



UNIVERSITAT DE BARCELONA



Departament de Biologia Animal
Facultat de Biologia
Universitat de Barcelona



Departamento de Ecología Evolutiva
Museo Nacional de Ciencias Naturales
Consejo Superior de Investigaciones Científicas

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

Memòria presentada per Oscar Gordo Villoslada
per optar al títol de Doctor

Programa de doctorat: Zoologia
Bienni 2002-2004

El doctorand

Oscar Gordo Villoslada

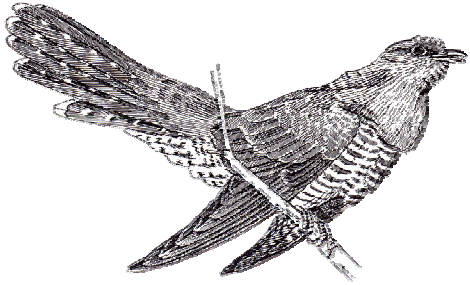
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Dr. Xavier Ferrer Parareda

Dr. Juan José Sanz Cid

Dr. Lluís Brotons i Alabau

Barcelona, Juliol 2006



Chapter 2

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

Oscar Gordo^{1,2}, Juan José Sanz², Jorge M. Lobo³

¹ Departament de Biologia Animal (Vertebrats), Universitat de Barcelona.

² Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC).

³ Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC).

Auk (submitted)

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 the cuckoo (*Cuculus canorus*) and the nightingale (*Luscinia megarhynchos*) recorded in thousands of sites throughout Spain was related to a set of potential predictors by partial least squares regression. Predictor variables (spatial, topography, basin, geographic, climate, abundance of species, vegetation productivity and land use) can affect first recorded singing dates in two ways: directly through individual decisions on singing activity and indirectly through spring migration route. Final model predictions indicated weak spatial structure in singing onset although well modelled by the environmental variables employed. Of the variables, climate was the most influential. Males of both species sing earlier in warmer and drier sites, which are closely related with geographic and topographic gradients in the Iberian Peninsula. Although some variables affected the singing activity of both species equally, final model predictions for the cuckoo, which colonizes most of Iberia in its first migratory wave, were quite different from predictions for the nightingale, which does so in its second migratory wave. In summary, the onset of singing of two migratory species, encountering very similar environmental conditions during nearly identical spring migratory periods, falls into different geographic patterns.

INTRODUCTION

Birdsong is the major means of communication among birds (Kroodsma *et al.*, 1982). 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 birdsong is highly dependent on environmental conditions and this, in turn, affects later stages of the life cycle (Slagsvold, 1977; Hegelbach & Spaar, 2000). Migratory bird reproduction is constrained by the period of suitable ecological conditions in breeding grounds (Coppack & Both, 2002). In fact, migrant birds have a greater urgency to reach their breeding grounds earlier as possible due to the benefits of an early arrival (Møller, 1994; Kokko, 1999; Forstmeier, 2002).

Singing is the only measurable observation possible for shier and more elusive species. Consequently, singing onset marks the annual spring arrival for many migrant birds most faithfully, although the date so derived may not entirely coincide with the date of arrival of the individual singer (Rendahl, 1965a; De Smet, 1967). Nevertheless, as singing is assumed to begin soon after arrival, spurred on by the reproduction urge of migrants, the measure of singing onset is assumed to reflect arrival date accurately enough (Slagsvold, 1977; Huin & Sparks, 2000). In any case, environmental variables can affect singing onset indirectly through time of colonization of breeding grounds, through spring migration timing, and directly through stimulus to singing, once individuals have arrived in breeding territories. Singing onset may then be influenced by individual characteristics (e.g., Ilyna & Ivankina, 2001), population density (e.g., Olinkiewicz & Osiejuk, 2003), weather variability (e.g., Lengagne & Slater, 2002) or habitat type (e.g., Doutrelant *et al.*, 1999). Changes in singing activity can consequently affect the timing of detection of individuals in each population, since greater singing activity increases the chance of detection (De Smet, 1967; Sparks *et al.*, 2001; Tryjanowski *et al.*, 2005). Unfortunately, in some cases indirect and direct effects can be indistinguishable (e.g., bad weather both delays migration and also inhibits singing activity).

Singing onset has been used in numerous studies as a measure of spring migratory phenology (e.g., Huin & Sparks, 2000). As far back as the

nineteenth century, Middendorff (1855) used singing onset of the cuckoo *Cuculus canorus* to study the migratory progression of this species 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; Brestcher, 1935; Sliwinsky, 1938; Verheyen, 1951; Bruns & Nocke, 1959; Rendahl, 1965a,b; De Smet, 1967; De Smet, 1970; Munteanu, 1982; Huin & Sparks, 2000). All of them took advantage of the popularity of this species among amateurs to compile huge amounts of first singing records in their countries. Unfortunately, these studies are purely descriptive and suffer from an exhaustive search into environmental factors behind the observed geographical patterns.

Despite of the popularity of such migrants as the cuckoo, studies similar to those previously cited are lacking in the Iberian Peninsula for any species (Pérez-Tris & Santos, 2004). Moreover, the information available on any aspect of migration for Iberian populations is scarce or virtually absent in the case of most trans-Saharan bird species. As Iberian and North-African cuckoo populations belong to the subspecies *bangsi*, information available on other European populations may not be fully applicable. The too, information available on another popular migrant, the nightingale *Luscinia megarhynchos*, does not go beyond anecdotal singing-onset records for a few sites (Bernis, 1963; Fernández-Cruz & Sáez-Royuela, 1971) and some few ringing recoveries (Bueno, 1990).

The aim of this study is to determine the geographic and environmental factors influencing spatial patterns of singing onset for the cuckoo and the nightingale in the Iberian Peninsula. The song of both species, common and widespread in the Iberian Peninsula (Martí & Del Moral, 2003), is easily detectable (Tryjanowski *et al.*, 2005). Such shared features are very important because they could seriously bias phenologic measurements (De Smet, 1967; Sparks *et al.*, 2001; Tryjanowski *et al.*, 2005). Furthermore, both populations encounter similar ecological conditions during their nearly identical spring migration dates. However, these seem to be their only shared features, as the rest of their ecology and behaviour is completely different (Cramp, 1985;

Cramp, 1988). Therefore, they provide an ideal test of how a shared scenario (i.e. ecological conditions during the spring migration into Iberia) may have led to convergent or analogous migratory strategies, or, alternatively, how particular ecological requirements may have led to specific migratory strategies.

MATERIAL AND METHODS

Bird phenological data

Singing phenology data for the cuckoo and nightingale were obtained from the phenological database of the Spanish *Instituto Nacional de Meteorología*. This database is the result of a volunteer observer network set up several decades ago by the *Instituto Nacional de Meteorología* to better understand the timing of seasons and improve agricultural practices, as has been done in other European countries (e.g., UK; Huin & Sparks, 1998). 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 (Anon., 1943). Selected species characteristics, lending themselves to a phenological monitoring scheme, are: i) broad distribution throughout Spain (anyone can become a volunteer observer), ii) great abundance (observation of phenological events would not be constrained by number of individuals), iii) unmistakable morphology and/or behaviour (making the data highly reliable). Therefore, homogeneity of data is assured.

Singing phenology of both species was measured as the date of singing onset for the first male in each study locality and year. All available records from 1945 to 2004 from original registers were collected and computerized to obtain a total of 8621 data from 898 localities (see Fig. 2.1). Dates were transformed to a Julian day scale (1 = first day of January), taking into account leap-years by adding 1 day after 28 February. Previous to analysis, we attempted to eliminate potential bias from long-term singing date trends in the UTM values recorded by regressing singing dates for both species with the year and its quadratic term. Residuals obtained were added to original data to remove temporal trends. Corrected dates were then used in all subsequent analyses.

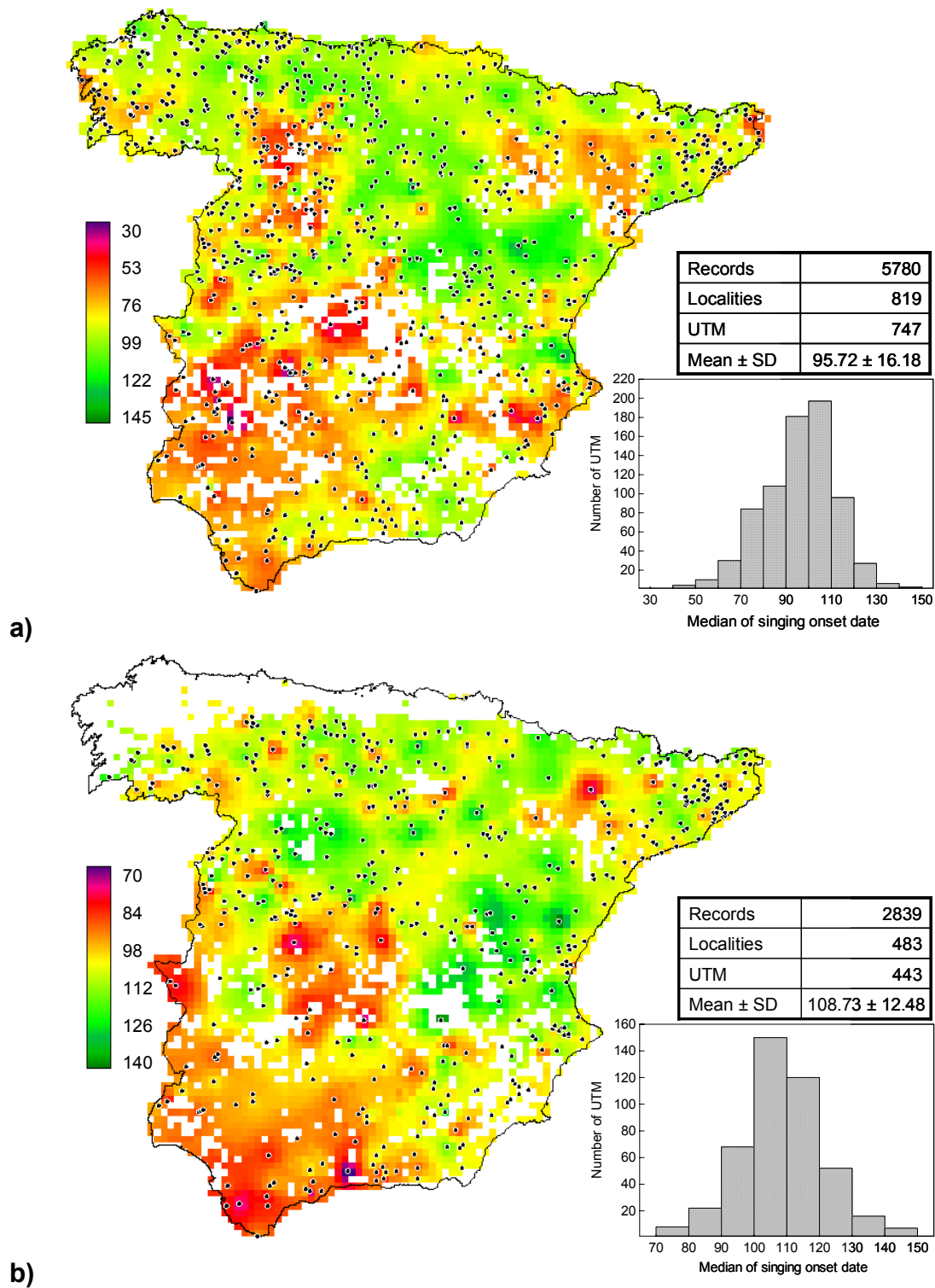


Figure 2.1 Interpolation map of singing onset for the cuckoo (a) and nightingale (b). Values only for those UTM cells where the species breed, according to Martí & Del Moral (2003). Black dots represent localities of the Spanish phenological network with records. Scale colour bar in Julian day (1 = 1 January). Details of number of records, localities, UTM cells, mean, standard deviation (SD) and histogram of the distribution of these observations are given for each species.

The median value of all records for the same UTM 100 km² cell was calculated in both species (Fig. 2.1). 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. 2.1). Median values for each UTM cell could have been biased due to differing number of records. This possible dependence was tested for by means of Spearman correlations between mean 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 mean singing onset was not found to be dependent on the number of records, all UTM cells with available records for both species were used.

Explanatory variables

A total of 51 explanatory variables in eight categories were used to model singing phenology of the studied species (see Table 2.1). Five topographic and ten climatic variables were extracted for each one of the 100 km² UTM Iberian squares (n=6063) using IDRISI 32 Geographic Information System (Clark Labs, 2001). Topographic variables were obtained from a Digital Elevation Model (Clark Labs, 2000). Mean altitude for all 100 pixels of 1 km² in each 100 km² UTM were used to calculate the altitude range in each cell from the maximum and minimum altitude values, together with the slope, aspect (the mean direction of the slope) and diversity of aspect for each UTM cell. Delayed singing onset is expected in more mountainous UTM cells (Angot, 1900; Bernis, 1970; Huin & Sparks, 2000).

Climate variables were rainfall and mean temperatures during each of the 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 climate variables were provided by the *Instituto Nacional de Meteorología*. We expect certain collinearity in the effect of temperature and rainfall, since the warmest Iberian sites are also the driest. If a negative relationship with temperature is assumed (i.e., higher temperatures lead to earlier singing onset)

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>Basins</i>	
CAN	Cantabrica
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>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>Abundance</i>	
P30	% of 10x10 km UTM where species is present in the 30x30 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 Uses</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)

Table 2.1 List of variables used in analyses. The acronym, complete description and units (in brackets) are given for each.

as in previous studies (e.g., Slagsvold, 1977; but see De Smet, 1970), then the opposite correlation with rainfall would be expected (i.e., higher precipitation should lead to later singing onset).

Three geographic variables were: the distance from each UTM cell to the Straits of Gibraltar; distance to the nearest major Iberian river; and cost of dispersion from the Straits of Gibraltar. We expect later singing onset for cuckoos and nightingales in sites far from Gibraltar reached by means of a costly arrival route. However, first-to-sing males would be heard earlier near major rivers, 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 IDRISI 32 software (Eastman, 2001). The friction surface image was the product of altitude times the distance-to-river variables, which takes into account the variable 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 before multiplying them. 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. 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. 1.2) was included in the model as categorical predictors. A 0-1 code was assigned to all UTM cells in each basin. The Cantabrian basin was excluded from the analysis for the nightingale since this species does not occur there. Basins are a natural partitioning of territory and could be associated with regional differences in singing onset.

A relative abundance index for both species was calculated for each 10x10 km UTM cell from the Spanish bird breeding atlas (Martí & Del Moral, 2003), to differentiate core (with 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 (Sparks *et al.*, 2001, Tryjanowski *et al.*, 2005); the singing of a male can stimulate its neighbours (Olinkiewicz & Osiejuk, 2003), increasing overall singing activity in the given zone. This could result in earlier singing onset for core areas with a larger number of males, since increased singing activity should increase the opportunity for earlier recording.

We have assumed that the main core and marginal areas have been consistently so throughout recent decades. Presence/absence data from the Spanish breeding atlas was used to count the number of 10x10 km UTM cells with presences in the surrounding 30x30 km square (range from 0 to 9). This value was divided by the number of available (i.e. terrestrial) UTM cells in the 30x30 km square to obtain the percentage of occupancy, thus distinguishing UTM cells completely surrounded by terrestrial cells from coastal and frontier cells surrounded by fewer than 9 terrestrial cells.

Vegetation productivity was also evaluated as a possible explanatory variable for geographic patterns in the onset of singing of studied species. This variable could affect, on the one hand, 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 for these birds). Finally, population density may 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 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 & 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 (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 of red wavelength absorption by chlorophyll, which is proportional to leaf chlorophyll density, and 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 average monthly values, 1982–2000, at a spatial resolution of 0.1 degree (Clark Labs, 2001). These maps were rescaled to our 10x10 km UTM grid for the Iberian Peninsula and afterwards combined in seasonal quarters.

Land use types were also included because features of the environment may affect singing onset in two ways (Doutrelant *et al.*, 1999; Partecke *et al.*, 2004; Tryjanowski *et al.*, 2005): on the one hand, habitat composition directly affects species presence and abundance, which in turn can affect singing activity (see above); on the other, environment type in each locality of the phenological network can affect species detectability (e.g. open habitats favour listening opportunities whereas dense forests do not). However these effects on record dates would probably be offset by the degree of detectability of our 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 100x100 m resolution (see Table 2.1). Land use based on present data may not necessarily be fully representative of use in past decades. The percentage of coverage of each category within each 10x10 km UTM cell was calculated and used as 15 predictor variables for analyses. A new variable measuring the heterogeneity of landscape was used to summarize variability of land use in each UTM cell, calculated as the Shannon diversity index.

Finally, spatial variables, the central latitude and longitude of each UTM cell, were included in the analysis as a third degree polynomial (Trend Surface Analysis or TSA; see Legendre & Legendre, 1998). The nine terms of a TSA can help to incorporate the effects of other historical, biotic or environmental variables not otherwise taken into consideration (Legendre & Legendre, 1998). Latitude and longitude were standardized (mean=0 and standard deviation=1) as were topographic, climate, geographic and vegetation productivity variables, in order to eliminate their measurement scale effects.

Statistical analyses

Associations between environmental and geographic variables and singing onset were analyzed 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 dependent variable and explanatory variables (i.e., predictors). Particularly useful for a (very) large set of predictors, the PLSR combination copes 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), account for successively smaller proportions of variance explained by the original variables, and become the independent variable, on which singing onset depends. Regression is simplified by the reduction of the large original set of predictors to fewer components, which summarize the really relevant features of explanatory variables. The meaning of PLSR components was derived from significant correlations with the original variables. The significance level for all PLSR analyses was established as $P < 0.001$ to avoid spurious relationships due to the large number of correlations performed (Bonferroni correction $\alpha_B = 0.05/58 \approx 0.001$). Since the variation explained by each successive component is smaller, relevant components (and consequently their number) in final models were limited to those significant at a previously-established significance level. Predicted scores from final PLSR models were mapped and examined for both species. All these analyses were conducted with STATISTICA (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 can be left out (Cliff & Ord, 1981; Legendre & Legendre, 1998; Keitt *et al.*, 2002). These analyses were conducted with GS+ (Gamma Design Software, 2002).

RESULTS

Cuckoo

No evident geographic pattern in the map of dates interpolated between localities can be seen (Fig. 2.1a). Earlier singing onset seems to occur in the southern half of the Iberian Peninsula and also in northeast, and in the western part of the Duero basin (see Fig. 1.2). The latest dates were recorded in the Iberian Mountain System. The earliest and latest median singing onset dates were 29 January and 26 May (range of 118 days) and extend previously reported dates (Bernis, 1963; Bernis, 1970; Fernández-Cruz & Sáez-Royuela, 1971), as a result of the broader temporal and spatial range of our data. Data was approximately normal, very slightly skewed towards the left (Skewness = -0.416, $P < 0.05$). As the skewness of the distribution usually does not greatly affect estimates of parametric statistics (StatSoft, 2001), analyses were carried out on original, 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 this species throughout Spain (Table 2.2). The first model component, accounting for the major part of variability, related early singing onset to southern UTM cells, especially those located in the Guadiana basin, at low altitude, reached by a short and inexpensive pathway from the Straits of Gibraltar, with warmer temperatures throughout the year, lower rainfall during spring and summer and, consequently, low vegetation productivity during summer and autumn. These UTM cells also were surrounded by areas with low

Variable	Cuckoo			Nightingale		
	Comp1	Comp2	Comp3	Comp1	Comp2	Comp3
LAT	0.179	-0.066	-0.069	0.240	-0.027	-0.064
LAT2	0.036	-0.058	0.180	-0.228	-0.220	-0.094
LAT3	0.151	-0.079	-0.035	0.275	0.078	0.034
LONG	0.073	0.242	0.131	0.146	0.105	0.000
LONG2	0.003	-0.077	-0.082	0.046	-0.064	-0.043
LONG3	0.006	0.007	-0.105	0.042	-0.086	-0.100
LONGXLAT	-0.044	-0.046	-0.229	-0.038	-0.224	-0.225
LONG2XLAT	0.047	-0.152	-0.142	0.047	-0.171	-0.130
LAT2XLONG	0.017	0.126	-0.115	0.113	0.041	-0.058
MEA	0.209	0.233	-0.071	0.182	0.054	0.034
AR	0.129	-0.013	-0.159	-0.057	-0.097	0.072
ASP	-0.027	-0.043	-0.149	-0.071	-0.143	-0.147
DASP	0.015	-0.037	-0.024	0.001	0.023	0.098
SLP	0.141	-0.005	-0.114	-0.061	-0.108	0.087
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	-0.155
DUE	0.033	-0.017	-0.218	0.093	-0.038	-0.116
GDN	-0.191	-0.253	-0.302	-0.112	-0.052	-0.025
GDQ	-0.086	0.031	0.180	-0.172	-0.022	0.174
MIÑ	0.019	-0.133	0.058	0.013	0.023	0.213
TAJ	0.025	0.141	0.194	-0.052	-0.075	-0.143
SEG	-0.046	0.057	0.034	-0.149	-0.061	-0.168
TUR	0.053	0.182	0.096	0.194	0.365	0.378
DSG	0.188	0.005	-0.008	0.256	0.018	-0.039
DIR	0.131	0.232	0.112	0.035	-0.037	-0.153
CSG	0.237	0.381	0.229	0.277	0.168	0.035
WIP	0.088	-0.187	-0.016	-0.132	-0.232	0.080
SPP	0.170	-0.113	0.011	0.028	-0.179	0.089
SUP	0.221	-0.012	-0.018	0.216	-0.050	0.007
AUP	0.140	-0.142	0.017	-0.039	-0.216	0.064
WIMET	-0.223	-0.158	0.162	-0.248	-0.007	0.073
SPMET	-0.288	-0.178	0.031	-0.250	-0.021	-0.008
SUMET	-0.291	-0.113	-0.065	-0.243	-0.011	-0.055
AUMET	-0.280	-0.164	0.057	-0.263	-0.024	0.005
ATR	-0.092	0.067	-0.207	0.024	0.020	-0.161
AI	-0.218	0.045	0.002	-0.048	0.197	-0.009
P30	0.202	0.194	0.235	-0.037	-0.218	-0.366
WINDVI	0.032	-0.199	-0.006	-0.117	-0.212	0.044
SPNDVI	0.119	-0.186	-0.099	0.009	-0.213	0.032
SUNDVI	0.188	-0.096	-0.009	0.055	-0.198	0.018
AUNDVI	0.144	-0.108	0.023	-0.011	-0.173	0.093
URB-IND	-0.063	-0.024	0.070	-0.119	-0.142	-0.230
DRY-CROP	-0.099	0.003	-0.087	0.072	0.064	-0.076
IRR-CROP	-0.122	-0.114	-0.210	-0.005	0.054	-0.004
VINE	-0.050	0.038	0.065	0.060	0.146	0.169
FRUIT	-0.013	0.102	0.162	-0.088	-0.076	-0.209
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	-0.122	-0.048	-0.088	-0.047	-0.029
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
R^2	19.04	4.70	2.66	19.73	5.32	3.03

Table 2.2 Predictor weights in significant components (Comp's 1 to 3) of the partial least squares regression models for the cuckoo and the nightingale. Significant associations between predictors and components are in bold type ($P < 0.001$). The percentage of variance (R^2) in the geographic pattern of population singing onset accounted for each by component is also shown.

occupancy rates, with extensive cropland cover (especially irrigated areas), and with little moorland or transitional areas from scrubland to forest. Climate contributed overwhelmingly to this component (Table 2.3).

The second component (Table 2.2) associated delays in cuckoo singing onset with eastern localities from the Turia basin at high altitude and far from major rivers, with an expensive pathway from the Straits of Gibraltar, extensive scrubland cover or with 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. We want to stress the major relevance of the cost of migration from the Straits of Gibraltar, as reflected in the gradient of geographic and environmental conditions (Table 2.3).

Finally, the third component (Table 2.2) associated delayed singing onset with eastern UTM cells with low altitude and temperature ranges, with northern exposure, with expensive pathways, milder winter temperatures, high density of individuals, and highly diverse landscapes with large scrubland and fruit tree cover, but little coniferous forest, grassland or other crops. Basins and land-use accounted for the major part of the variation explained by this component (Table 2.3).

Variables group	Cuckoo			Nightingale		
	Comp1	Comp2	Comp3	Comp1	Comp2	Comp3
Spatial	6.57	11.97	15.94	22.72	15.89	9.70
Topographic	8.12	5.79	6.61	4.52	4.50	4.52
Climatic	45.64	17.08	7.89	32.18	17.53	5.28
Basins	6.00	14.73	23.90	11.80	16.16	30.60
Geographic	10.86	19.92	6.52	14.37	3.01	2.61
Abundance	4.06	3.75	5.51	0.14	4.74	13.37
Vegetation productivity	7.12	9.51	1.05	1.69	15.95	1.20
Land Uses	11.63	17.24	32.57	12.59	22.24	32.71

Table 2.3 Percentage of variance (R^2) in the geographic pattern of population singing onset accounted for by each type of variable in each component of the partial least squares regression models.

In the case of cuckoo, some explanatory variables appeared to be significantly linked to all components, in that they characterized the

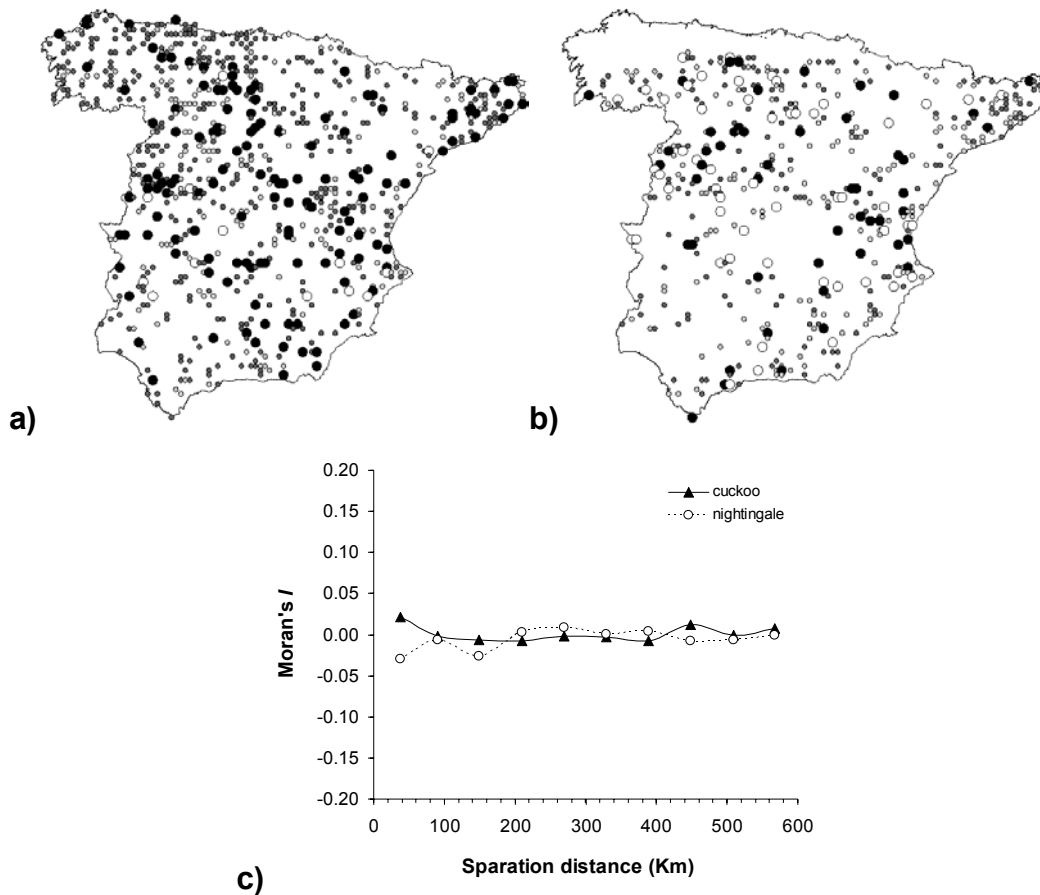


Figure 2.2 Geographic distribution of residuals of partial least squares regression models for the cuckoo (a) and nightingale (b). Residuals are divided into four quartiles in which large white circles represent localities with high negative residuals (predicted scores higher than observed), and large black circles localities with high positive residuals. c) Spatial autocorrelation of residuals from partial least squares regression models. Isotropic correlograms represents the variation in the scores of Moran's I spatial autocorrelation statistic with increase in the separation distance between 10x10 km UTM cells (in km), using a lag distance of 60 km and an active lag of 600 km.

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 2.2).

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. 2.2).

Predictions from the PLSR model are mapped in Fig. 2.3a. 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 the most part of Iberia, including all the 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 and the north coast (see Fig. 1.2).

Nightingale

The picture obtained from the onset date interpolation between localities is not very clear (Fig. 2.1b). Earlier localities pop up throughout most of Spain, bereft of any obvious spatial pattern. The Turia basin was the only large area where nightingale singing onset was reported late, contrasting with an early zone in the south of Spain. The distribution of data was normal, with earliest and latest mean values (10 March and 24 May) also extending previously reported dates for this species (Bernis, 1963; Fernández-Cruz & Sáez-Royuela, 1971).

The final model obtained from the PRLS analysis accounted for more variability of singing onset (up to 28%; Table 2.2) than in the case of the cuckoo. The first component explained more than 70% of total model variability. This component associated earlier singing onset with southern localities from the Guadalquivir basin 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. Temperatures and latitude trend (both latitude and distance from Gibraltar) were the most relevant variables (Table 2.3).

Both remaining components explained about 8% of spatial variability in singing onset for this species (Table 2.2). 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, with low vegetation productivity throughout the year as a result of low precipitation in most seasons, causing arid conditions. These localities had low nightingale densities and were dominated by coniferous forests and transitional areas from scrubland to forest with absence of deciduous forests and moorlands. Finally, the meaning of the

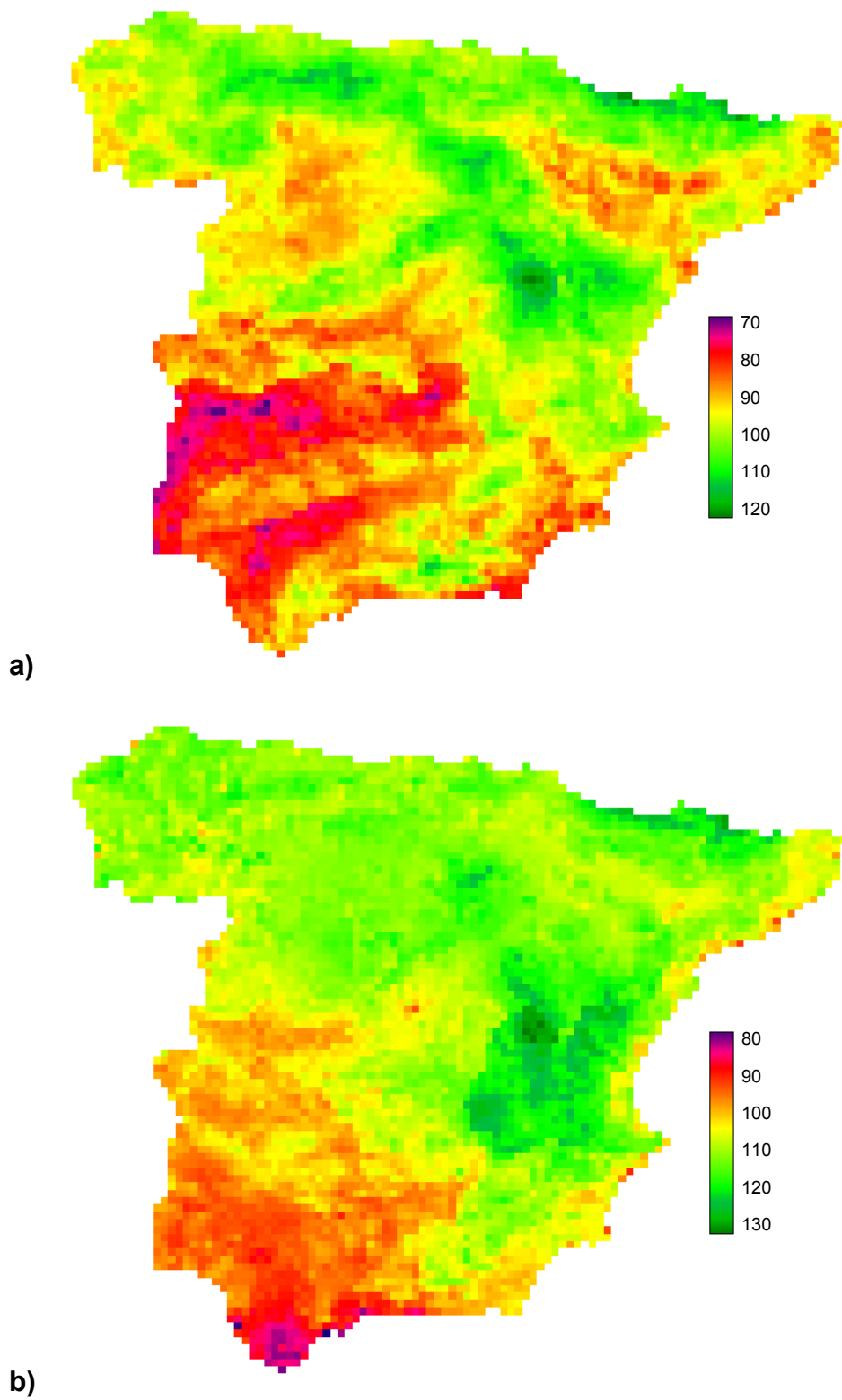


Figure 2.3 Geographic representation of predicted scores for 10x10 km UTM cells from the partial least squares regression models for (a) the cuckoo and (b) nightingale. Scale colour bar in Julian day (1 = 1 January).

third component was less clear. It related delayed singing onset with localities from the north-eastern corner of the Iberian Peninsula and the Turia basin 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, and with transition from scrubland to forest, and with several basins. Residual scores were not significantly spatially autocorrelated (Fig. 2.2b).

The meaning of the components can be seen much more clearly in Fig. 2.3b. Model predictions of singing onset appear in a more spatially structured pattern than do field observations (Fig. 2.1b). The areas where nightingales are heard earliest (purple in Fig. 2.3b) are those located near the Straits of Gibraltar. Afterwards (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 can be reached in a very short interval of 10 days (110-120), leaving a highly delayed zone in only the Turia basin, the Iberian Mountain System and the Pyrenees.

DISCUSSION

Final partial least squares regression models for both species moderately explained the variability in singing onset. A look at maps of interpolated field data (see Fig. 2.1) reveals a complicated picture for both species, making modelling difficulties not surprising a priori. But the complete absence of residual spatial autocorrelation (see Fig. 2.2) is an indication that probably no other variables, on our working scale, would help to improve model predictions. Therefore, we can conclude that at least in the Iberian Peninsula, population differences in singing onset phenology are spatially structured, although weakly, and caused by environmental factors.

In spite of these difficulties, models can help to considerably clarify the complicated picture offered by raw data (see Fig. 2.1), by revealing subtle underlying patterns. 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. 2.4). 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; Huin & Sparks, 2000). A marked latitude 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; Sanz, 1997; Fargallo, 2004). Moreover, the cost of migration from Gibraltar also appeared as highly explicative, but in this case especially relevant for the cuckoo. The warmest and driest Iberian regions' location in the south, at low altitudes, near the Straits of Gibraltar, leads to the pronounced collinearity of these variables, well-summarized by the environmental dependence defined by the first component in both species.

We would like to stress the part played by other variables with more specific effects. Some basins were strongly and consistently associated with phenology. In the case of the cuckoo, the small populations from the Guadiana basin sing markedly earlier than the rest of Spanish populations. In the case of the nightingale, the effect of the Turia basin was even stronger, although in this case populations in this basin stood out due to their late singing phenology.

Overall, vegetation productivity and land use were not highly relevant. This is especially disappointing in the case of land use, where a multitude of variables was introduced in models, but few were strongly related with the principal environmental gradients described by components. 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. 2.5). This relationship remains little changed by the removal by trend surface analysis of spatial structure in the onset of cuckoo singing (Legendre & Legendre, 1998; see Fig. 2.5), which would be in agreement with supposed earlier detection in more frequented habitats (De Smet, 1967; Sparks *et al.*, 2001, Tryjanowski *et al.*, 2005).

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%). The sign of the relationship for the cuckoo confounded

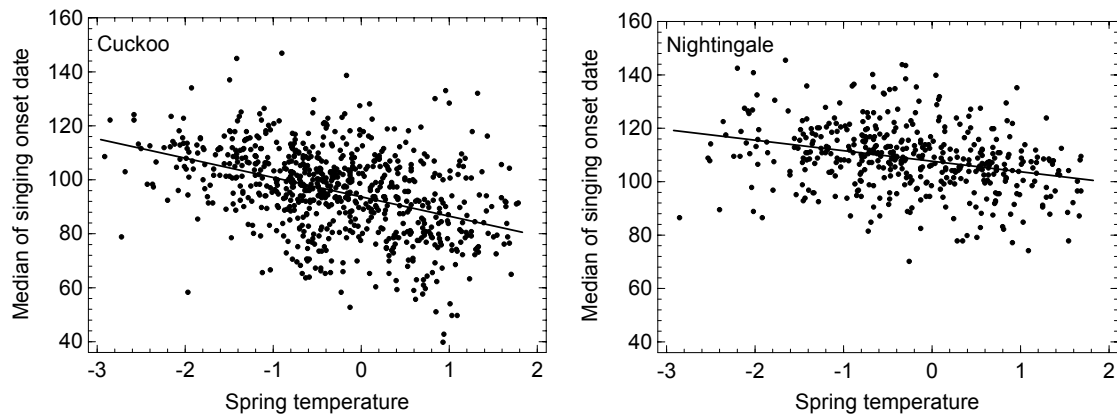


Figure 2.4 Relationship between singing dates and mean spring temperature in the 10x10 km UTM cells for the cuckoo ($n=747$) and nightingale ($n=453$). Solid line represents the best linear-fit model.

predictions, since earlier onset was expected in areas with denser populations, where chances for earlier detection should be greatest (Sparks *et al.*, 2001; Tryjanowski & Sparks, 2001; Tryjanowski *et al.*, 2005). This finding verifies absence of bias towards early detection in more densely populated sites, and thus data reliability. Singing onset in core and densely populated areas with ecological conditions optimum for this species may be delayed by their distance from Gibraltar and by a later arrival of spring weather. Early singing onset in sparsely populated areas may also be linked with the specific reproduction method of the cuckoo, involving the parasitic use of other bird species nests (Cramp, 1985). While their potential host spectrum is broad, the cuckoo lays its invading egg 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, sparsely populated or unpopulated by cuckoos (see Fig. 2.1a), are mainly those with little abundance, or even absence, of host breeder pairs (e.g., wren *Troglodytes troglodytes*, dunnock *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 due to distribution retreat during recent decades. In areas with a low density of potential host pairs, we suggest that cuckoos suffer from increased intra-specific competition. The favourability for cuckoo reproductive success of an

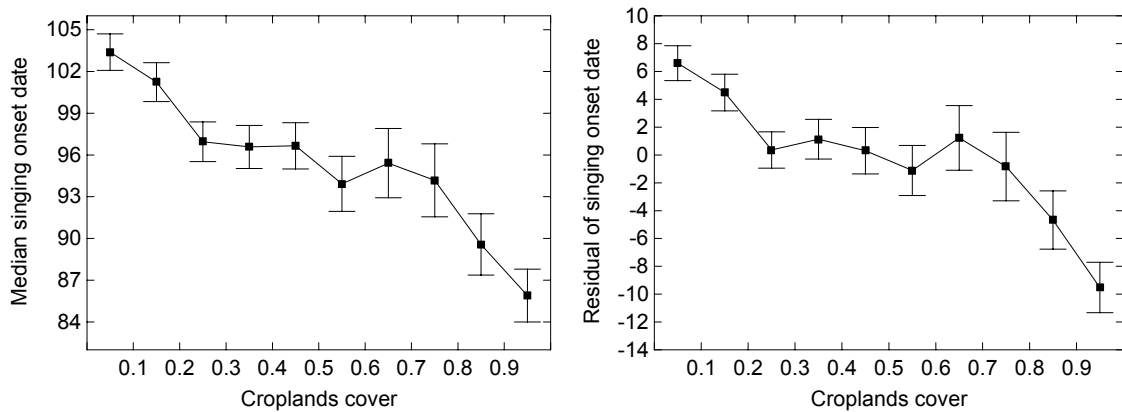


Figure 2.5 Mean and residual from a trend surface analysis of singing onset in the 10x10 km UTM cells for the cuckoo ($n=747$), according to percentage of cover provided by all types of crops (sum of the variables urb-ind, dry-crop, irr-crop, vine, fruit, olive, mos-crop and crop-nat, see Table 1). Bars indicate standard error.

early spring arrival, when non-parasitized nests would still be available in largest 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 phylopatric, 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 lacking.

As we have seen, there are some common patterns in singing onset variability among populations of both species, which can be summarized as: 1) singing onset occurs in the Iberian System, Pyrenees and the Turia basin later than in the rest of Spain. Cost of dispersion from the Straits of Gibraltar and altitude are mainly responsible for onset delay in these areas, mountainous or the most expensive to reach. 2) Singing onset occurs earliest in the SW corner of Iberia, close to Gibraltar, easily accessible, and with mild climate at winter's end. 3) Singing onset occurs early along the Mediterranean coast, thanks to its milder, seaside climate.

The spatial configuration of the Iberian Peninsula imposes unavoidable constraints that condition these common geographic pattern features. In addition, specific environmental variable influence on each species modifies this spatial pattern in singing onset in the Iberia Peninsula quite differently for each.

The cuckoo sings early (first migratory wave) in the southern half of Iberia, and in other Ebro and Duero basin areas (Fig. 2.3a), whereas nightingale migration takes place as a timid first wave (purple and red areas in Fig. 2.3b) mainly in the south-western corner of Iberia. In a second wave (yellow to green colours in Fig. 2.3) the cuckoo reaches only a minor portion of Iberia, especially mountainous regions, whereas the nightingale appears in most parts of Spain.

Singing onset variability was low in the major part of the Iberian Peninsula. The standard deviation in both species was about 15 days, whereas it is ca. 25 days for the swallow and the swift in the same area and years (unpublished author's data). In fact, final models predicted a range of singing onset, between the earliest and latest dates shorter than two months. Moreover, final maps (Fig 4) show that singing males are first detected in most parts of Spain with a variation of approximately 15 days (between March 20-April 5 for the cuckoo and April 15-30 for the nightingale). However, it is interesting to note again that this pattern is reversed for the two species. Iberia is colonized by the cuckoo mainly in its first migratory wave, whereas the nightingale does so in a second and later wave.

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RESUM

Variació geogràfica de les dates d'inici del cant entre poblacions en dos aus migratòries

Tot i que el cant juga un paper fonamental en la comunicació de les aus, encara no s'ha estudiat quines són les variables ambientals que determinen la variació geogràfica observable en les dates d'inici del cant per àrees extenses. Es va relacionar la fenologia de cant del cucut (*Cuculus canorus*) i del rossinyol (*Luscinia megarhynchos*) enregistrada en centenars de localitats de tota Espanya amb un conjunt de predictors potencials mitjançant la regressió de mínims quadrats parcials. Les variables predictives (de caire espacial, topogràfic, conques de rius, geogràfic, climàtic, abundància de les espècies, producció vegetal i usos del sòl) poden afectar les dates de primer cant de dues maneres: directament a través de les decisions individuals sobre el cant o indirectament a través de la ruta migratòria primaveral. Els models finals van tenir un poder explicatiu moderat, el que seria indicatiu de l'absència d'una forta estructura espacial de l'inici del cant. De les variables predictives, el clima va ser el factor amb més influència. Els mascles d'ambdues espècies canten abans en àrees caloroses y seques, el que està molt lligat a d'altres gradients geogràfics i topogràfics de la Península Ibèrica. Encara que algunes variables van afectar igualment a les dues espècies, les prediccions finals del model pel cucut van ser diferents de les del rossinyol. El primer colonitza la península en una primera onada migratòria mentre que el segon ho fa en una segona onada. En resum, l'inici del cant en aquestes dues espècies, que troben condicions

ecològiques semblants a la península degut a que tenen fenologies d'inici del cant similars, mostra patrons geogràfics diferents.