 2 – Topographical map of the Iberian Peninsula with the main geographical features cited in the text. Black dashed lines indicate political borders. River basins are numbered (codes: 1-Miño, 2-Cantabrian, 3-Duero, 4-Ebro, 5-Catalan, 6-Tajo, 7-Southwestern (not included in analyses), 8-Guadiana, 9-Turia, 10-Guadalquivir, 11-Segura) and their boundaries marked by black solid lines. The main rivers in each basin are shown as white dashed lines.**

of red wavelength absorption by chlorophyll, which is proportional to leaf chlorophyll density. It is also measured by reflectance of near infrared radiation, which is proportional to green leaf density (Tucker et al., 1985). Therefore, NDVI correlates well with such variables as green leaf biomass, leaf area index, total accumulated dry matter and annual net primary productivity (Nicholson et al., 1990). NDVI data, from Clark Labs world images, are monthly values, from 1982 to 2000, at a spatial resolution of 0.1 degree (approximately 11.1 km; Clark Labs, 2001a,b). These maps were rescaled for this study to the 100 km<sup>2</sup> UTM grid for the Iberian Peninsula and combined afterwards to obtain a single average value of vegetation productivity per UTM corresponding to each season.

Land use types were also included because habitat features of the environment may affect singing onset in at least two ways (Doutrelant et al., 1999; Partecke et al., 2004; Tryjanowski et al., 2005): (1) directly by means of species presence and abundance, which in turn can affect singing activity (see above); and (2) indirectly by means of species' detectability according to dominant environment type in each locality of the phenological network (e.g. open habitats favour listening opportunities whereas dense forests do not). However, these effects on recorded dates would probably be offset by the degree of detectability of the studied species, whose song is certainly among the loudest (Tryjanowski et al., 2005). The distribution of 15 land use types for the Iberian Peninsula was obtained from Corine Land Cover 2000 at a 100 × 100 m resolution (see Table 1). Land use based on present data may not be fully representative of use in past decades but, as in the case of species abundance, it was expected that

distribution of major types of habitats in a macroscale (like Spain) would not change during the temporal work scale of this study. The percentage of coverage of each category within each 100 km<sup>2</sup> UTM cell was calculated and used as 15 predictor variables for analyses. The heterogeneity of landscape in each UTM cell was summarized by the Shannon diversity index based on the 15 land use variables.

Finally, the central latitude and longitude of each UTM cell were included in the models in order to incorporate the effects of other historical, biotic or environmental variables not otherwise taken into consideration that may impose spatial trends on singing onset (Legendre and Legendre, 1998). Latitude and longitude were included as a third degree polynomial with nine terms (see Table 1) to take into account possible non-linear spatial trends (Legendre and Legendre, 1998). Latitude and longitude were standardized (mean = 0 and standard deviation = 1) as were topographic, climate, geographic and vegetation productivity variables, in order to eliminate their measurement scale effects.

### 2.3. Statistical analyses

Associations between environmental and geographic variables and singing onset were analysed by means of univariate Partial Least Squares Regression (PLSR). This technique generalizes and combines principal component analysis and multiple regression features to model relationships between the response and explanatory variables (i.e., predictors). Particularly useful for a (very) large set of predictors, the PLSR combination deals with the multi-collinearity problem (Abdi, 2003). Original predictors are linearly combined to obtain components (like principal component analyses) that maximize the explained variance in the dependent variable (Garthwaite, 1994; Abdi, 2003). PLSR components are orthogonal (i.e., independent of each other), and account for successively smaller proportions of variance (i.e.,  $R^2$ ) explained by the original variables (Geladi and Kowalski, 1986). Regression is simplified by reducing the large original set of predictors to fewer components that summarize latent factors from explanatory variables (in this case, environmental gradients). Therefore, components become the independent variables, on which singing onset depends. The meaning of PLSR components was derived from weights of original predictors on each component. The significance level for weights in all components analyses was established as  $P < 0.001$  to avoid spurious relationships due to the large number of original explanatory variables (Bonferroni correction  $\alpha_B = 0.05/58 \approx 0.001$ ). The sum of all squared weight of a component yields one (Geladi and Kowalski, 1986). This property of weights is extremely useful to perform a partitioning of variance (i.e.,  $R^2$ ). It was used to establish the partial  $R^2$  of each group of variables within each component. Since the variation explained by each successive component diminishes, components in final models were limited to those that were significant at the previously-established significance level of  $P < 0.001$ . Predicted scores from final PLSR models were mapped and examined for both species. All these analyses were conducted with STATISTICA software (StatSoft, 2001).

To examine if singing dates predicted by PLSR models are spatially structured, Moran's  $I$  autocorrelation coefficient



with a Bonferroni-corrected significance level (Sawada, 1999) was calculated for ten classes with a lag distance of 60 km between 60 and 600 km. If regression analysis residuals are found to be spatially autocorrelated, one or several important spatially structured explanatory variables are likely to have been left out (Cliff and Ord, 1981; Legendre and Legendre, 1998; Keitt et al., 2002). These analyses were conducted with GS+ software (Gamma Design Software, 2002).

### 3. Results

#### 3.1. Cuckoo

Regression models with the quadratic function for year showed a significant relationship of singing onset dates with the two terms of the function (year and squared year), as it was expected (Gordo and Sanz, 2006). However, this trend towards earlier singing onset dates in the last decade is almost negligible (Adjusted  $R^2 = 0.272\%$ ;  $P = 0.0001$ ) and its strong significance is due to the huge number of records (Fig. 1). This fact denotes that intra-annual variability (i.e., variability among study sites) is much larger than inter-annual variability (i.e., variability among years). Therefore, the potential bias of the long-term trends in the last six decades in this species can be considered of minor importance for the geographic variability in its singing onset.

The map of dates interpolated between localities did not offer clear spatial patterns (Fig. 1). Earlier singing onset occurs mainly in the southern half of the Iberian Peninsula except the Sierra Nevada area in the southeastern corner of Iberia (Fig. 2). There is also scattered early singing onset in parts of the Ebro and Duero basin (Fig. 2). The latest singing onset dates were recorded in the mountainous Iberian System. The earliest and latest median singing onset dates were January 29 and May 26 (range of 118 days), which is an extension of previously reported dates for singing onset phenology of Cuckoos in

Spain (Bernis, 1963, 1970; Fernández-Cruz and Sáez-Royuela, 1971). This was a result of the broader temporal and spatial range of the data. Data was approximately normally distributed (Fig. 1), slightly skewed towards the left (Skewness =  $-0.416$ ,  $t_{746} = 4.646$ ,  $P < 0.001$ ). Slight deviations from normality due to skew does not greatly affect estimates of parametric statistics (StatSoft, 2001), and consequently analyses were carried out with untransformed data.

The final model obtained from the partial least squares regression (PLSR) accounted for more than 26% of geographic variability in the singing onset of the Cuckoo throughout Spain (Table 2). The first component accounted for the major part of the model explanatory capacity (around 19%). The first component related early singing onset to southern UTM cells, especially those located in the Guadiana basin, which are at low altitude and can be reached by a short and inexpensive pathway from the Straits of Gibraltar. It has warmer temperatures throughout the year, lower rainfall during spring and summer and, consequently, low vegetation productivity during summer and autumn (Table 3). These UTM cells were also surrounded by areas with low occupancy rates, with extensive cropland cover (especially irrigated areas), and with little moorland or transitional areas from scrubland to forest.

The second component (around 5% of total variability; see Table 2) associated delays in Cuckoo singing onset with eastern localities from the Turia basin, which are at high altitude and far from major rivers (Table 3). The second component was also related to places with an expensive pathway from the Straits of Gibraltar, extensive scrubland cover or transitional areas tending towards forest, high density of the species, low temperatures in most seasons, dry winters, and, consequently, winters and springs with low vegetation productivity (Table 3).

Finally, the third component (around 3% of total variability; Table 2) associated delayed singing onset with eastern UTM cells. These cells had low altitude and temperature ranges, northern exposure, expensive pathways, milder winter

**Table 2 – Detailed explanatory capacity of the partial least squares regression models in the geographic pattern of singing onset of Cuckoo and Nightingale Spanish populations. Topographic, climatic, basins and geographic groups of variables can be considered as indirect effects on singing onset through migratory progression and arrival date of individuals. Abundance, vegetation productivity and land use can be considered as directly acting on singing activity of already established males. The percentage of variance (partial  $R^2$ ) accounted for by each group of variables is shown for each component, together with its relative weight (% of the components'  $R^2$  in brackets). A summary column (total) is also included to denote the relative importance of each group of variables in the model as a whole. In the last row, the total of variance ( $R^2$ ) accounted for by each component is shown in italics. The total variance accounted for by the model is in bold italics**

Variables group	Cuckoo				Nightingale			
	Comp1	Comp2	Comp3	Total	Comp1	Comp2	Comp3	Total
Spatial	1.25 (6.57)	0.56 (11.97)	0.42 (15.94)	2.24 (8.48)	4.48 (22.72)	0.85 (15.89)	0.29 (9.70)	5.62 (20.02)
Topographic	1.55 (8.12)	0.27 (5.79)	0.18 (6.61)	1.99 (7.55)	0.89 (4.52)	0.24 (4.50)	0.14 (4.52)	1.27 (4.52)
Climatic	8.69 (45.64)	0.80 (17.08)	0.21 (7.89)	9.70 (36.74)	6.35 (32.18)	0.93 (17.53)	0.16 (5.28)	7.44 (26.51)
Basins	1.14 (6.00)	0.69 (14.73)	0.64 (23.90)	2.47 (9.36)	2.33 (11.80)	0.86 (16.16)	0.93 (30.60)	4.11 (14.65)
Geographic	2.07 (10.86)	0.94 (19.92)	0.17 (6.52)	3.18 (12.04)	2.84 (14.37)	0.16 (3.01)	0.08 (2.61)	3.07 (10.95)
Abundance	0.77 (4.06)	0.18 (3.75)	0.15 (5.51)	1.10 (4.15)	0.03 (0.14)	0.25 (4.74)	0.40 (13.37)	0.68 (2.43)
Vegetation productivity	1.35 (7.12)	0.45 (9.51)	0.03 (1.05)	1.83 (6.93)	0.33 (1.69)	0.85 (15.95)	0.04 (1.20)	1.22 (4.34)
Land use	2.21 (11.63)	0.81 (17.24)	0.87 (32.57)	3.89 (14.75)	2.48 (12.59)	1.18 (22.24)	0.99 (32.71)	4.66 (16.59)
Total $R^2$	19.04	4.70	2.66	<b>26.40</b>	19.73	5.32	3.03	<b>28.08</b>

**Table 3 – Predictor weights in significant components (Comps 1–3) of the partial least squares regression models for the Cuckoo and the Nightingale. Significant associations between predictors and components are in bold type ( $P < 0.001$ )**

Variable	Cuckoo			Nightingale		
	Comp1	Comp2	Comp3	Comp1	Comp2	Comp3
<i>Spatial</i>						
LAT	<b>0.179</b>	–0.066	–0.069	<b>0.240</b>	–0.027	–0.064
LAT <sup>2</sup>	0.036	–0.058	<b>0.180</b>	<b>–0.228</b>	<b>–0.220</b>	–0.094
LAT <sup>3</sup>	<b>0.151</b>	–0.079	–0.035	<b>0.275</b>	0.078	0.034
LONG	0.073	<b>0.242</b>	<b>0.131</b>	0.146	0.105	0.000
LONG <sup>2</sup>	0.003	–0.077	–0.082	0.046	–0.064	–0.043
LONG <sup>3</sup>	0.006	0.007	–0.105	0.042	–0.086	–0.100
LONG × LAT	–0.044	–0.046	<b>–0.229</b>	–0.038	<b>–0.224</b>	<b>–0.225</b>
LONG <sup>2</sup> × LAT	0.047	<b>–0.152</b>	<b>–0.142</b>	0.047	<b>–0.171</b>	–0.130
LAT <sup>2</sup> × LONG	0.017	<b>0.126</b>	–0.115	0.113	0.041	–0.058
<i>Topographic</i>						
MEA	<b>0.209</b>	<b>0.233</b>	–0.071	<b>0.182</b>	0.054	0.034
AR	<b>0.129</b>	–0.013	<b>–0.159</b>	–0.057	–0.097	0.072
ASP	–0.027	–0.043	<b>–0.149</b>	–0.071	–0.143	–0.147
DASP	0.015	–0.037	–0.024	0.001	0.023	0.098
SLP	<b>0.141</b>	–0.005	–0.114	–0.061	–0.108	0.087
<i>Climatic</i>						
WIP	0.088	<b>–0.187</b>	–0.016	–0.132	<b>–0.232</b>	0.080
SPP	<b>0.170</b>	–0.113	0.011	0.028	<b>–0.179</b>	0.089
SUP	<b>0.221</b>	–0.012	–0.018	<b>0.216</b>	–0.050	0.007
AUP	<b>0.140</b>	<b>–0.142</b>	0.017	–0.039	<b>–0.216</b>	0.064
WIMET	–0.223	<b>–0.158</b>	<b>0.162</b>	<b>–0.248</b>	–0.007	0.073
SPMET	<b>–0.288</b>	<b>–0.178</b>	0.031	<b>–0.250</b>	–0.021	–0.008
SUMET	<b>–0.291</b>	–0.113	–0.065	<b>–0.243</b>	–0.011	–0.055
AUMET	<b>–0.280</b>	<b>–0.164</b>	0.057	<b>–0.263</b>	–0.024	0.005
ATR	–0.092	0.067	<b>–0.207</b>	0.024	0.020	<b>–0.161</b>
AI	<b>–0.218</b>	0.045	0.002	–0.048	<b>0.197</b>	–0.009
<i>Basins</i>						
CAN	0.085	–0.055	0.101			
CAT	0.000	–0.057	–0.071	0.006	–0.108	–0.029
EBR	0.044	0.038	–0.036	0.067	–0.044	<b>–0.155</b>
DUE	0.033	–0.017	<b>–0.218</b>	0.093	–0.038	–0.116
GDN	<b>–0.191</b>	<b>–0.253</b>	<b>–0.302</b>	–0.112	–0.052	–0.025
GDQ	–0.086	0.031	<b>0.180</b>	<b>–0.172</b>	–0.022	<b>0.174</b>
MIN	0.019	<b>–0.133</b>	0.058	0.013	0.023	<b>0.213</b>
TAJ	0.025	<b>0.141</b>	<b>0.194</b>	–0.052	–0.075	–0.143
SEG	–0.046	0.057	0.034	–0.149	–0.061	<b>–0.168</b>
TUR	0.053	<b>0.182</b>	0.096	<b>0.194</b>	<b>0.365</b>	<b>0.378</b>
<i>Geographic</i>						
DSG	<b>0.188</b>	0.005	–0.008	<b>0.256</b>	0.018	–0.039
DIR	<b>0.131</b>	<b>0.232</b>	0.112	0.035	–0.037	–0.153
CSG	<b>0.237</b>	<b>0.381</b>	<b>0.229</b>	<b>0.277</b>	<b>0.168</b>	0.035
<i>Abundance</i>						
P30	<b>0.202</b>	<b>0.194</b>	<b>0.235</b>	–0.037	<b>–0.218</b>	<b>–0.366</b>
<i>Vegetation productivity</i>						
WINDVI	0.032	<b>–0.199</b>	–0.006	–0.117	<b>–0.212</b>	0.044
SPNDVI	0.119	<b>–0.186</b>	–0.099	0.009	<b>–0.213</b>	0.032
SUNDVI	<b>0.188</b>	–0.096	–0.009	0.055	<b>–0.198</b>	0.018
AUNDVI	<b>0.144</b>	–0.108	0.023	–0.011	<b>–0.173</b>	0.093
<i>Land use</i>						
URB-IND	–0.063	–0.024	0.070	–0.119	–0.142	<b>–0.230</b>
DRY-CROP	–0.099	0.003	–0.087	0.072	0.064	–0.076
IRR-CROP	<b>–0.122</b>	–0.114	<b>–0.210</b>	–0.005	0.054	–0.004
VINE	–0.050	0.038	0.065	0.060	0.146	<b>0.169</b>
FRUIT	–0.013	0.102	<b>0.162</b>	–0.088	–0.076	<b>–0.209</b>
OLIVE	–0.084	0.010	0.113	–0.151	–0.074	–0.022
MOS-CROP	–0.043	–0.052	0.070	0.007	0.073	–0.027
CROP-NAT	–0.053	<b>–0.122</b>	–0.048	–0.088	–0.047	–0.029

(continued on next page)



Table 3 (continued)

Variable	Cuckoo			Nightingale		
	Comp1	Comp2	Comp3	Comp1	Comp2	Comp3
DEC-FOR	0.108	−0.005	0.072	−0.051	−0.164	0.040
CON-FOR	0.085	0.006	−0.193	0.162	0.159	0.259
MIX-FOR	0.028	−0.128	−0.020	0.055	−0.046	0.036
MOOR	0.128	−0.035	0.074	−0.036	−0.231	−0.209
SCRUB	0.080	0.264	0.219	0.001	0.042	−0.038
TRANS-SF	0.133	0.121	0.086	0.169	0.181	0.258
GRASS	0.000	−0.101	−0.203	−0.055	−0.113	−0.026
DIVSH	0.114	0.130	0.272	−0.002	−0.021	0.108

temperatures, high density of individuals, and highly diverse landscapes with large scrubland and fruit tree cover, but little coniferous forest, grassland or other crops (Table 3).

In the case of the Cuckoo, some explanatory variables appeared to be significantly linked to all components. They characterized the environmental gradients described by the three components in the same way, highlighting their relevance to Cuckoo singing phenology. The Guadiana basin is a region where Cuckoos sing early, while the species was heard later in those areas with low population density and far from the Straits of Gibraltar (Table 3).

PLSR residuals were not significantly autocorrelated at any lag distance, an indication that no spatially structured variation remained to be included in the model (Fig. 3).

Predictions from the PLSR model are mapped in Fig. 4. The model predicts earliest singing onset in the Guadiana and Guadalquivir basins (in purple). Afterwards, in a short interval of only 15 days (red to yellow), the Cuckoo can be heard for the first time in most of Iberia, including the entire southern half of Spain, most of the Ebro and Duero basins, and all of the Mediterranean coast. The Cuckoo is heard much later (green) in the rest of the areas, which are associated mainly with mountainous regions (e.g., Iberian System, Pyrenees, Cantabrian Mountains) and the Cantabrian coast.

### 3.2. Nightingale

As in the previous case, it is difficult to detect clear spatial trends by a visual inspection of the picture obtained from the interpolation of singing onset data between localities (Fig. 1). The Turia basin was the only area where Nightingale singing onset was reported late in all localities. Duero and Ebro basins (northern Spain) showed in general late dates but some early localities pop up throughout these regions. The southern half of Spain was early, especially the Gibraltar area. The distribution of data was normal, with earliest and latest mean values (March 10 and May 24) also extending previously reported dates for this species (Bernis, 1963; Fernández-Cruz and Sáez-Royuela, 1971).

The final model obtained from the PLSR analysis accounted for a bit more variability of singing onset for the Nightingale (up to 28%; Table 2) than in the case of the Cuckoo, which demonstrates the existence of a spatial structure of data hidden to visual inspection (Fig. 1). The explanatory capacity ( $R^2$ ) of each component in the Nightingale model was quite similar

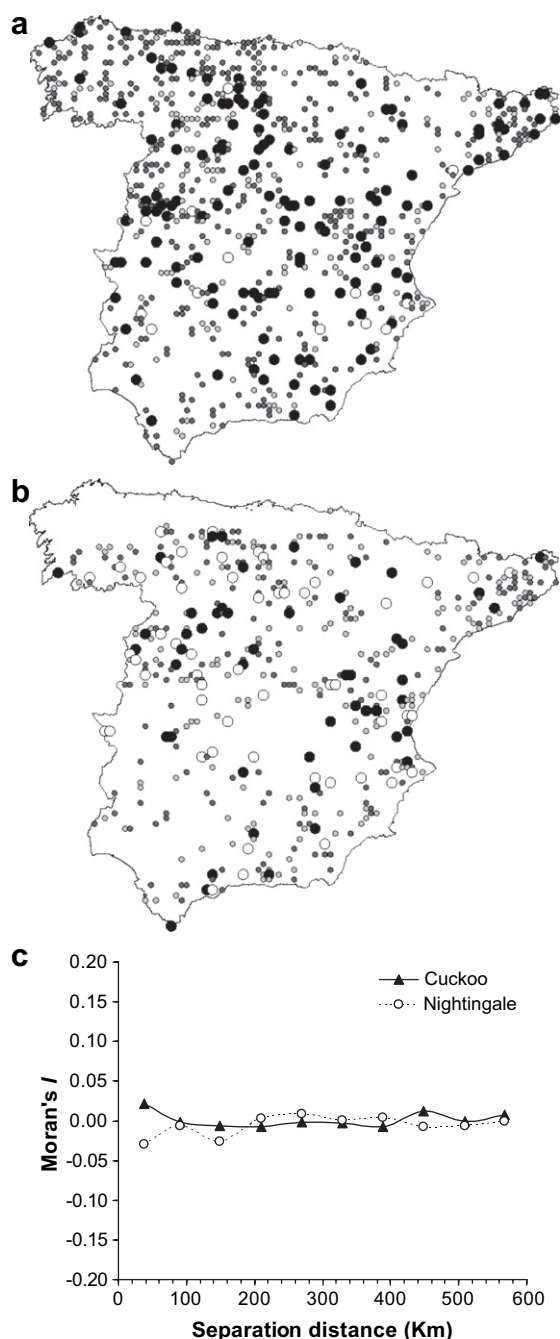
to the Cuckoo model, although the relative contribution of each group of variables to each component was different (Table 2). The first component explained almost 20% of total model explanatory capacity. This component associated earlier singing onset with southern localities from the Guadalquivir basin. These localities are at low altitude, with a short and relatively inexpensive pathway from the Straits of Gibraltar, mild temperatures throughout the year and dry summers, and sparse cover of coniferous forest or scrubland-to-forest transitional areas (Table 3).

Both remaining components together explained about 8% of spatial variability in singing onset for this species (Table 2). The second component associated later dates for singing onset detection with localities in the north-eastern corner of the Iberian Peninsula, especially in the Turia basin. These localities showed low vegetation productivity throughout the year as a result of low precipitation in most seasons, causing arid conditions (Table 3). These localities had low Nightingale densities and were dominated by coniferous forests and transitional areas from scrubland to forest with an absence of deciduous forests and moorlands. Finally, the meaning of the third component was less clear (Table 3). It related delayed singing onset with localities from the north-eastern corner of the Iberian Peninsula and the Turia basin. These are areas with low densities of pairs of this species and little human influence, and with extensive vineyard cover and few fruit trees. This component also related delayed singing onset with sites with coniferous forest cover, transition from scrubland to forest, and with several basins. Residual scores were not significantly spatially autocorrelated (Fig. 3b).

Environmental gradients described by PLSR components can be much more easily interpreted by mapping model scores (Fig. 4). The areas where Nightingales are heard earliest (purple in Fig. 4) are those located near Gibraltar. Next (red and yellow), males singing first are heard in southwestern Iberia, and in a narrow strip along the entire Mediterranean coast. Finally, the major part of Iberia is reached by Nightingales in a very short interval of 10 days (between April 20 and 30), leaving a highly delayed zone (predicted singing onset in May) in only the Turia basin, the Iberian Mountain System and the Pyrenees.

### 3.3. Relative importance of each type of variables

The importance of each group of variables (i.e., partial  $R^2$ ) showed marked heterogeneity both between components



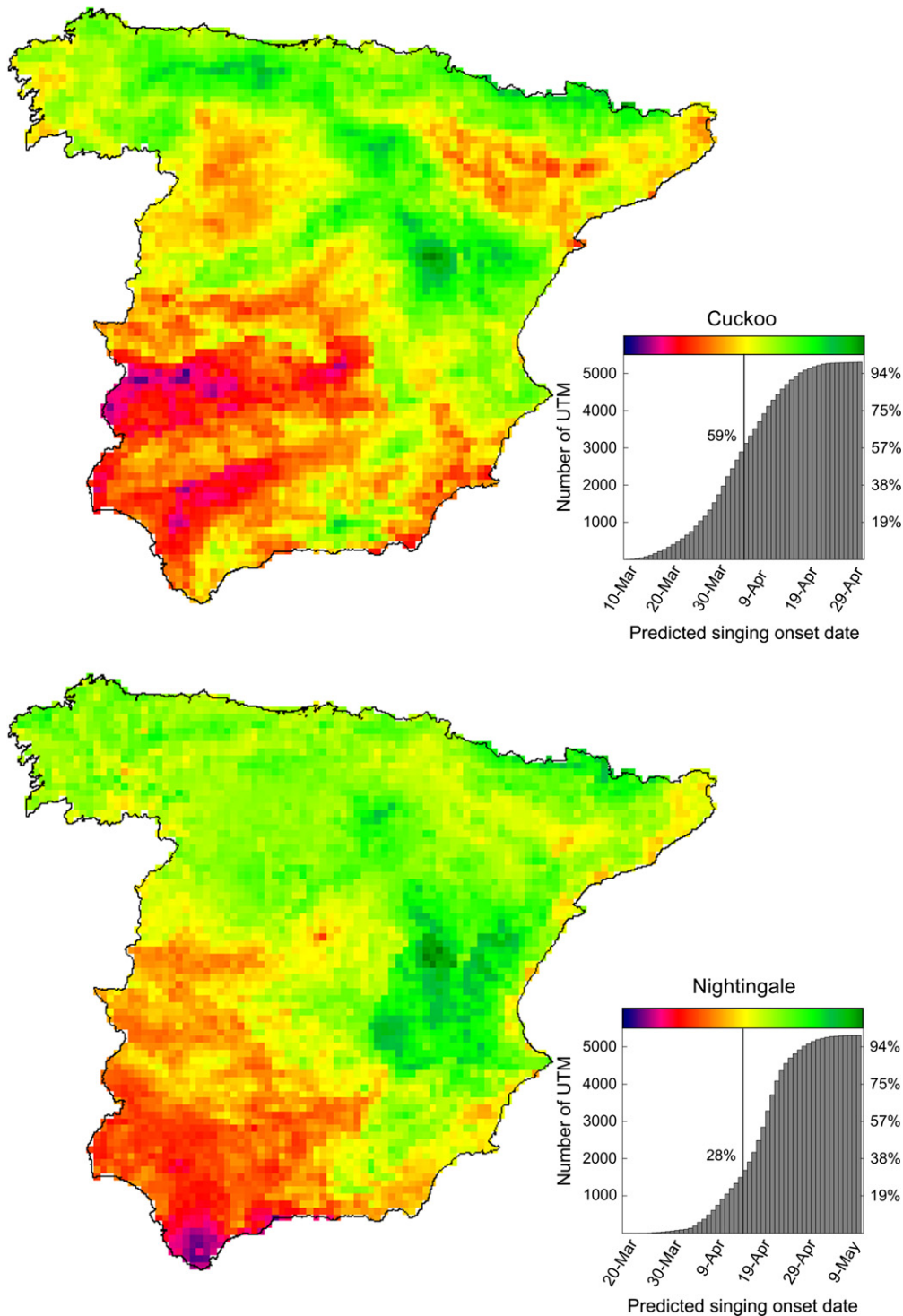
**Fig. 3 – Geographic distribution of residuals of partial least squares regression models for the Cuckoo (a) and Nightingale (b). Residuals are divided into four quartiles in which large white circles represent localities with high negative residuals (predicted scores lower than observed), and large black circles are localities with high positive residuals. (c) Spatial autocorrelation of residuals from partial least squares regression models. Isotropic correlograms represent the variation in the scores of Moran's  $I$  spatial autocorrelation statistic with increase in the separation distance between 100 km<sup>2</sup> UTM cells (in km), using a lag distance of 60 km and an active lag of 600 km.**

and between species (Table 2). In the case of the Cuckoo, climatic variables stand out notably. This is especially true for the gradient defined by the first component, where climate represented almost half of the variability explained in singing onset dates. Geographic variables were the most important for the explanatory capacity of the second component, but climate and land use also played a notable role. However, since the total amount of variability explained by the second component was about 5%, the real contribution of each of these groups was of low relevance. Similarly, the greater importance of the basins and land uses in the third component of the Cuckoo implied only a very small real contribution to the full model explanatory capacity (between 0.6% and 0.8%). Overall (total column in Table 2), those variables hypothetically more related to the indirect effect of environment through effects on migratory progression and arrival of individuals (i.e., topography, climate, basins and geography) accounted for most of the variability of the final model (about 66%). However, those variables that we supposed were related to the direct effect of the environment on singing activity of males (i.e., abundance, vegetation productivity and land uses) were of less relevance (about 26% of final explanatory variance). It must also be noted that the spatial terms represented more than 8% of the final  $R^2$  model, which highlights the existence of a remaining spatial structure of singing onset dates not accounted for by any of the rest of the explanatory variables.

In the case of the Nightingale, climate variables were again the most important in the first component (Table 2). However its dominance in the overall model is not as overwhelming as in the Cuckoo (26% vs. 36%, respectively). In the Nightingale model, the relevance of spatial variables, which account for a fifth of the total variability explained by the model, also stands out. This means that a notable part of the spatial patterns in singing onset dates of the Nightingale have an unknown origin, such as other non-considered environmental or geographic explanatory variables or historical processes. In summary, variables related to indirect effects were also the most important (about 57% of total  $R^2$ ) in the Nightingale, while those related to direct effects had even less importance (about 23% of total  $R^2$ ).

#### 4. Discussion

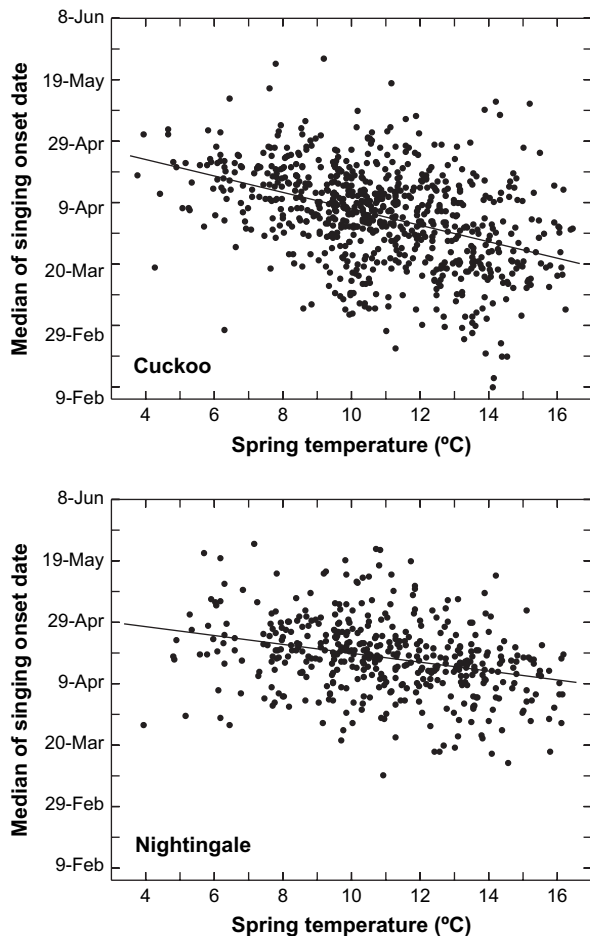
Differences in singing onset phenology among populations of Cuckoos and Nightingales are spatially structured and strongly correlated with some environmental factors. The complicated picture obtained by means of interpolation of raw data (see Fig. 1) was clarified by predictions of partial least squares regression models (see Fig. 4), which revealed the underlying spatial patterns of variability in singing onset in both species. Climate appears as the most important type of variable influencing variability in singing onset among populations of both species. Individuals singing earliest are heard in the warmest and driest regions of Iberia (see Fig. 5). This, in turn, is closely related to the effect of other variables. Altitude is related positively in all cases (i.e., later detection in more elevated zones), in agreement with predictions (Angot, 1900; Bernis, 1970; Slagsvold, 1976; Huin and Sparks, 2000). A



**Fig. 4 – Geographic representation of predicted singing onset dates for 100 km<sup>2</sup> UTM cells from the partial least squares regression models for the Cuckoo and the Nightingale. A cumulative histogram with the number of Spanish UTM occupied each day (in the right y-axis the percentage) is shown. In the upper part of the histogram a colour bar gives the scale of dates for the map. A vertical line within the histogram marks the halfway point in the range of dates. The precise percentage for this date value is showed.**

marked latitudinal gradient (i.e., later in northern sites), measured both as latitude and as distance from the Straits of Gibraltar, was especially relevant for the Nightingale. This result was also to be expected (Bernis, 1970; Slagsvold, 1976;

von Haartman and Söderholm-Tana, 1983). Moreover, the cost of migration from Gibraltar also appeared as a highly explicative variable, and was especially relevant for the Cuckoo. The warmest and driest Iberian regions located in the south at



**Fig. 5 – Relationship between singing dates and mean spring temperature in the 100 km<sup>2</sup> UTM's for the Cuckoo ( $n = 747$ ) and Nightingale ( $n = 453$ ). Solid line represents the best linear-fit model.**

low altitudes near the Straits of Gibraltar leads to the pronounced collinearity of these variables, and was well-summarized by the environmental dependence defined by the first component in both species. Therefore, from a purely descriptive point of view, we can conclude that in both species, earliest singing onset occurs in southern Spain, close to Gibraltar, in easily accessible sites located at low altitude and with mild and dry climate. This pattern concurs broadly with patterns described recently for the Common Swift *Apus apus*, the Barn Swallow *Hirundo rustica* (Gordo et al., 2007a) and the White Stork *Ciconia ciconia* (Gordo et al., 2007b) in Spain. This fact would reinforce the hypothesis suggested by those authors that spatial configuration imposes unavoidable constraints for the spring progression of migratory birds.

Common gradients described by the Cuckoo and the Nightingale models and shared with other species (Gordo et al., 2007a,b) disagree with observable differences in the pictures resulting from both the interpolated (Fig. 1) and the predictive maps (Fig. 4). However, these spatial differences arose mainly from differences in the rate of progression of singing onset through Spain rather than by true differences in the spatial patterns. There are indeed subtle differences in the spatial

structure of the singing onset (e.g., the Nightingale has a bit more marked south–north axis than the Cuckoo), but with our data resolution and explanatory capacity of predictive models, only those broader patterns (i.e., those described by the first component) are reliable. According to the prediction of the final model, the Cuckoo sings early in the southern half of Iberia and in other Ebro and Duero basin areas (purple and red areas in Fig. 4), while the earliest areas for the Nightingale occur only in the south-western corner of Iberia. Areas where singing occurs later (yellow to green colours in Fig. 4) are only in a minor portion of Spain, especially in mountainous regions in the case of the Cuckoo. The late singing areas for the Nightingale correspond to most parts of the country. The different rate of progression of singing onset through Spain of Cuckoos and Nightingales is well-illustrated by the percentage of Spanish territory occupied during the predicted calendar range (Fig. 4). At half of the dates, the Cuckoo has been heard for the first time in almost 60% of Spain, while in the case of the Nightingale only in 28%. Therefore, Cuckoo singing onset spreads quickly at the beginning of the predicted singing onset period, whereas the Nightingale does it at the end of the period.

Singing onset variability was low in the major part of the Iberian Peninsula. The standard deviation in both species was about 15 days. It is c. 25 days for the Barn Swallow *Hirundo rustica*, the Common Swift *Apus apus* or the White Stork *Ciconia ciconia* in the same area and years (Gordo et al., 2007a,b). In fact, final models predicted a range of singing onset, between the earliest and latest dates, of shorter than 2 months (Cuckoo = 3-Apr  $\pm$  9 days; Nightingale = 17-Apr  $\pm$  7 days; mean  $\pm$  SD). Moreover, final maps (Fig. 4) showed that singing males are first detected in most parts of Spain within a rough range of 15 days (between March 20–April 5 for the Cuckoo and April 15–30 for the Nightingale; see histograms of Fig. 4). Therefore, singing onset has lower spatial variability than other measures of arrival dates, such as first sighted individuals (Gordo et al., 2007a,b). Unfortunately, we cannot determine to what extent this fact is due to peculiarities of this phenological measure or to species-specific characteristics.

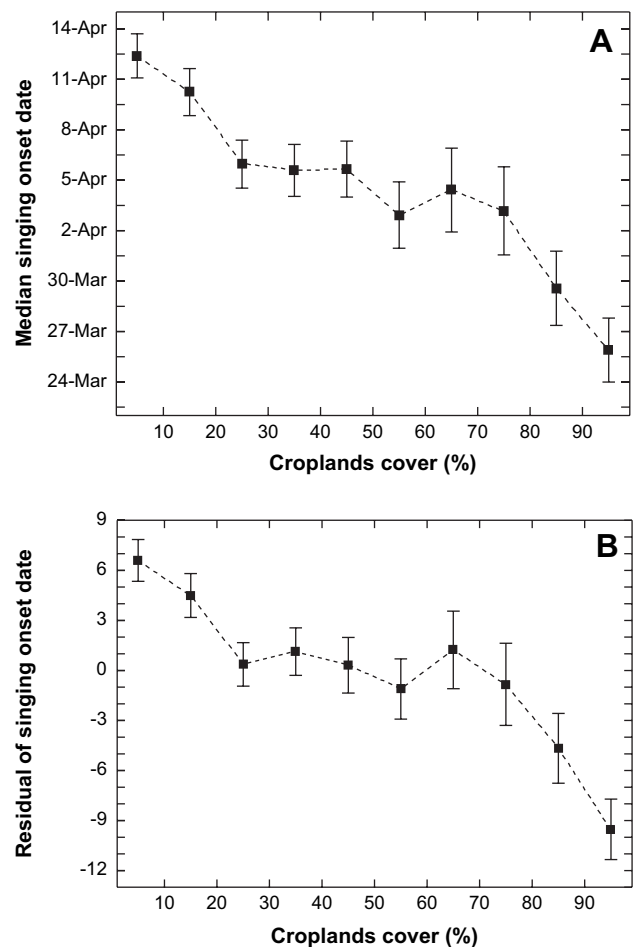
The variability in singing onset accounted for by the final models (i.e.,  $R^2$ ) of the Cuckoo and Nightingale was also lower than that accounted for by models for the first arrival dates in other migrants (Gordo et al., 2007a,b). The worse explanatory capacity of singing onset models cannot be attributed to the employed predictor variables, since they were the same as in previous studies (i.e., Gordo et al., 2007a,b) along with others related to the direct effect of local conditions on males' singing onset decisions. Furthermore, the complete absence of residual spatial autocorrelation (see Fig. 3) is an indication that most likely no other variables, at our working resolution and extent, would help to improve model predictions. The lower explanatory capacity could be related to the above mentioned shorter range of dates, which does not create strong phenological gradients. Alternatively, the dual nature of first listening dates (i.e., depends on individuals' arrival and their singing activity) could blur spatial differences due, for example, to spatial differences in the lag between arrival and singing onset. Results for both species suggest that the latter hypothesis could be true. For example, in the case of the Cuckoo, dates predicted in the Duero basin as well as in the north-eastern



Mediterranean coast (about March 25; see Fig. 4) are similar to those predicted for some regions from the southernmost parts of Spain. However, in these latter zones, Cuckoos may arrive earlier because of the greater proximity to Africa.

To the best of our knowledge, this is the first time that potential relationships between spatial variability in singing phenology and vegetation productivity and land uses have been tested. Both groups of variables were included because they may influence singing onset by local environmental conditions acting over male decisions. Overall, vegetation productivity was not relevant in either studied species. Therefore, singing onset is almost independent of the amount of vegetation productivity and thus on resource availability. Land use was especially important for the second and third components both in the Cuckoo and the Nightingale. Nevertheless, the absolute contribution to model explanatory variability (see Table 2) is a bit disappointing because this group was constituted by the larger number of predictor variables (16). Few land use variables were strongly related with the principal environmental gradients described by the first (and most important) component (see Table 3). In the case of the Cuckoo, their song seemed to be heard earlier in areas with any type of crop cover (negative sign in all types of cover in the first component; see Fig. 6A). This relationship remains little changed by the removal of spatial structure in the onset of Cuckoo singing by means of the third degree polynomial of latitude and longitude (Legendre and Legendre, 1998; see Fig. 6B), which would be in agreement with the local influence of this type of variable.

The influence of the relative abundance index on the Cuckoo was noteworthy, even though it accounted for little total variability in each component (4–5%, but note that it is a single variable). Earlier onset was expected in areas with denser populations. Here, chances for earlier detection should be greatest (Sparks et al., 2001; Tryjanowski and Sparks, 2001; Tryjanowski et al., 2005). However, the effect of abundance on its singing onset was in the opposite direction, i.e., the Cuckoo is heard for the first time earlier in the less populated areas. Singing onset in core areas may be delayed due to being coincident with those areas far from Gibraltar and with a later arrival of spring weather. Nevertheless, the relationship is maintained even when removing the spatial structure of singing data by means of the third degree polynomial of latitude and longitude (Legendre and Legendre, 1998), which suggests that the abundance index effect is not due to spatial collinearity. Alternatively, early singing onset in sparsely populated areas may also be linked with the breeding biology of the Cuckoo, which involves the parasitic use of other bird species' broods (Cramp, 1985). While their potential host spectrum is broad, the Cuckoo lays its eggs only in nests of those host species with greatest abundance of breeding pairs in a given region (Soler et al., 1999; Álvarez, 2003; Reichholf, 2005). Iberian areas that are sparsely populated or unpopulated by Cuckoos (see Fig. 1) are mainly those with little abundance, or even absence, of host breeder pairs (e.g., wren *Troglodytes troglodytes*, dunnoek *Prunella modularis*, rufous bush robin *Cercotrichas galactotes*, or robin *Erithacus rubecula*). These regions, sparsely populated by Cuckoos, were already identified several decades ago (Bernis, 1970). Hence, we are confident that empty cells are not an artefact of distribution retreat during recent decades. In areas with a low density of potential host



**Fig. 6 – Median (A) and residual from a trend surface analysis (B) of singing onset in the 100 km<sup>2</sup> UTM cells for the Cuckoo ( $n = 747$ ), according to percentage of cover provided by all types of crops (sum of the variables urb-ind, dry-crop, irr-crop, vine, fruit, olive, mos-crop and crop-nat, see Table 1). Bars indicate standard error.**

pairs, we suggest that Cuckoos suffer from increased intra-specific competition. The favourability for Cuckoo reproductive success of an early spring arrival, when non-parasitized nests would still be available in large number, would seem obvious (Palomino et al., 1998; Soler et al., 1999). Therefore, in this situation, selective pressure for earlier arrivals would be high. Since Cuckoos are strongly philopatric, this situation could be maintained over time. Unfortunately, neither precise information on host reproductive phenology, nor the parasitism rate for each population in a comparable geographic range is available to confirm our hypothesis.

Singing onset can be affected indirectly through factors influencing migratory progression and arrival date of individuals, or directly by affecting males' decisions on singing activity once they have established a breeding territory. To discern, in a precise way, between both effects we would ideally need to know the exact arrival date of males. Unfortunately, our data only recorded the singing onset of them because they are a very shy and skulking species and it is almost impossible to sight quiet males. Therefore, our dates are indeed a sum of

the arrival date plus the time passed until the singing onset. Traditionally, it has been assumed that the first singing date is a good proxy of the arrival date because the passed time between the arrival and the singing onset is short due to the urgency of males to get a territory and a mate as early as possible. Our results give support to this assumption. Those groups of explanatory variables such as abundance, land use or vegetation productivity would be better related to the singing decisions of individuals once they arrived (i.e., direct effects). However, all of these mentioned variables were of low relevance (see Table 3). This fact suggests that those mechanisms acting on a local scale among individuals (Doutrelant et al., 1999; Ilyna and Ivankina, 2001; Lengagne and Slater, 2002; Olinkiewicz and Osiejuk, 2003) are not relevant to explain broader geographical patterns among populations on a large scale. The greater importance of those fixed abiotic variables such as geography, topography or climate features of each site suggests that singing onset is determined mainly by environmental factors related to the progression during spring migration and the arrival of individuals, rather than by decisions of individuals on singing activity. Therefore, phenological maps for singing onset can be assumed as a good reflection of the arrival and progression in some migratory bird species (Bernis, 1970; Tryjanowski et al., 2005), most likely as a result of the urgency of males to start singing just after they arrive. In conclusion, our study suggests that singing onset is a good proxy for the arrival dates of migratory birds.

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