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

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Chapter 1

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

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ABSTRACT

Aims Still poorly identified, 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 36.02ºN-43.68ºN; longitude from 9.05ºW-3.17ºE; altitude from 0-1595 m a.s.l. for 482 common swift and 812 barn swallow Spanish localities, spread widely over the Iberian breeding grounds of both species.

Methods Our dataset, covering the years 1960-1990, consisted of 3206 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 (GRM). GRM 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. GRM were applied in two steps. First, we searched for the best model in each one of the previous five types of variables. To cope with the unavoidable correlation between explanatory variables, the relative importance of each type of variables was assessed by hierarchical variance partitioning. Secondly, we searched for that model able to explain the maximum amount of the observed variability of 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 to the southwestern Iberian Peninsula, where summers are warmer and drier. From there, both species follow the main southern Iberian river basins towards the northeast, however several mountainous regions impede the colonization of eastern Iberia. Best models for each type of variable explained 19%-47% of 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. Best predictive models built with all variables accounted for 52% of variability in common swift arrival dates and 50% in those of the barn swallow. Residuals from both models were not spatially autocorrelated, an indication that all major spatially structured variation had been accounted for.

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

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 (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, to afterwards 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 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 authors throughout the last century. The pioneering studies of Sliwinsky (1938) and Southern (1938 a,b, 1939, 1940, and 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 on the scale of 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 southwestern Europe, about two weeks earlier than in similar Eastern European latitudes. Most later studies focussed on particular countries and species (Zabłocka, 1959; De Smet, 1970; Monteanu & Maties, 1978; Beklová *et al*., 1983; Munteanu 1985; Grischtschenko *et al*., 1995; Grishchenko, 2001; Grishchenko 2002; Grishchenko, 2003) and applied the methodology used by Sliwinsky and

Southern decades earlier to describe broad geographical patterns of the progression of migration. Applying GIS techniques, Huin and Sparks (1998 and 1999) mapped more comprehensively the arrival and progression through Britain of four migratory birds, but did not investigate potential environmental or geographical factors underlying the spatial patterns observed. Therefore, studies have yet to go beyond mere description of migration progression through large territories.

Huin and Sparks (1998 and 2000) offered evidence of the effect of climate on migratory arrival dates. 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, would be 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 spatial patterns of spring migration through the Iberian Peninsula of the common swift (*Apus apus*) and barn swallow (*Hirundo rustica*), two of the most abundant and widespread species in this region (Martí & Del Moral, 2003). Their specialized feeding on airborne insects has led both species to develop very similar migration strategies and requirements (Cramp, 1985; Cramp 1988), though their timing of migration both in the spring and autumn are quite different. The common swift arrives in Spain, on average, 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 to offer 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 main 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 are a basis from which to compare their migratory pathways through the same territory and determine the relative influence of: constant (on our time scale) characteristics of Iberian Peninsula geography and topography; changes in ecological conditions during the course of spring; and/or the influence of the evolutionary history of each species on their migration patterns.

MATERIAL AND METHODS

Bird arrival dates

Arrival dates for the common swift and barn swallow were obtained from the Spanish *Instituto Nacional de Meteorología* phenological database gathered by 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, 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 (Anon., 1943). The characteristics of these events include: *i*) broad distribution of species throughout Spain (volunteers can observe everywhere in the country), *ii*) considerable abundance (phenological observation unconstrained by number of individuals), *iii*) unmistakable morphology and/or behaviour (increased data reliability) making them ideal for phenological monitoring and ensure data homogeneity, independent of the observer.

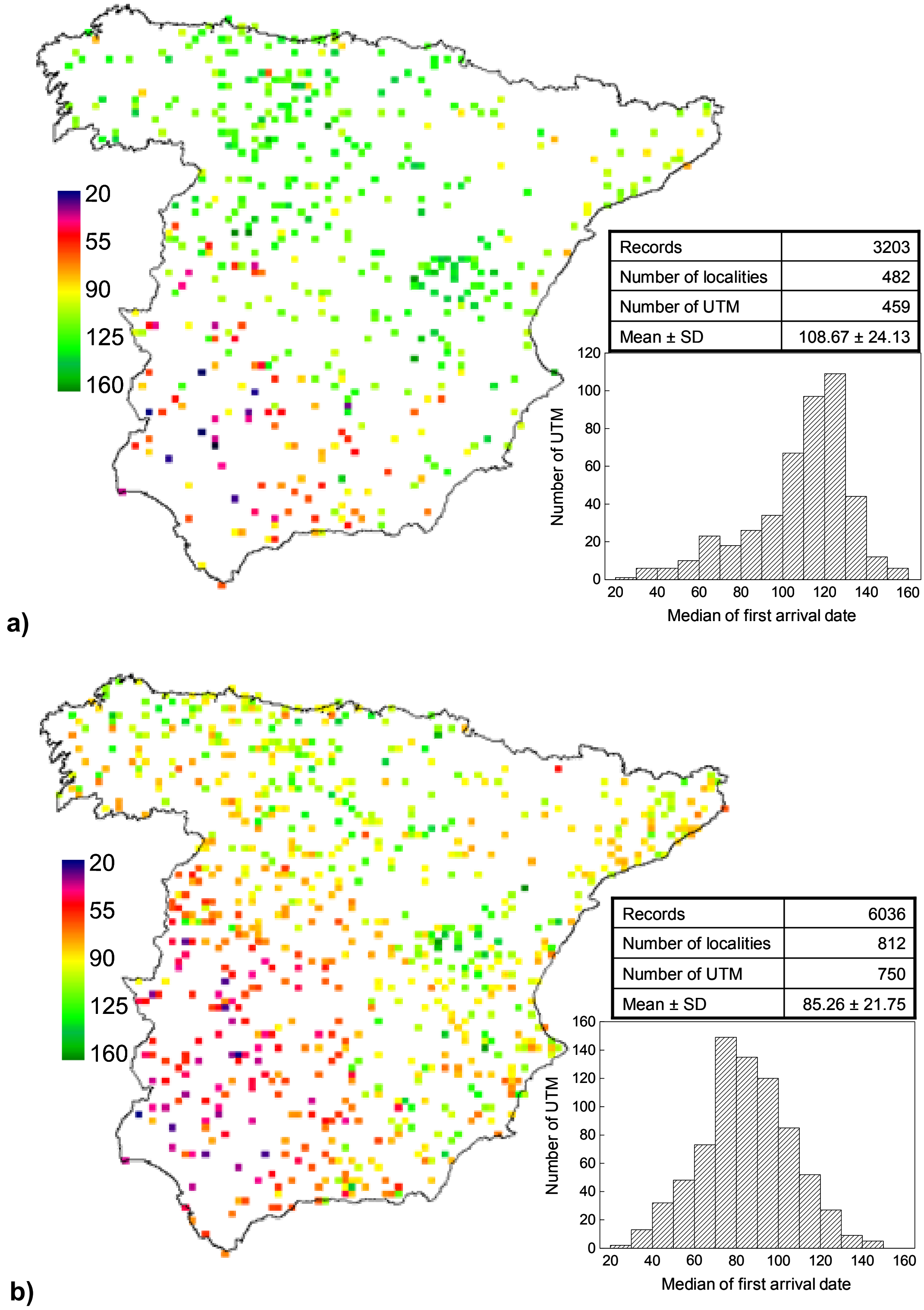
Spring migratory phenology of both species was measured as the date of the first sighted individual in each study site and year. The first sighted individual thus is interpreted as the first nesting individual arriving at a certain locality. This observation method produces data with very few undetectable misidentifications, as there is little probability of mistaking passing individuals, on their way to more northerly or higher areas, for nesting individuals (Slagsvold, 1973). Another potential source of error would be misidentification of species. Their similarity in feeding habits and body shape does not extend to their different colouring, behaviour and voice (Cramp, 1985; Cramp, 1988), nor to their very different migratory calendar; barn swallows arrive on average nearly one month (23.8 days) before common swifts (see Fig. 1.1).

All collected and computerized original records (9239, from 829 localities; see Fig. 1.1 for species details), from 1960 to 1990, correspond to the period for which meteorological data is 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 tendencies within date distributions) for all records from the same 100 km^2 UTM cell (Fig. 1.1) was selected. 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 (see Fig. 1.1). The difference in number of records from each UTM could have biased median values, but coefficients of Spearman rank correlation of median values with number of records did not indicate such a bias (Common swift: $r_S = 0.026$; Barn swallow: $r_S = -0.072$).

Explanatory variables

A set of 40 explanatory variables, used to model migratory arrival dates of the study species (Table 1.1), fall into topographic, climatic, river basin, geographic, and spatial groups. For each 100 km^2 Iberian Peninsula UTM cell (n = 6063) seven topographic and eighteen 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 its diversity were calculated from mean, minimum and maximum altitude 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



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

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

Figure 1.1 Median common swift (**a**) and barn swallow (**b**) arrival dates. Maps of the geographic distribution of recorded data in Spain (square = UTM). Scale colour bar in Julian day (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).

Variables	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 (ºC)
SUMIT	Summer minimum temperature (ºC)
AUMIT	Autumn minimum temperature (ºC)
WIMIT	Winter minimum temperature (ºC)
SPMET	Spring mean temperature (ºC)
SUMET	Summer mean temperature (ºC)
AUMET	Autumn mean temperature (ºC)
WIMET	Winter mean temperature (ºC)
SPMXT	Spring maximum temperature (ºC)
SUMXT	Summer maximum temperature (ºC)
AUMXT	Autumn maximum temperature (ºC)
WIMXT	Winter maximum temperature (ºC)
ATR	Annual temperature range (ºC)
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)

Table 1.1 Topographical, climatic, river basin, geographical and spatial variable groups used in general regression models along with their acronym, complete description and units (in brackets).

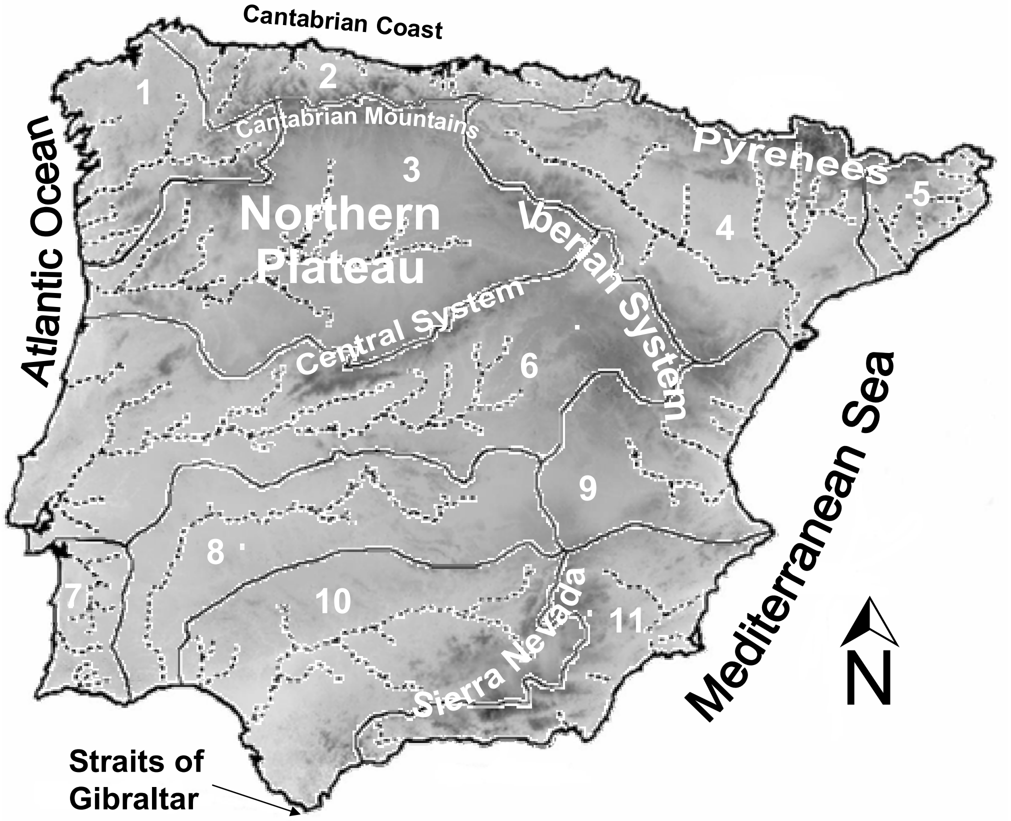


Figure 1.2 Topographic map of the Iberian Peninsula with the main geographic features cited in text. River basins are numbered (codes: 1-Miño, 2-Cantabrian, 3-Duero, 4-Ebro, 5-Catalan, 6-Tajo, 7-Southwestern (not included in analyses), 8-Guadiana, 9-Turia, 10-Guadalquivir, 11-Segura) and their boundaries marked by solid lines. The main rivers in each basin are shown as dashed lines.

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. 1.2) 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

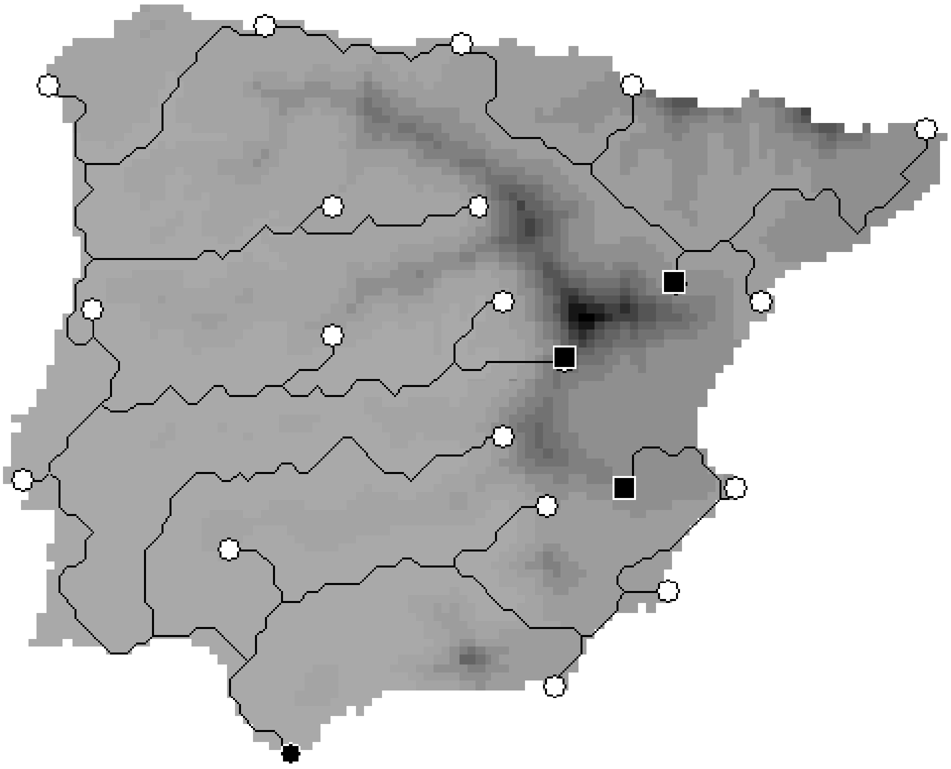


Figure 1.3 Map of the cost of moving from the Straits of Gibraltar along valleys through the Iberian Peninsula. This cost surface was obtained from the costgrow algorithm module of idrisi 32 software, taking the product of altitude x distance-to-rivers as friction surface. Darker UTMs are those with the more costly pathway 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 by the pathway module of IDRISI 32 software.

image was the product of (standardized) altitude x (standardized) distance-to-rivers (see Fig. 1.3). 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, the friction surface. Finally, a 0-1 code, identifying UTM falling within (1) or outside (0) of major Iberian river basins (Fig. 1.2) 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 analyzed by means of General Regression Models (GRM) using STATISTICA (StatSoft, 2001), in two steps. Firstly, the explanatory variables from the same 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 final group models. 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 eliminated non-significant variables. Predicted scores of this complete model were mapped and examined.

Arrival dates were examined for possible spatial structure after accomplishing GRM 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 such spatial autocorrelation would indicate that one or more important spatially structured explanatory variables may have been left out (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; MacNally, 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

Factors related to variability in common swift arrival dates

Median values of first arrival dates were earlier in UTM in the southern Iberian Peninsula and near the Mediterranean coast (Fig. 1.1a). Common swifts arrived last in the Northern Plateau and in the Iberian System (see Fig. 1.2). The earliest and latest arrival dates were separated by 132 days (end January to the beginning of June), longer than previously reported (Bernis, 1951; Bernis, 1970), a result of the broader temporal and spatial range of our data. The distribution, slightly skewed to the left (Skewness = -1.052, t_{458} = 9.233, $P < 0.001$), had a larger proportion of early arrivals than in a normal distribution. As distribution skewness does not usually have an appreciable effect on the F statistic (StatSoft, 2001), all analyses were performed with original untransformed data.

Climatic and geographical models were the most explanatory (Table 1.2). Of the climatic variables, summer rainfall and mean temperature as well as the aridity index were retained in the final model. The signs of variables pointed towards earlier arrivals in areas with drier and warmer summers (Fig. 1.4). Of the geographical variables, both distance to- and cost of dispersion from- the Straits of Gibraltar were related with common swift arrivals (Table 1.2), later in localities remote from the Straits of Gibraltar and reached by an expensive pathway. While the general relevance of geographical variables highlighted the importance of the spatial configuration of 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 variability ($F_{3,455}$ = 110.77, $P < 0.001$).

The topographical model was the least relevant (Table 1.2). Its prediction of later arrival in high altitude plains concurs exactly with observations in the Northern Plateau, one of the areas where individuals arrive latest. On the other hand, the final model of the five river basin variables explained a notable

Group of variables	Model	R^2_{adj}	F	d.f.	Pure R^2_{adj}
Topography	$100.61 + 12.13MIA + 6.49MIA^2 - 2.99MIA^3 - 3.73SLP$	18.57	27.11	4, 454	2.40
Climate	$114.84 + 11.58SUR - 11.88SUR^2 + 2.96SUR^3 + 11.26AI - 13.24SUMET - 2.27SUMET^2$	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
Geography	$113.50 + 16.32DSG - 8.16DSG^2 - 2.86DSG^3 + 4.42CSG$	44.87	94.19	4, 454	6.57
Space	$112.67 + 13.23X - 5.71X^2 + 21.60Y - 5.01Y^2 - 4.33Y^3 - 11.92XY$	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	

Table 1.2 Best regression models of common swift spring arrivals. The regression equation, adjusted R^2 (R^2_{adj}), F-test (F) and degree 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. All models were significant at $P < 0.0001$ and included only significant variables at $P < 0.05$. See Table 1 for explanatory variable acronyms.

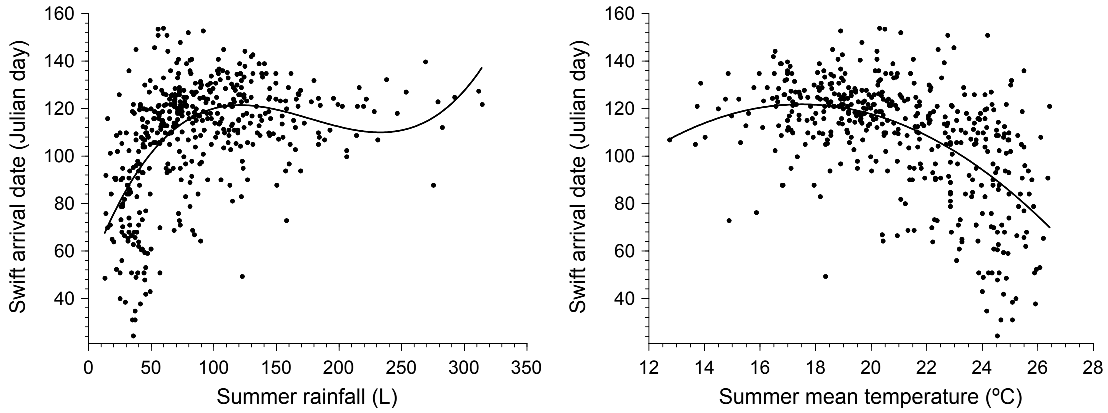


Figure 1.4 Illustrative scatterplots of the most relevant climatic variables and the common swift arrival date. The continuous line is the best fitted polynomial model.

amount of original data variability (Table 1.2). The negative effect of Guadalquivir, Guadiana and Segura basins (see Fig. 1.2) fully agrees with the previously mentioned earlier arrivals in southern Iberia (Fig. 1.1a).

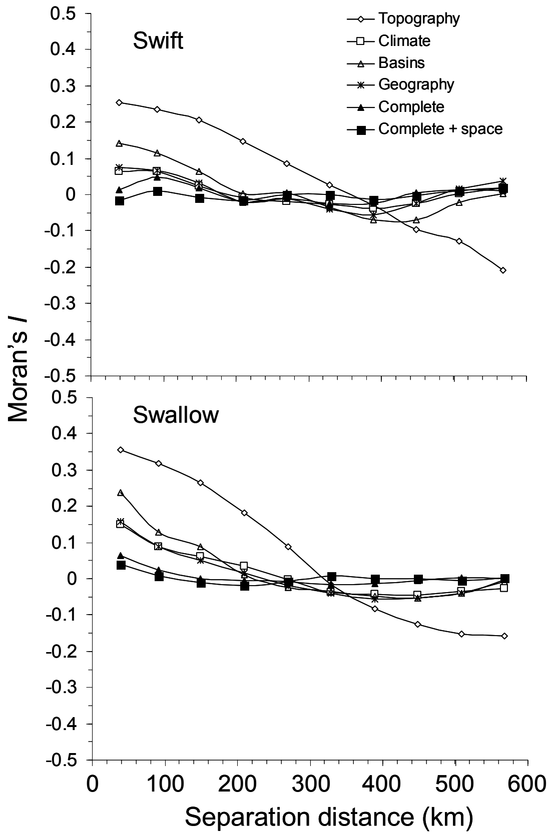


Figure 1.5 Spatial autocorrelation of model residuals for each type of variable and for the final model of all variables. Isotropic correlograms represent the variation in the scores of Moran's *I* spatial autocorrelation statistic with the increase in the separation distance between 10 x 10 km UTM cells, using a lag distance of 60 km and an active lag of 600 km.

Backward stepwise selection of all significant variables from the five groups (Table 1.2) together produced a final model that explained around 50% of total variability. Spatial variables, by themselves highly relevant, accounted for around 47% of total variability (Table 1.2), indicating that common swift spring arrival is highly spatially structured. The slight increase in the percentage of explained variability, to 52%, due to the inclusion of spatial terms, after the environmental and geographic variables, shows that some spatial structure in the data had not been explained by the environmental and geographical variables. Residuals from models for each type of variable (other than topography and river basin; Fig. 1.5) were not significantly spatially autocorrelated, nor were those from the complete final model.

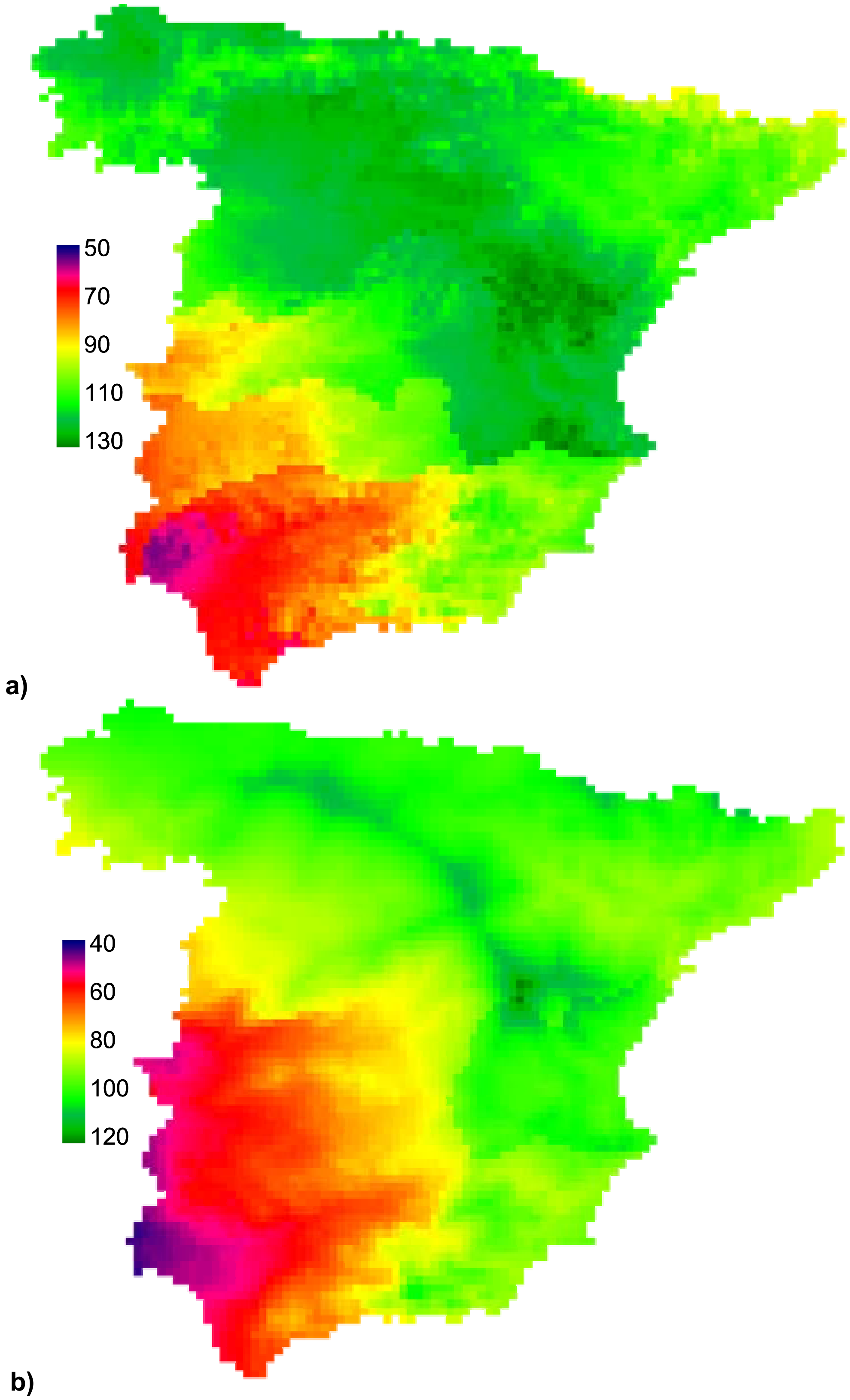


Figure 1.6 Map of predicted common swift (**a**) and barn swallow (**b**) arrivals according to the best final complete model. Scale colour bar in Julian day (1 = 1 January).

The small average percentage of variability accounted for by each type of variable (see Pure R^2_{adj} in Table 1.2) indicates that most of the variability is due to 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 by themselves.

These models point towards earlier spring arrivals of common swifts in southernmost localities, with low altitudes, higher temperatures and little precipitation. The map drawn from the final model (Fig. 1.6a) displays the spring migratory spatial pattern of this species, where an earlier arrival region appears in the southernmost river basins. Later arrivals occurred on the Cantabrian coast, in the Northern Plateau and the mountainous region of the Iberian System, while arrivals seem to be earlier in the north-eastern corner of the Iberian Peninsula and the Ebro basin than in some neighbouring regions.

Factors related to variability in barn swallow arrival dates

A pattern of earliest arrivals in the southwestern Iberian corner (Fig. 1.1b) can be seen in the geographical variation in data. The distribution of dates was normal ($SW\text{-}W = 0.997$; $P = 0.106$), with earliest and latest first arrival dates between 29 January and 28 May. The early arrivals coincide with those reported in the literature, while the later ones extend the migratory period by nearly one month (Saunders, 1871; Bernis, 1971).

Climatic and geographical models for this species were also the most explanatory (Table 1.3). The climatic model for barn swallow arrivals, while including a positive quadratic function of temperature range, highlighted the role of summer rainfall and maximum temperatures. A model including only the quadratic function of this latter summer variable accounted for 33.38% ($F_{2,747} = 188.66$, $P < 0.001$) of barn swallow arrival date variability. A quite similar picture to that described for the common swift emerged, of earliest arrivals where summer temperatures are highest and rainfall lowest; arrivals were especially early where conditions are most arid and temperatures less variable throughout the year.

Group of variables	Model	R^2_{adj}	F	d.f.	Pure R^2_{adj}
Topography	$80.82 - 6.00MIA + 8.09MIA^2 + 11.62MEA - 4.94MEA^2$	13.52	30.29	4, 745	2.34
Climate	$86.29 + 9.85SUR - 2.31SUR^2 + 8.83AI - 16.91SUMXT - 3.44SUMXT^2 + 6.80ATR + 2.40ATR^2$	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
Geography	$87.70 + 12.02DSG - 2.26DSG^2 - 2.73DSG^3 + 11.92CSG - 5.01CSG^2 + 0.77CSG^3$	41.21	88.50	6, 743	7.07
Space	$83.54 + 21.38X - 3.89X^2 - 2.54X^3 + 9.52Y -7.9XY + 2.97X^2Y - 2.19XY^2$	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	

Table 1.3 Best regression models of barn swallow spring arrivals. The regression equation, adjusted R^2 (R^2_{adj}), F-test (F) and degree 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. All models were significant at $P < 0.0001$ and included only significant variables at $P < 0.05$. See Table 1 for explanatory variable acronyms.

The geographical model explained a slightly smaller percentage of variability than did the climatic one (Table 1.3), included only the cubic function of two variables (distance to- and cost of dispersion from- the Straits of Gibraltar) and highlighted 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. Topographical and river basin variables seemed to have a smaller influence (Table 1.3). High altitude localities were colonized later, while arrivals were clearly earlier in the Guadiana and Guadalquivir basins (see Fig. 1.2), nearest to the Straits of Gibraltar.

The correlation of many of the explanatory variables caused their real contribution to the percentage of variability accounted for them to be much smaller than such a percentage accounted for by the model developed from them alone (Table 1.3). While geographical and climatic variables contributed most, spatial variables were also highly explicative by themselves due to the most, spatial variables were also highly explicative by themselves due to the spatial structure in barn swallow arrival dates. However, the inclusion of spatial variables after considering the remaining environmental and geographic variables increased the explained variability by only 1.66% in the complete final model (see Table 1.3). The inclusion of four climate variables in these final models highlights their relevance.

While residuals of the various models developed from each type of variable were spatially autocorrelated (Fig. 1.5), both complete stepwise models were not significantly autocorrelated at any lag distance, evidence that any important spatially structured variation had been included (Fig. 1.5).

The geographical pattern (Fig. 1.6b) reflected earlier barn swallow arrivals in the southwestern Iberian corner, with its high temperatures and little precipitation, and mainly, along the Guadiana and Guadalquivir basins. They arrive much later in the mountainous zones of southeastern (Sierra Nevada), northwestern (Cantabrian Mountains) Iberian Peninsula, but mainly in those of the Iberian System.

DISCUSSION

Final models for both species were similar in their explanatory capacity and variable composition. 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), so do earlier arrivals at the end of winter in areas of less rainfall and higher temperatures during the summer (see Fig. 1.2). Distance to- and cost of dispersion from- the Straits of Gibraltar were also very important in explaining migrant bird 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. 1.3). The Cantabrian Mountains, Iberian System and Sierra Nevada (darker areas in Fig. 1.3) 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 from southwestern 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 southwestern to northeastern gradient for both species, disrupted only by the Catalan and Ebro basins (see Fig. 1.2). Earlier arrivals to northeastern Spain suggest that there may be a direct crossing of the Mediterranean Sea from North Africa via the Balearic Islands (Moreau, 1953; Bernis, 1962; Bernis, 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 migration of these two species, which determine their similar spatial patterns.

These common patterns for spring colonization suggest the existence of some environmental constraints due to the inevitable spatial configuration of the Iberian Peninsula 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 (due to abiotic constraints; see Fig. 1.3) of the pattern of their spring migration through the Iberian Peninsula (see Fig. 1.6) would be in accordance with the adaptability to environmental conditions of migratory patterns (Berthold *et al*. 1992; Pulido *et al*. 1996). The similarity of their ecological niche should imply that both species search for similar ecological conditions during migration and, as a consequence, have similar migration 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. 1.3). 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, due to its spatial configuration. After leaving Africa and reaching Iberia, individuals do not seem to 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. 1.6b). 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 southwestern 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. 1.2) seem to act as effective barriers to the eastward migration of barn swallows across the Guadalquivir, Guadiana and Tajo basins. A direct crossing of the sea from North Africa to the southeastern Spanish Mediterranean coast does not seem to be undertaken by many individuals (Bernis, 1971, but see Glainville & Walker, 1962); the Straits of Gibraltar provides the main access to Europe for this species (Moreau, 1953; Bernis, 1962). As a consequence the colonization of southeastern 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, though it also exists (see Fig. 1.6a). Probably the greater mobility of this species (Koskimies, 1947; Lack, 1955; Lack 1958; Bernis, 1970) helps it to more easily overcome geographical barriers. Such barriers limit pathways to spring breeding grounds and constrain the migratory 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 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. 1.3).

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 to their breeding grounds in southwestern 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. 1.1b). 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 the observers from the Spanish phenological network skip over passing individuals. 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, 1973).

As we have shown, summer climate parameters seem to strongly influence arrival dates. This was unexpected, since summer conditions affect individuals only some months after their arrival to breeding grounds. However, summer climatic conditions in the Mediterranean region are of the most limiting ecological conditions for organisms (Richardson, 1965; Carbonell & Tellería, 1999; Garcia & 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 nonexistent) precipitations. The shape of the arrival date relationship with summer climate (see Fig. 1.4) reflects the occurrence of earlier arrival dates in areas with warmer and drier summers. This pattern can readily be seen to be due to the very temperate winters in these areas (Font Tullot, 1983) and, consequently, to ecological conditions suitable for reproduction at the beginning of the year (Isenmann *et al.*, 1990; Sanz, 2002). Earlier arrival in such places would lessen individual 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 southeastern corner of Spain exhibits similar temperature scores to the southwestern corner, but the latter is colonized about one 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 southeast of the Iberian Peninsula from Gibraltar, the main point of access. 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 due 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 eastward, where the Sierra Nevada rises.

Final model explanation, for both species, of only about half of the variability in observed arrival dates could be due to 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 different African regions and/or reach the Iberian Peninsula by different routes. Hence, regardless of the similarity in environmental and geographical conditions between neighbouring Spanish localities, later arrivals observed at one locality could be due to population migration from more distant wintering quarters or to 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 outside of 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 models should be due mainly to the nature of data; first arrival dates are subject to several well-known biases (Sparks *et al*., 2001; Tryjanowsky *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 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 due to 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 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 from which to study migration through and colonization of large territories. Unfortunately, this measurement is subject to potential biases which reduce the resolution of results to that of broad patterns.

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RESUM

Factors ambientals i geogràfics limitants en els patrons migratoris de falciots negres i orenetes vulgars a través de la Península Ibèrica

Les principals rutes migratòries a través de la Península Ibèrica encara són desconegudes per a la majoria d’aus trans-saharianes, tot i el paper clau que té

aquesta àrea en el sistema migratori europeu-africà. Es van descriure els patrons d'arribades per al falciot negre (*Apus apus*) i l'oreneta vulgar (*Hirundo rustica*) i van estudiar quins són els millors factors ambientals i geogràfics capaços d'explicar-los. Els nostre anàlisi va permetre buscar limitants ecològics en comú en dues espècies migratòries amb una morfologia i tipus de vol similars.

Es van emprar 482 localitats per al falciot negre i 812 per a l'oreneta vulgar àmpliament distribuïdes per la Península Ibèrica. Rang latitudinal: 36.02ºN-43.68ºN, rang longitudinal: 9.05ºW-3.17ºE, rang altitudinal: 0-1595 m.

Es van utilitzar 3206 registres d e primeres arribades per al falciot negre i 6036 per a l'oreneta vulgar entre 1960 i 1990. Es van usar 40 variables predictives (de caire topogràfic, climàtic, conques del rius, geogràfic i espacial) en models generals de regressió (GRM). Els GRM van incloure termes polinomials fins al cub en totes aquelles variables on foren significatius. Es va aplicar selecció per passos fins obtenir models compostos només de termes significatius. Els GRM es van aplicar en dos fases. Primer es va buscar el millor model dintre de cada un dels tipus de variables esmentats anteriorment. Degut a que les variables predictives estan inevitablement correlacionades entre sí, la importància relativa de cadascuna d'elles es va determinar mitjançant una partició jeràrquica de la variança. Després vam cercar el model capaç d'explicar més quantitat de la variabilitat observada en les dates d'arribada. Per obtenir-lo, totes les variables significatives es van incloure en un únic model. Un cop obtingut, a més, es van afegir les variables de caire espacial per tal de tenir en compte qualsevol estructura espacial romanent a les dades. L'autocorrelació espacial es va avaluar mitjançant el coeficient *I* d'autocorrelació de Moran.

Ambdues espècies van arribar abans a aquelles localitats amb estius més calorosos i secs prop de l'Estret de Gibraltar, el que correspon al sud-oest de la península. Els millors models per a cada tipus de variable van ser capaços d'explicar entre el 19 i el 47 % de la variabilitat en les dates d'arribada del falciot negre, i entre el 14 i el 44 % en les de l'oreneta vulgar. La partició de la variança va demostrar que les variables climàtiques i geogràfiques són les més explicatives. Els millors models predictius van explicar el 52 % de la variabilitat en les dates del falciot negre i el 50 % en l'oreneta vulgar. Ambdós models no van tenir residus espacialment autocorrelacionats, el que vol dir que no van deixar de banda cap mena de variabilitat estructurada espacialment.

Podem concloure que la colonització primaveral depèn molt de la configuració geogràfica de la Península Ibèrica. L'Estret de Gibraltar actua com una mena d'embut pel qual passen la majoria dels individus que migren cap al nord. Des d'aquí la progressió de les espècies analitzades segueix un eix del sud-oest cap el nord-est degut a l'orientació de les conques dels principals rius ibèrics. Aquesta limitació obliga a ambdues espècies a convergir en un patró molt similar pel que fa a la seva migració pre-nupcial. Els falciots negres i les orenetes vulgars, per tant, s'han d'enfrontar a un *trade-off* imposat per l'existència d'unes les rutes òptimes per a la migració i la presència de condicions ecològiques adequades en els territoris de nidificació a l'inici de la temporada.