ORIGINAL ARTICLE

Environmental and geographical constraints on common swift and barn swallow spring arrival patterns throughout the Iberian Peninsula

Oscar Gordo[1,2]*, Juan José Sanz[1] and Jorge M. Lobo[3]

[1]*Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal 2, E-28006 Madrid, Spain,* [2]*Departament de Biologia Animal (Vertebrats), Universitat de Barcelona, Av. Diagonal 645, E-08028 Barcelona, Spain and* [3]*Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal 2, E-28006 Madrid, Spain*

ABSTRACT

Aim Still poorly understood, the main migratory pathways for most trans-Saharan species pass through the Iberian Peninsula, which acts as a gateway to the European–African migratory system. Arrival patterns in this region for the common swift (*Apus apus*) and barn swallow (*Hirundo rustica*), of similar morphology and flight capabilities, were described, and the environmental and geographical factors best explaining them were examined, in a search for common ecological constraints on these two migratory species.

Location Latitude ranged from 36.02 to 43.68°N, longitude from 9.05°W to 3.17°E, and altitude from 0 to 1595 m a.s.l. for 482 common swift and 812 barn swallow Spanish localities spread widely over the Iberian breeding grounds of the two species.

Methods Our data set, covering the years 1960–1990, consisted of 3206 first-arrival dates for common swifts and 6036 for barn swallows. Forty topographical, climatic, river basin, geographical and spatial variables were used as explanatory variables in general regression models (GRMs). GRMs included polynomial terms up to cubic functions in all variables when they were significant. A backward stepwise selection procedure was applied in all models until only significant terms remained. GRMs were applied in two steps. First, we searched for the best model in each one of the five types of variables (topographical, climatic, river basin, geographical and spatial). To cope with the unavoidable correlation between explanatory variables, the relative importance of each type of variable was assessed by hierarchical variance partitioning. Secondly, we searched for that model able to explain the maximum amount of the observed variability in arrival date. To obtain this model all significant explanatory variables were subjected jointly to a GRM. Spatial variables were then added to this model to take any remaining spatial structure in the data into account. Moran's *I* autocorrelation coefficient was used to check for spatial autocorrelation.

Results Both species arrived earlier in the south-western Iberian Peninsula, where summers are warmer and drier. From there, both species followed the main southern Iberian river basins towards the north-east; however, several mountainous regions impede the colonization of eastern Iberia. The best models for each type of variable explained 19–47% of the variability in common swift arrival dates and 14–44% in barn swallow arrival dates. Variance partitioning indicated that climatic and geographical variables best explained variability. The best predictive models built with all variables accounted for 52% of the variability in common swift arrival dates and 50% for the barn swallow. Residuals from both models were not spatially autocorrelated, an indication that all major spatially structured variation had been accounted for.

*Correspondence: Oscar Gordo, Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), C/José Gutiérrez Abascal 2, E-28006 Madrid, Spain.
E-mail: ogordo@mncn.csic.es

O. Gordo, J. J. Sanz and J. M. Lobo

Main conclusions Spring arrival patterns are highly dependent on the geographical configuration of the Iberian Peninsula. This spatial constraint forces both species to converge very closely in their spring migration, because common swifts and barn swallows are subject to a trade-off between optimum migratory pathways and territories ecologically suitable for breeding.

Keywords

Apus apus, arrival date, bird migration, geographical patterns, *Hirundo rustica*, modelling, phenology, Spain.

INTRODUCTION

The migration of trans-Saharan birds northwards in spring and southwards in autumn has long been recognized as one of the most remarkable biological phenomena in the world (Moreau, 1972). Millions of individuals of some 200 European bird species overwinter south of the Sahara in Africa, then fly to breeding grounds in Europe, only to then return to Africa, year after year. For western European populations, the Iberian Peninsula plays two prominent roles, as the first European territory reached during the spring migration, and as the last left by migrants prior to their autumn return flight to Africa (Moreau, 1956; Pérez-Tris & Santos, 2004).

The onset of migration by long-distance migratory birds is triggered by photoperiod through endogenous rhythms (Berthold, 1996; Gwinner, 1996), an environmental cue enabling birds to be in the right place at the right time (Coppack & Both, 2002). Migratory arrival- and departure-date variation (e.g. Lehikoinen et al., 2004; Sparks et al., 2005), an adjustment in timing to specific environmental conditions at each place and time, has been of interest to many researchers throughout the last century. The pioneering studies of Sliwinsky (1938) and Southern (1938a,b, 1939, 1940, 1941) described spring European colonization patterns for nine trans-Saharan birds. Both authors mapped isophenes, lines connecting points of equal arrival dates, a technique used first by Middendorff (1855) to help visualize the movement of the migratory wave through a given territory. Both Sliwinsky and Southern pointed out the paucity of data from southern Europe, and in particular from the Iberian Peninsula.

Unfortunately, most trans-Saharan bird migratory patterns involving the Iberian Peninsula are still unexplored (Pérez-Tris & Santos, 2004; but see Gordo & Sanz, 2006). Based on arrival data for Gibraltar only, Southern claimed that the earliest European arrivals occurred in south-western Europe, about 2 weeks earlier than at similar eastern European latitudes. Most later studies focused on particular countries and species (Zabłocka, 1959; De Smet, 1970; Munteanu & Mǎtieș, 1978; Beklová et al., 1983; Munteanu, 1985; Grischtschenko et al., 1995; Grishchenko, 2001, 2002, 2003) and applied the methodology used by Sliwinsky and Southern decades earlier to describe broad geographic patterns of the progression of migration. Applying GIS techniques, Huin & Sparks (1998, 2000) mapped the arrival and progression through Britain of four migratory birds more comprehensively, but did not investigate potential environmental or geographical factors underlying the spatial patterns observed. Therefore, studies have yet to go beyond a mere description of migration progression through large territories.

Huin & Sparks (1998, 2000) offered evidence of the effect of climate on arrival dates of migratory birds. Temperatures in both Britain and in Spanish and French pathways affected the timing of recorded arrivals year after year: warmer years, with their earlier spring providing greater food availability sooner, corresponded with rapid northward progression and earlier arrivals. Such early migrant bird arrival dates in response to increasing temperatures have been reported repeatedly during recent decades (Crick, 2004). Therefore, an accurate knowledge of the factors governing migratory phenology, both temporally and spatially, is critical in providing a better assessment of the potential hazards to migratory birds posed by current and future climate change (Møller et al., 2004).

This study examines the spatial patterns of spring arrival dates through the Iberian Peninsula of the common swift (*Apus apus* Linnaeus, 1758) and barn swallow (*Hirundo rustica* Linnaeus, 1758). Their specialized feeding on airborne insects has led both species to develop very similar requirements and migration strategies (Cramp, 1985, 1988), although the timings of their migration both in the spring and autumn are quite different. On average, the common swift arrives in Spain in April and departs in August (Bernis, 1970), whereas the barn swallow arrives in March and departs in September (Bernis, 1971). Therefore, we can compare how similar species with similar requirements have evolved the best response to the same spatial scenario (the Iberian Peninsula) but under different ecological conditions, since the barn swallow arrives at the beginning of spring and the common swift at its end.

The primary aims of this study are to describe the spatial patterns of spring arrivals, and to ascertain the principal environmental and geographical constraints on the arrival dates of common swifts and barn swallows. Specifically, we examine the variability explained by each climatic, topographical, river basin, geographical and spatial group of explanatory variables. Our data on two ecologically similar species allow us to compare their migratory pathways through the same territory, and also to determine the relative influences of (1) constant (on our time-scale) characteristics of Iberian Peninsula geography and topography, (2) changes in ecological

conditions during the course of spring, and/or (3) the effects of the evolutionary history of each species on their migratory phenology patterns.

MATERIALS AND METHODS

Bird arrival dates

Arrival dates for the common swift and barn swallow were obtained from the Spanish *Instituto Nacional de Meteorología* phenological data base, compiled from a volunteer observer network set up several decades ago, as in other European countries (e.g. UK, Huin & Sparks, 1998), to improve the understanding of the timing of seasons and thus of agricultural practices (García, 1963; Gordo & Sanz, 2006). Volunteers apply standard observation rules to record phenological events of plants and animals from a list of common species (Anonymous, 1943). The characteristics of these events include: (1) a broad distribution of species throughout Spain (volunteers can observe everywhere in the country), (2) considerable abundance (phenological observation is unconstrained by the number of individuals), (3) unmistakable morphology and/or behaviour (increased data reliability), making them ideal for phenological monitoring and ensuring data homogeneity, independent of the observer. We note that the common swift and the barn swallow are two of the most abundant and widespread trans-Saharan birds in the Iberian Peninsula (Martí & Del Moral, 2003), as indeed they are in the rest of the Palaearctic (Cramp, 1985, 1988). The wide distribution of both species is favoured by man-made infrastructures, which provide suitable nesting places. The common swift has essentially an aerial lifestyle. It feeds on aeroplankton in groups over towns and cities but also in peripheral habitats. Barn swallows occupy all types of habitats (although especially pastures, meadows and farm crops), where they find a constant supply of small flying insects taken in flight. According to ringing recoveries, the primary wintering area in Africa for Spanish barn swallow populations is the Guinean Gulf (i.e. Ivory Coast, Ghana and Nigeria). The wintering area south of the Sahara Desert for the Spanish common swift is, however, unknown.

The spring arrival date for both species was taken as the date that the first individual was sighted in each study site and year. The first sighted individual is thus interpreted as the first arrived and settled individual from the local population. Observation rules of the Spanish phenological network state that migratory birds must be observed daily in the study site after the first sighting in order to avoid erroneous records of arrival dates resulting from aberrant or non-autochthonous individuals (e.g. individuals passing on their way to more northerly breeding areas). This methodology produces data with very few undetectable misidentifications, as there is a low probability of mistaking passing individuals for local individuals. Another potential source of error would be misidentification of species. Although the two species have similar feeding habits and body shape, however, they have distinctive colouring, behaviour and voice (Cramp, 1985, 1988), and very

different migratory calendars: barn swallows arrive on average nearly 1 month (23.8 days) before common swifts.

We collected and computerized all original records (9239 records from 829 localities) from 1960 to 1990, because this is the period for which meteorological data are also available for each UTM (see below). Dates were transformed to Julian days (1 = first of January); 1 day was added after 28 February to take leap-years into account.

For both species, the median value (less influenced by extreme observations and thus a better estimate of central tendencies within date distributions) for all records from the same 100-km^2 UTM cell was calculated. As some UTM cells contained more than one locality, the final number of records (UTM cells) available for calculations was smaller than the number of original localities. The difference in the number of records from each UTM could have biased median values, but coefficients of Spearman rank correlation of median values with numbers of records did not indicate such a bias (common swift: $r_S = 0.026$; barn swallow: $r_S = -0.072$).

Explanatory variables

The 40 explanatory variables used to model the migratory arrival dates of the study species (Table 1) fall into topographical, climatic, river basin, geographical, and spatial groups. For each 100-km^2 Iberian Peninsula UTM cell ($n = 6063$), seven topographical and 18 climatic variables were extracted using IDRISI 32 Geographic Information System (Clark Labs, 2001). Topographical variables were obtained from a digital elevation model (Clark Labs, 2000). Altitude range, together with slope, aspect (mean direction of slope) and diversity of aspects were calculated from the mean, minimum and maximum altitudes of all 100 1-km^2 pixels (in each UTM). Climate variables, courtesy of the *Instituto Nacional de Meteorología*, were rainfall and mean, maximum and minimum temperatures during each of the spring, summer, autumn and winter seasons, together with annual temperature variation, and an aridity index expressed as

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

where P is the mean annual precipitation and T the mean annual temperature. The geographical group of variables included distance from each UTM cell to the Straits of Gibraltar, distance to the closest major Iberian river (Fig. 1), and the cost of dispersion from the Straits of Gibraltar. Cost from the Straits of Gibraltar was calculated considering a friction surface image (a variable that impedes or facilitates movement through space) and the costgrow algorithm module of IDRISI 32 software (Eastman, 2001). The friction surface image was the product of (standardized) altitude with (standardized) distance-to-rivers (see Fig. 2). This product accounts for the varying effect of the altitude on probable routes of dispersion along major Iberian rivers (low vs. high valleys). The surface generated by costgrow represents the cost of dispersion from a source point, the Straits of Gibraltar, along valleys followed as routes of migration. Finally, a 0–1

Table 1 Topographical, climatic, river basin, geographical and spatial variable groups used in the general regression models along with their acronyms, complete description and units (in brackets).

Variable	Description
Topographical	
MIA	Minimum altitude (m)
MEA	Mean altitude (m)
MXA	Maximum altitude (m)
AR	Altitude range (m)
SLP	Slope (degrees)
ASP	Aspect (degrees)
DASP	Diversity of aspects
Climatic	
SPR	Spring rainfall (L)
SUR	Summer rainfall (L)
AUR	Autumn rainfall (L)
WIR	Winter rainfall (L)
AI	Aridity index
SPMIT	Spring minimum temperature (°C)
SUMIT	Summer minimum temperature (°C)
AUMIT	Autumn minimum temperature (°C)
WIMIT	Winter minimum temperature (°C)
SPMET	Spring mean temperature (°C)
SUMET	Summer mean temperature (°C)
AUMET	Autumn mean temperature (°C)
WIMET	Winter mean temperature (°C)
SPMXT	Spring maximum temperature (°C)
SUMXT	Summer maximum temperature (°C)
AUMXT	Autumn maximum temperature (°C)
WIMXT	Winter maximum temperature (°C)
ATR	Annual temperature range (°C)
River basins	
MIÑ	Miño
CAN	Cantabrian
DUE	Duero
EBR	Ebro
CAT	Catalan
TAJ	Tajo
GDN	Guadiana
TUR	Turia
GDQ	Guadalquivir
SEG	Segura
Geographical	
DSG	Distance to Straits of Gibraltar (km)
CSG	Cost from Straits of Gibraltar
DIR	Distance to rivers (km)
Spatial	
X	Longitude (m)
Y	Latitude (m)

Figure 1 Topographical map of the Iberian Peninsula showing the main geographical features cited in the text. Black dashed lines indicate political borders. River basins are numbered (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 are marked by black solid lines. The main rivers in each basin are shown as white dashed lines.
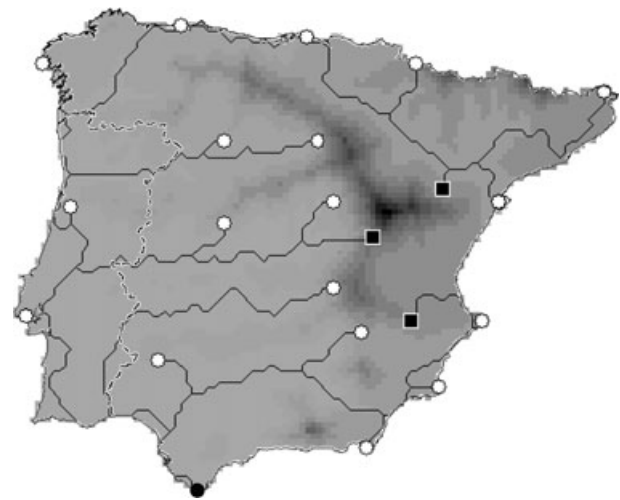
Figure 2 Map of the cost of moving from the Straits of Gibraltar along valleys through the Iberian Peninsula. This cost surface was obtained from the costgrow algorithm module of IDRISI 32 software, taking the product of altitude with distance-to-rivers as friction surface. Darker UTMs are those with the more costly pathways from the Straits of Gibraltar. The black dot represents the target point, the Straits of Gibraltar, while white dots are destination points arbitrarily selected throughout the Iberian Peninsula. Black squares are the localities with the latest barn swallow arrivals. Lines representing the lowest-cost route linking the target point with destination points were calculated using the pathway module of IDRISI 32 software. The black dashed line indicates a political boundary.

code, identifying a UTM falling within (1) or outside (0) a major Iberian river basin (Fig. 1), was included in the model as a categorical predictor.

Spatial variables, the central latitude and longitude of each UTM cell, were included in models as a third-degree polynomial (trend surface analysis – TSA; see Legendre & Legendre, 1998), as an aid to the incorporation of effects caused by otherwise unaccounted-for historical, biotic or environmental
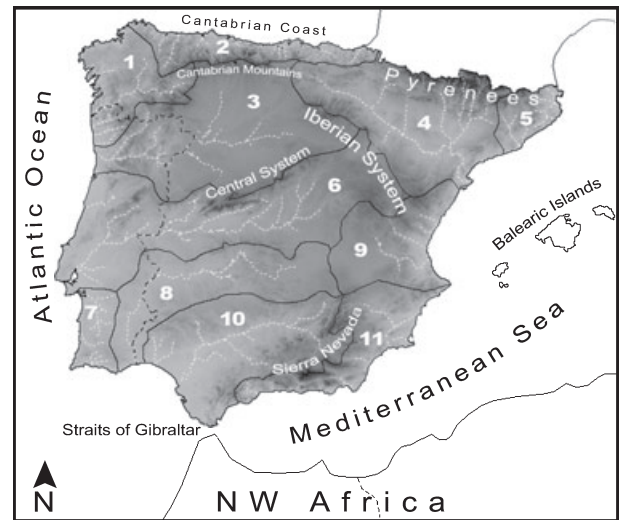
variables (Legendre & Legendre, 1998). Latitude and longitude were standardized (mean = 0 and standard deviation = 1), as were all other continuous explanatory variables, in order to eliminate measurement scale effects.

Statistical analyses

The relationship of arrival date to explanatory variables was analysed by means of general regression models (GRMs) using STATISTICA (StatSoft, Inc., 2001), in two steps. First, the explanatory variables from each group (topographical, climatic, river basin, geographical and spatial) were backward stepwise ranked according to their explanatory capacity, and each statistically significant linear, quadratic or cubic variable term was included in a final model for each group. Next, all significant explanatory variables so obtained were jointly backward stepwise selected to yield a complete model from all groups. Then, the nine terms of the third-degree polynomial of central latitude and longitude were incorporated into this complete model, and another backward stepwise selection was used to eliminate non-significant variables. Predicted scores of this complete model were mapped and examined.

Arrival dates were examined for possible spatial structure after obtaining GRMs by calculating Moran's I autocorrelation coefficient with a Bonferroni-corrected significance level (Sawada, 1999) against ten classes separated by a lag distance of 60 km (from 60 to 600 km). Autocorrelation of residuals from a regression model of arrival times developed from the various groups of explanatory variables was checked because any spatial autocorrelation would indicate that one or more important spatially structured explanatory variables may have been excluded (Cliff & Ord, 1981; Legendre & Legendre, 1998; Keitt *et al.*, 2002).

The inherent correlation of environmental variables hinders the estimation of their explanatory power. To ascertain the relative importance of each type of explanatory variable, a hierarchical variance partitioning was implemented (Birks, 1996; MacNally, 2000, 2002). The 2^k ($k = 5$, types of explanatory variables) possible models were constructed and the average of the variability explained by each type of variable was calculated.

RESULTS

A pattern of earliest arrivals in the south-western corner of Iberia can be seen in the geographical variation in data for both species (Fig. 3). UTMs with the latest animals were located in the mountainous Iberian System and, in the case of the common swift, also in the Northern Plateau (see Fig. 1). The extreme dates recorded among UTMs, i.e. earliest and latest arrival dates, were separated by 132 days (end of January to beginning of June) in the case of the common swift, and by 120 days (end of January to end of May) in the barn swallow (Fig. 3). In both species, this period is longer than previously reported (Saunders, 1871; Bernis, 1951, 1970, 1971), as a result of the broader temporal and spatial range of our data. The distribution of dates was normal (Shapiro-Wilk = 0.997;

$P = 0.106$) for the barn swallow (Fig. 3), while it was slightly skewed to the left for the common swift (skewness = −1.052, $t_{458} = 9.233$, $P < 0.001$), i.e. it had a larger proportion of early arrivals than would be expected in a normal distribution. As distribution skewness does not usually have an appreciable effect on the F-statistic (StatSoft, Inc., 2001), all analyses were performed with original untransformed data.

Climatic and geographical models were the most explanatory (Table 2). Of the climatic variables, summer rainfall and temperature as well as the aridity index were retained in the final model for both species. The signs of these variables pointed towards earlier arrivals in areas where summer temperatures are highest and rainfall lowest (Fig. 4); arrivals were especially early where conditions are most arid. In the case of the common swift, the best adjusted summer temperature was mean temperature, while in the barn swallow it was maximum temperature. A model including only the quadratic function of this latter variable accounted for 33.38% ($F_{2,747} = 188.66$, $P < 0.001$) of barn swallow arrival-date variability. In this species, the climatic model also included a positive quadratic function of temperature range; that is, barn swallows arrive earlier where temperatures are less variable throughout the year.

The geographical model explained a slightly smaller percentage of variability than did the climatic one in the barn swallow, while it was better fitted to data in the common swift (Table 2). Geographical models in both species included both distance to and cost of dispersion from the Straits of Gibraltar. Individuals arrive later in localities remote from the Straits of Gibraltar and reached by a costly pathway. These models highlight the importance of the geographical configuration of the Iberian Peninsula. This configuration shapes the most probable migration routes, probably limited to only one optimum pathway through the territory. The cubic function of the distance to the Straits of Gibraltar was particularly relevant to common swift arrivals. Modelling of this variable alone accounted for 41.83% of the variability ($F_{3,455} = 110.77$, $P < 0.001$).

The topographical model was the least relevant (Table 2). In both species studied, high-altitude localities were colonized later. River basin models explained a notable amount of the original data variability (Table 2). The negative effect of the Guadalquivir and Guadiana basins (see Fig. 1) fully agrees with the aforementioned earlier arrivals to south-western Iberia in both species (Fig. 3). However, the inclusion of the Segura basin in the common swift model instead of the Tajo basin included in the barn swallow model indicates the earlier arrivals of the latter species to the southern regions of the Northern Plateau (see Fig. 1) than to the south-eastern corner of Spain (Fig. 3). Turia basin showed a positive effect for both species (i.e. later arrivals), as data maps revealed (Fig. 3).

Spatial models were highly relevant (Table 2), indicating that spring arrivals in both species are strongly spatially structured. Common swift and barn swallow arrive later to north and east Iberia. In fact, for both species the interaction of latitude with longitude was included with a negative sign.

Backward stepwise selection with all significant variables from topographical, climatic, river basin and geographical
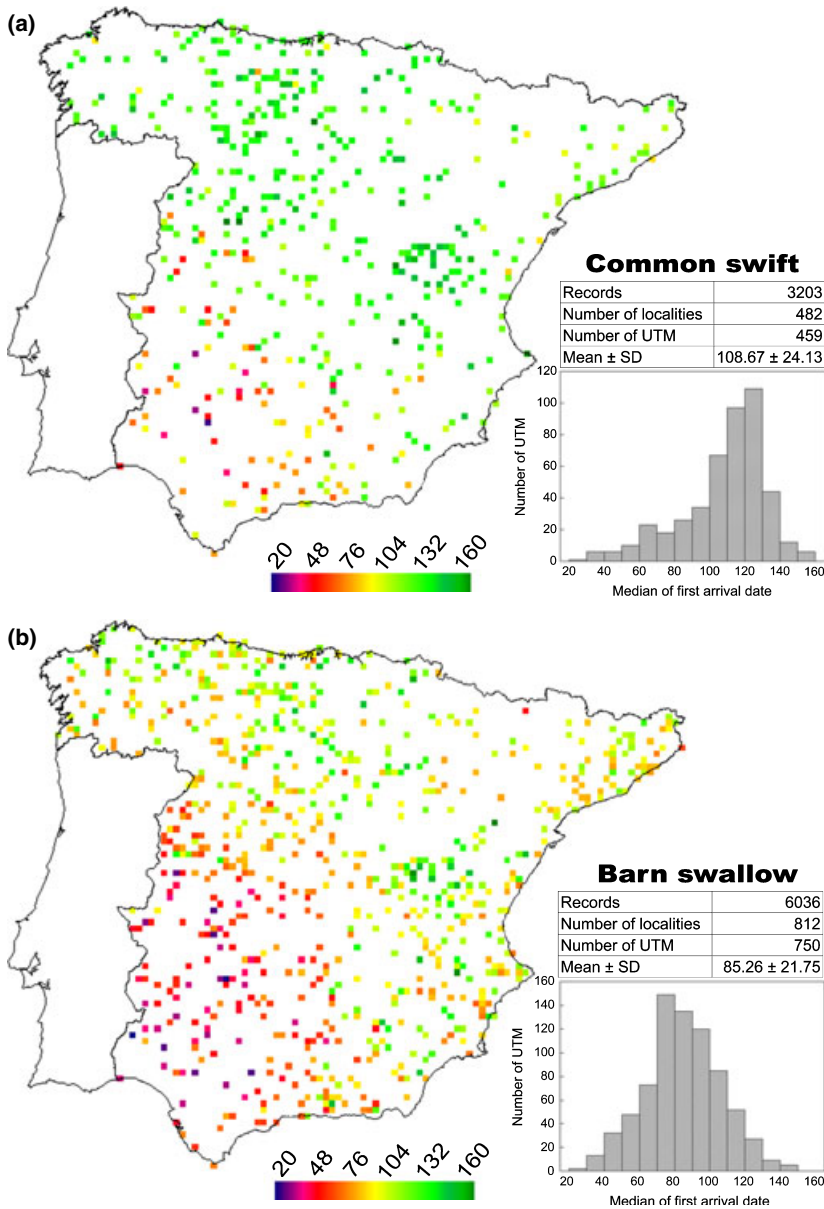
(a)

Common swift

Records	3203
Number of localities	482
Number of UTM	459
Mean ± SD	108.67 ± 24.13

(b)

Barn swallow

Records	6036
Number of localities	812
Number of UTM	750
Mean ± SD	85.26 ± 21.75

Figure 3 Median common swift and barn swallow arrival dates. Maps of the geographic distribution of recorded data in Spain (square = UTM). Scale colour bar in Julian days (1 = 1 January). The number of records, localities and UTMs, together with the mean value and the standard deviation (SD) for all records are also specified for each species. The histogram with the distribution of observations is also shown (scale of *x*-axis in Julian days).

models together produced a final complete model that explained about half of the total variability in both species. The variables included and their signs were quite similar for the two species, with a clear dominance of climatic variables, especially in the barn swallow model. In both models, a positive effect of the Turia basin and the cost of dispersion from Gibraltar were included. The slight increase in the percentage of explained variability, 2.27% in the common swift and 1.67% in the barn swallow, resulting from the inclusion of spatial terms in these complete models shows that some spatial structure in the data had not been explained by the environmental and geographical variables.

While residuals of the various models developed from each type of variable were spatially autocorrelated (Fig. 5), neither of the complete stepwise models were significantly autocorrelated at any lag distance – evidence that no important spatially structured variation had been excluded (Fig. 5).

The small average percentage of variability accounted for by each type of variable (see pure R^2_{adj} in Table 2) indicates that most of the variability is a result of the high degree of variable collinearity (e.g. warmest areas are also the driest). In any case, the groups of explanatory variables from which the best models were developed also accounted for greater fractions of variability on their own.

The map drawn from the complete models (Fig. 6) reflects similar geographical patterns for spring arrivals in both species. First, individuals colonize Iberia between the outlets of the Guadiana and Guadalquivir rivers. From there, they spread through these rivers basins and also through the Tajo basin. This northward movement through only the western half of Iberia is especially clear for the barn swallow map. On the other hand, later arrivals occurred on the Cantabrian coast, the Northern Plateau and the mountainous region of the Iberian System in the common swift, while in the barn swallow later

Table 2 Best regression models of (a) common swift and (b) barn swallow spring arrivals. The regression equation, adjusted R^2 (R^2_{adj}), F-test (F) and degrees of freedom (d.f.) are shown for each type of variable, the complete model, and the complete model with spatial terms. The effect of each type of variable alone, according to hierarchical partitioning of variance, is indicated by the pure R^2_{adj} column.

Group of variables	Model	R^2_{adj}	F	d.f.	Pure R^2_{adj}
Common swift					
Topographical	$100.61 + 12.13MIA + 6.49MIA^2 - 2.99MIA^3 - 3.73SLP$	18.57	27.11	4, 454	2.40
Climatic	$114.84 + 11.58SUR - 11.88SUR^2 + 2.96SUR^3 + 11.26AI - 13.24SUMET - 2.27SUMET^2$	43.33	59.36	6, 452	7.44
Basins	$111.11 + 9.46DUE - 24.25GDN + 12.53TUR - 34.88GDQ - 18.09SEG$	37.93	56.97	5, 453	5.45
Geographical	$113.50 + 16.32DSG - 8.16DSG^2 - 2.86DSG^3 + 4.42CSG$	44.87	94.19	4, 454	6.57
Spatial	$112.67 + 13.23X - 5.71X^2 + 21.60Y - 5.01Y^2 - 4.33Y^3 - 11.92XY$	47.37	69.69	6, 452	9.23
Complete model	$110.09 - 3.45SLP - 12.52SUR + 4.56SUR^2 - 11.46SUMET - 2.84SUMET^2 + 8.57TUR + 10.55DSG - 5.74DSG^2 + 2.95CSG$	49.69	51.27	9, 449	
Complete model + spatial terms	$114.44 - 5.70SLP - 9.44SUMET - 2.19SUMET^2 - 9.56GDN - 21.29GDQ - 17.17SEG + 10.77X - 3.83X^2 - 8.17XY$	51.96	56.04	9, 449	
Barn swallow					
Topographical	$80.82 - 6.00MIA + 8.09MIA^2 + 11.62MEA - 4.94MEA^2$	13.52	30.29	4, 745	2.34
Climatic	$86.29 + 9.85SUR - 2.31SUR^2 + 8.83AI - 16.91SUMXT - 3.44SUMXT^2 + 6.80ATR + 2.40ATR^2$	43.10	82.06	7, 742	8.52
Basins	$90.11 + 8.99CANT - 16.82TAJ - 24.65GDN + 8.59TUR - 24.65GDQ$	31.23	69.02	5, 744	4.82
Geographical	$87.70 + 12.02DSG - 2.26DSG^2 - 2.73DSG^3 + 11.92CSG - 5.01CSG^2 + 0.77CSG^3$	41.21	88.50	6, 743	7.07
Spatial	$83.54 + 21.38X - 3.89X^2 - 2.54X^3 + 9.52Y - 7.90X \cdot Y + 2.97X^2Y - 2.19XY^2$	43.57	83.62	7, 742	9.75
Complete model	$82.93 + 7.06SUR - 1.52SUR^2 + 7.57AI - 14.78SUMXT - 1.89SUMXT^2 + 5.77ATR + 2.65ATR^2 + 9.81TUR - 6.37GDN + 3.23CSG$	48.24	70.81	10, 739	
Complete model + spatial terms	$80.09 - 6.36SUMXT - 2.07SUMXT^2 + 3.93ATR + 5.69TUR + 3.59CSG + 9.60X - 2.24X^2 + 7.27Y + 3.74Y^2 - 7.33XY$	49.91	75.62	10, 739	

All models were significant at $P < 0.0001$ and included only variables significant at $P < 0.05$. See Table 1 for explanatory variable acronyms.
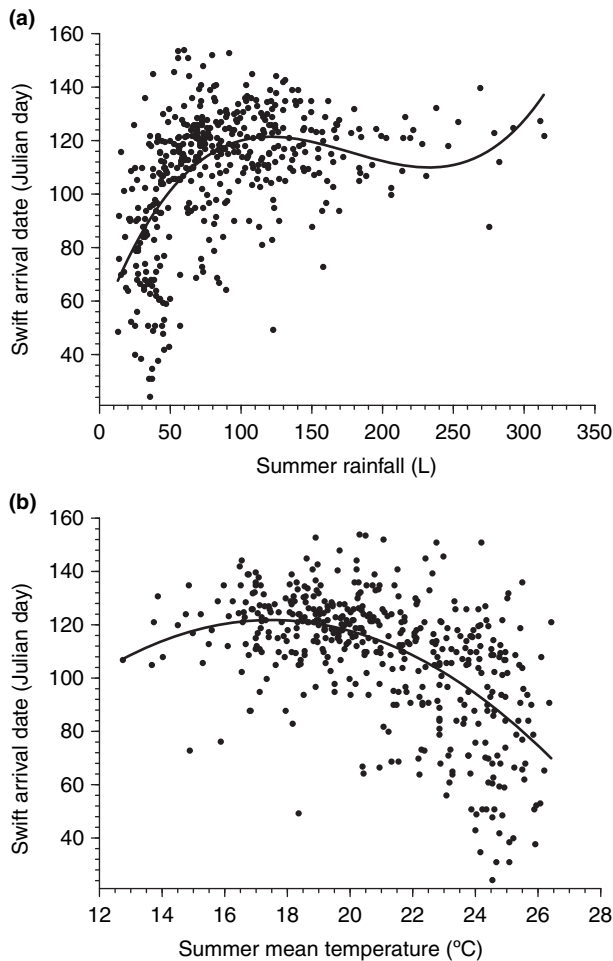
(a)

(b)

Figure 4 Illustrative scatterplots of the most relevant climatic variables and the common swift arrival date. The continuous line is the best-fitting polynomial model.

Figure 5 Spatial autocorrelation of model residuals for each type of variable and for the final model of all variables. Isotropic correlograms represent the variation in the scores of Moran's I spatial autocorrelation statistic with the increase in the separation distance between 10×10 km UTM cells, using a lag distance of 60 km and an active lag of 600 km.

arrivals were located in elevated regions in the Cantabrian Mountains, Iberian System and Pyrenees. In both species, the north-eastern corner (i.e. Catalan and Ebro basins) appeared as an early region, this being especially clear in the case of the common swift.

DISCUSSION

Final models for both species were similar in their explanatory capacity and composition of variables. The absence of autocorrelation in the final models, as well as the irrelevance of spatial variables (added to the models after environmental and geographical variables), indicated that most of the arrival-date variability was explained well enough by the environmental and geographical variables selected. Even though the correlation of the five types of variables employed reduces the reliability of causal factor identification, climatic and geographical variables still seemed to be especially relevant. Just as the occurrence of breeding common swifts and barn swallows in Spain correlates most strongly with both temperature and rainfall (Martí & Del Moral, 2003), there is a strong association between earlier
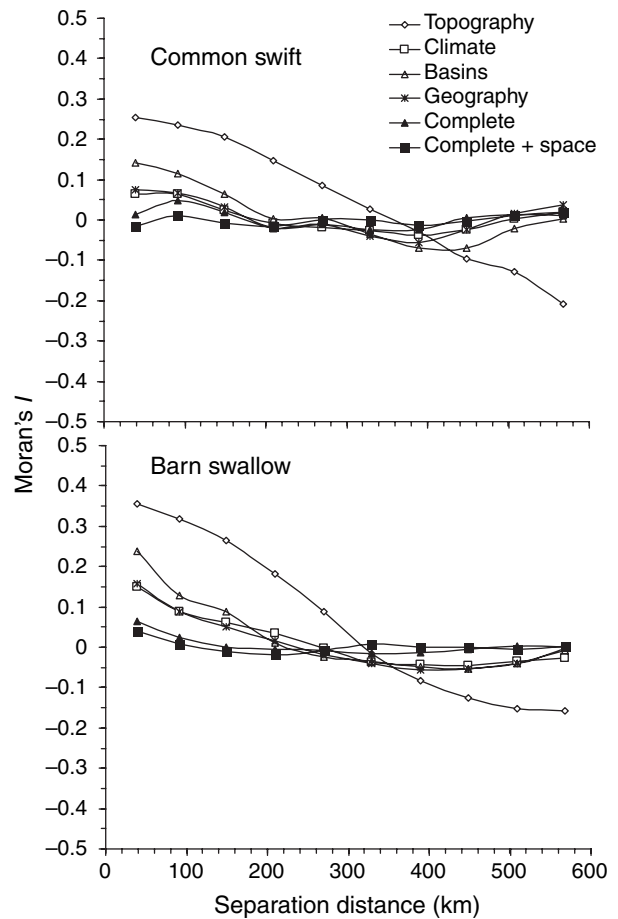
arrivals at the end of winter and areas of less rainfall and higher temperatures during the summer. Distance to and cost of dispersion from the Straits of Gibraltar were also very important factors in explaining arrival dates. Arrivals were later at localities more distant and more costly to reach from the Straits. Lowest-cost routes much longer than a straight line can be seen on the map drawn from the variable (friction surface) used to calculate the cost of dispersion from the Straits of Gibraltar (see Fig. 2). The Cantabrian Mountains, Iberian System and Sierra Nevada (darker areas in Fig. 2) form a nearly continuous geographical barrier, raising the cost of routes traversing them and impeding direct flight to the eastern Iberian Peninsula from the first colonized areas in south-western Spain. Thus the lowest-cost route for common swifts and barn swallows becomes a longer journey across the Iberian Peninsula, leading to delayed arrivals in the eastern breeding grounds. The greater cost of eastern localities is reflected in a longitudinal gradient in arrival dates. The combination of the latitudinal and longitudinal gradients derived from climatic and geographical variables leads to a south-western to north-
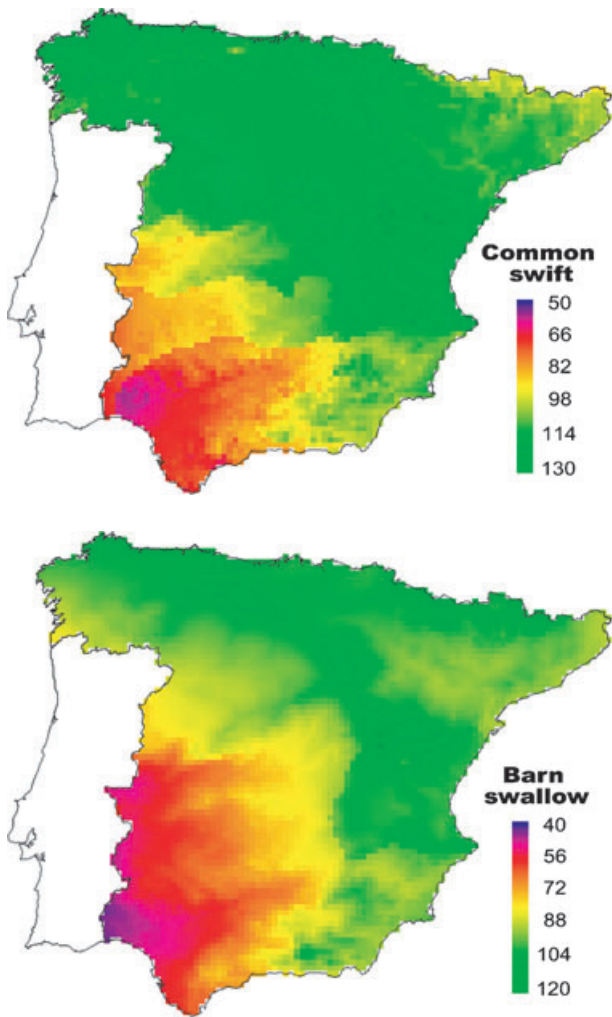
Figure 6 Map of predicted common swift and barn swallow arrivals according to the best final complete model. Scale colour bar in Julian days (1 = 1 January).

eastern gradient for both species, disrupted only by the Catalan and Ebro basins (see Fig. 1). Earlier arrivals to north-eastern Spain suggest that there may be a direct crossing of the Mediterranean Sea from North Africa via the Balearic Islands (Moreau, 1953; Bernis, 1962, 1971; Spina & Pilastro, 1998), although migration along the Spanish Mediterranean coast is also possible. Thus, there is evidence of very strong environmental constraints on the spring arrival dates of these two species, which determine their similar spatial patterns.

These common patterns for spring colonization suggest the existence of some environmental constraints resulting from the unavoidable spatial configuration of the Iberian Peninsula that go beyond possible preferential migratory routes for each species linked with the particular evolutionary history or ancient geographical distribution of each. As avian migration is strongly influenced by endogenous programmes which in turn have a genetic basis (Berthold, 1996), so too could common swift and barn swallow genes impose routes different for each species, as a result of their different phylogenetic origins.

However, the similarity (owing to abiotic constraints; see Fig. 2) in the patterns of their arrivals times to the breeding Iberian territories (see Fig. 6) would be in accordance with adaptability to environmental conditions of migratory patterns (Berthold et al., 1992; Pulido et al., 1996). The similarity of their ecological niches should imply that both species search for similar ecological conditions during spring migration, and, as a consequence, have similar arrival-date patterns.

There is a trade-off between the need for conditions ecologically suitable for reproduction at the beginning of spring and for pathways of lowest cost from the Straits of Gibraltar to breeding localities (see Fig. 2). This trade-off becomes especially evident in the case of the barn swallow, which arrives earlier in northern latitudes in the west than in the east of the Iberian Peninsula, owing to the spatial configuration of the Iberian Peninsula. After leaving Africa and reaching Europe, individuals do not advance northwards in all directions. They first occupy western areas along the southernmost river basins (Guadalquivir, Guadiana and Tajo), which empty into the Atlantic on the western side of the Iberian Peninsula (see Fig. 6). Furthermore, more migrants are seen to pass through the Straits of Gibraltar on days with easterly winds (Nisbet et al., 1961; Bernis, 1962; Hilgerloh, 1993), which would favour a drift of individuals towards the west. The early dates recorded in south-western Iberia could be attributed to swallows wintering in that area, but their small numbers (Bernis, 1971; Cramp, 1988) make them irrelevant to the massive spring colonization of migrants each year. Some mountainous systems (Sierra Nevada and Iberian System, see Fig. 1) seem to act as effective barriers to the eastward migration of barn swallows. A direct crossing of the sea from North Africa to the south-eastern Spanish Mediterranean coast does not appear to be undertaken by many individuals (Bernis, 1971, but see Glainville & Walker, 1962): the Gibraltar area provides the main access to Europe for this species (Moreau, 1953; Bernis, 1962). As a consequence, the colonization of south-eastern Iberia is delayed, despite its proximity to Gibraltar and early onset of conditions suitable for breeding. In the case of the common swift, this difference between arrival dates in western and eastern parts of the southern Iberian Peninsula is not so marked, although it does exist (see Fig. 6). Probably the greater mobility of this species (Koskimies, 1947; Lack, 1955, 1958; Bernis, 1970) helps it to overcome geographical barriers more easily. Such barriers limit pathways to spring breeding grounds and constrain the arrival patterns of our study species. The importance of the combination of altitude, distance to the Straits of Gibraltar, and disposition of river basins implies that the migration of these species through the Iberian Peninsula is partly determined by the location of the main dispersion routes to the most distant Iberian localities (Fig. 2).

A single optimum pathway, the least costly route, could even be used by populations passing through the Iberian Peninsula migrating towards northern breeding areas. The first barn swallows arrive at their breeding grounds in the south-west of the UK during the last week of March (Huin & Sparks, 1998). By this date, only half of our study localities have received barn

swallows (see Fig. 3). Ringing recoveries demonstrate that British barn swallows pass through the Iberian Peninsula both in spring and autumn. Barn swallows migrating during the day and near the land surface, feeding on airborne insects, are easily observable. Hence, it is very unlikely that British passing individuals go unnoticed by Spanish bird observers in those areas with later arrival dates of local breeders. Therefore, early barn swallows from northern European populations must travel only through areas already colonized by Iberian breeders, where ecological conditions have become suitable for both reproduction and migration (Stresemann, 1948; Slagsvold, 1976).

As we have shown, summer climate parameters seem to have a strong influence on arrival dates. This was unexpected, because summer conditions affect individuals only some months after their arrival to breeding grounds. However, summer climatic conditions in the Mediterranean region are some of the most limiting ecological conditions for organisms (Richardson, 1965; Carbonell & Tellería, 1999; García & Arroyo, 2001; Fortuna, 2003). Summer, and especially August, in most of the Iberian Peninsula is a difficult time for individual survival, as a result of high temperatures and scarce (or non-existent) precipitation. The shape of the arrival-date relationship with summer climate (see Fig. 4) reflects the occurrence of earlier arrival dates in areas with warmer and drier summers. This pattern can readily be seen to be the result of the very temperate winters in these areas (Font Tullot, 1983) and, consequently, of ecological conditions suitable for reproduction at the beginning of the year (Isenmann et al., 1990; Sanz, 2002). Earlier arrival in such places would lessen individuals' exposure to life-threatening summer conditions, allowing them to profit from their precocity. However, the spatial constraint again comes to the fore in this context of temperatures. The south-eastern corner of Spain exhibits similar temperature scores to the south-western corner, but the latter is colonized about 1 month earlier. Such a difference in arrival times cannot be attributed to a later onset of the summer season in this region, but rather to the difficulty in reaching the south-east of the Iberian Peninsula. The effect of this geographical asymmetry, and of its concomitant shorter period prior to the onset of summer conditions, on the reproduction of eastern populations should be of considerable interest. Earlier migration along the Atlantic Iberian coast is possible owing to its mild climate and the particular spatial configuration of the Iberian Peninsula. Once individuals cross the sea from Africa to Europe, they find it easier to migrate upstream, along the Guadalquivir and Guadiana basins, than eastwards, where the Sierra Nevada rises.

The final model explanation, for both species, of only about half of the variability in observed arrival dates could be the result of the conditions encountered by individuals during the non-breeding season (Marra et al., 1998; Sillett et al., 2000; Newton, 2006). Each Spanish population might overwinter in a different African region and/or reach the Iberian Peninsula by a different route. Hence, regardless of the similarity in environmental and geographical conditions between neighbouring Spanish localities, the later arrivals observed at one locality could be the result of population migration from more distant wintering quarters or of longer migratory routes. Unfortunately, this hypothesis cannot be verified, since at present the precise location of the wintering quarters of Spanish common swift and barn swallow populations is unknown. There is no information on the whereabouts of the common swift outwith the breeding season. In the case of the barn swallow, ringing recoveries do not seem to support a clearly segregated wintering area for each population, nor even strong individual fidelity to the same wintering grounds (Loske, 1986; Møller & Hobson, 2004).

In our opinion, the variability unexplained by the models is likely to be the result mainly of the nature of the data: first-arrival dates are subject to several well-known biases (Sparks et al., 2001; Tryjanowski et al., 2005). In our case, some of them (e.g. aberrant behaviour of first individuals) are absent from the median values per locality with which we worked. However, the density dependence of the first-arrival date cannot be tested because the number of breeding pairs in each study locality is unknown. Arrival dates for larger populations could be earlier than those for smaller ones, as the probability of earlier observation increases with population size. Another potential problem comes from the number of records (i.e. years) per locality. As we explained, bias resulting from the number of records should not be cumulative, because localities were sampled randomly throughout the study period. However, a potentially large amount of noise is introduced into the data. The probability of sampling in non-representative years (unusually late or early arrivals for given environmental and geographical conditions) increases as the number of records decreases. In conclusion, the first-arrival date produces huge amounts of data with which to study migration through and colonization of large territories. Unfortunately, this measurement is subject to potential biases that reduce the resolution of results to that of broad patterns.

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BIOSKETCHES

Oscar Gordo is interested in how plant and animal phenology is influenced by environment, with special regard to climate change. He is currently working on temporal and spatial migratory bird phenological patterns in the Iberian Peninsula in the Museo Nacional de Ciencias Naturales, Madrid.

Juan José Sanz is a researcher at the Museo Nacional de Ciencias Naturales, Madrid. He is interested in the life histories of songbirds. He is also working on the effects of global change on birds from the Mediterranean region, with special emphasis on their reproduction.

Jorge M. Lobo is a specialist in the biogeography and ecology of dung beetles (Scarabaeoidea) working in the Museo Nacional de Ciencias Naturales, Madrid. He is interested in the patterns and processes of species distribution from a macroecological perspective, in the management of biodiversity information and in conservation biology.

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