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

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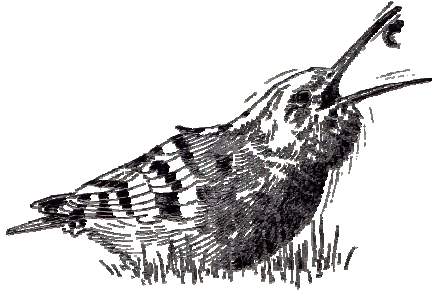
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Chapter 5

Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds?

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ABSTRACT

The life cycles of plants and animals are changing around the world in line with the predictions originated from hypotheses concerning the impact of global warming and climate change on biological systems. Commonly, the search for ecological mechanisms behind the observed changes in bird phenology has focussed on the analysis of climatic patterns from the species breeding grounds. However, the ecology of bird migration suggests that the spring arrival of long-distance migrants (such as trans-Saharan birds) is more likely to be influenced by climate conditions in wintering areas given their direct impact on the onset of migration and its progression. We tested this hypothesis by analysing the first arrival dates (FADs) of six trans-Saharan migrants (cuckoo *Cuculus canorus*, common swift *Apus apus*, hoopoe *Upupa epops*, barn swallow *Hirundo rustica*, house martin *Delichon urbica* and nightingale *Luscinia megarhynchos*), in a western Mediterranean area since 1952 to 2003. By means of multiple regression analyses, FADs were analysed in relation to the monthly temperature and precipitation patterns of five African climatic regions south of the Sahara where species are thought to overwinter and from the European site from where FADs were collected. We obtained significant models for five species explaining 9–41 % of the variation in FADs. The interpretation of the models suggests that: 1) The climate in wintering quarters, especially the precipitation, has a stronger influence on FADs than that in the species' potential European breeding grounds. 2) The accumulative effects of climate patterns prior to migration onset may be of considerable importance since those climate variables that served to summarise climate patterns 12 months prior to the onset of migration were selected by final models. 3) Temperature and precipitation in African regions are likely to affect departure decision in the species studied through their indirect effects on food availability and the build-up of reserves for migration. Our results concerning the factors that affect the arrival times of trans-Saharan migrants indicate that the effects of climate change are more complex than previously suggested, and that these effects might have an interacting impact on species ecology, for example by reversing ecological pressures during species' life cycles.

INTRODUCTION

Mean global temperature has increased about 0.6 °C worldwide over the last century (McCarthy *et al.*, 2001) with the consequent impact of global warming on a range of ecosystems. In recent years, a number of studies (Hughes, 2000; McCarty, 2001; Sanz, 2002; Walther *et al.*, 2002) have attempted to detect and evaluate the magnitude of such impacts on the structure and functioning of these ecosystems, and there is an accumulating body of evidence to indicate that the life cycle patterns and physiology of several organisms are indeed changing as a result of global warming (Parmesan & Yohe, 2003; Root *et al.*, 2003).

Birds constitute useful study models due to well-established monitoring programmes that provide time series detailing the ecological parameters of various species during the last decades, when the highest warming was detected (McCarthy *et al.*, 2001), and in some cases covering all last century (e.g. Butler, 2003). The temporal amplitude of these data allows to test the hypothetical effects of recent global climate change on three main features of birds: changes in reproductive success (e.g. Moss *et al.*, 2001), shifts in geographical distribution (e.g. Thomas & Lennon, 1999) and changes in the timing of life cycle events (e.g. Sparks, 1999).

The timing of migration in birds is of particular interest since migratory bird species are under considerable constraints of time and energy during this period (Wikelski *et al.*, 2003) and any changes in migratory phenology can have a severe impact on a bird's fitness (Both & Visser, 2001; Lemoine & Böhning-Gaese, 2003; Sanz *et al.*, 2003). The timing of migration is determined by a combination of environmental and endogenous factors (Zalakevicius, 1997; Berthold, 2001). Circannual rhythms, which are under the control of photoperiod (Gwinner, 1990; Berthold, 1996), are commonly accepted to be responsible for the initiation of spring migration, especially in long-distance migrants (Gwinner, 1996). However, photoperiod driven circannual rhythms may show a great degree of plasticity in their expression allowing individuals to adapt their departure timing in response to local ecological conditions (e.g. food availability) in wintering areas (Saino *et al.*, 2004). For those species with limited plasticity,

a change in climate may lead to a mismatch between the timing of migration and resource availability in the birds' wintering and breeding areas. This mismatch may be difficult to overcome by natural selection if climatic changes occur rapidly (Potti, 1998; Bradley *et al.*, 1999; Both & Visser, 2001; but see Møller, 2001; Pulido *et al.*, 2001; Yom-Tov, 2001).

Most studies analysing changes in migratory phenology in species breeding in northern boreal and temperate habitats report that the arrival dates of migratory birds have advanced in agreement with a temperature increase in these areas. However, a few studies (Mason, 1995; Loxton & Sparks, 1999; Sparks & Braslavská, 2001; Butler, 2003; Cotton, 2003) report the contrary for some species, suggesting that changes in migration phenology may show a strong geographical and species specific component (Ahas, 1999; Inouye *et al.*, 2000) which has been recently demonstrated for breeding parameters in the pied flycatcher (Sanz, 2003). Peñuelas *et al.* (2002) found that the spring arrival of five out of the six bird species analysed in a western Mediterranean area had been delayed over the last 50 years. However, other phenology events associated with spring, such as flowering, leaf unfolding, fruiting or insect appearance, were significantly advanced in the same area in agreement with local warming (Peñuelas *et al.*, 2002; Stefanescu *et al.*, 2003). In this particular case, one would expect bird fitness to be markedly affected by late arrival to the breeding ground as the birds encounter a general advancement in the phenological events due to local warming. Understanding all the causes of changes in bird migration timing is essential if we wish to assess accurately the effects of global change on bird biology.

Most studies analysing changes in the timing of bird migration have focussed on the role of shifting climate patterns in breeding areas. However, since it is more likely that decisions on departure are made in the wintering grounds, it appears that climate patterns in these areas rather than those in breeding grounds may influence the timing of arrival in the later (Mason, 1995; Huin & Sparks, 1998; Sparks, 1999; Huin & Sparks, 2000; Cotton, 2003). Here, we tested the hypothesis that for trans-Saharan migrants, the most important factor affecting the timing of the spring arrival is the climate in African wintering

quarters rather than the climate patterns in the potential European breeding grounds. If the hypothesis holds, we predict that the arrival patterns of migrant birds in Southern Europe will reflect more closely climatic variation in African wintering quarters than that in Europe.

MATERIAL AND METHODS

Collection of bird data

Field bird data has been collected since 1952 by one of the authors (P.C.) in the area surrounding the Cardedeu field station (NE Spain, 41°34'N - 2°21'E), as a part of a long-term meteorological and phenological monitoring programme (Peñuelas *et al.*, 2002). The first arrival date in the Cardedeu area (FAD, first sighting or recording of bird song) was recorded each year for six migratory bird species. The data included first sightings of the common swift *Apus apus*, the barn swallow *Hirundo rustica* and the house martin *Delichon urbica*, and the first singing of the cuckoo *Cuculus canorus*, the hoopoe *Upupa epops* and the nightingale *Luscinia megarhynchos*. All these species, but a small fraction of hoopoe populations, are sub-Saharan winterers. Recording the first individual of the species receive criticism because these data may not represent the migratory behaviour of the whole population and may be biased by recording effort and population size of the species (Mason, 1995; Sparks *et al.*, 2001; Tryjanowski & Sparks, 2001). In our case, no changes occurred in effort as the recording was always conducted by one of the authors using the same transect routes every year (P.C.). On the other hand, no significant tendencies in distribution range or population size in last 20 years have been found for five of the species (Estrada *et al.*, 2004.). Only a slight decline (6.3 %) in the distribution range of the hoopoe has been detected during this period.

As previously described in Peñuelas *et al.* (2002), bird monitoring was conducted by daily sighting and listening from key points, plus surveys carried out in a 5-10 km circuit within the 100 km² study site. This methodology ensures high accuracy of data (+/- 1 day). The study site is located in a plain valley with an average altitude of 200 m. The landscape is dominated by a mosaic of forests, agricultural fields and gardens with noteworthy human presence.

Climate data

We used temperature and precipitation variables calculated over two different temporal intervals to analyse the hypothetical long and short-term accumulative effects of climatic variation on the spring arrival of migrants. The long-term effects summarise climatic conditions during a complete annual cycle for a given species that is a 12-month interval starting with the predicted departure of the species from their African wintering quarters or with their arrival to the study site. To analyse the short-term effects, we used the two-month period prior to the onset of migration or to the first arrival for each species. Temperature variables for each available meteorological station were calculated as the monthly mean averages for each temporal interval (2 or 12 months), whereas for precipitation, we used total accumulated monthly values for the corresponding interval. Since, the species included in the analysis showed significant idiosyncrasy in their FADs ($F_{4,112} = 274.36$; $P < 0.001$), possibly reflecting different timing of migration, we used four different temporal intervals (Table 5.1) according to the expected departure dates from wintering grounds for each species as gathered from the literature (Moreau, 1961; Cramp, 1985; Cramp, 1988; Fry *et al.*, 1988; Keith *et al.*, 1992). Temperature and precipitation data for the Cardedeu area were collected by P.C. since 1950 at Cardedeu meteorological station, whereas for Africa, temperature and precipitation data were gathered from the Global Historical Climatology Network data files (NCDC, 2003) which provided data on 1990 African meteorological stations belonging to the World Meteorological Organization network from 1950 to 2003.

Unfortunately, at present the available information about wintering sites for the NE Iberian populations of the species included in our analyses is too scarce to select specific stations in Africa to directly test our main hypothesis. This problem led us to use a conservative approach of which we included climatic information covering all potential areas where species may overwinter (Curry-Lindahl, 1981; Cramp, 1985; Cramp, 1988; Fry *et al.*, 1988; Keith *et al.*, 1992). To do this, we first classified all stations south of Sahara into five

Species	AFRICA		CARDEDEU	
	Long-term	Short-term	Long-term	Short-term
Hoopoe	Feb-Jan	Des-Jan	Mar-Feb	Jan-Feb
Barn swallow House martin	Mar-Feb	Jan-Feb	Apr-Mar	Feb-Mar
Nightingale Cuckoo	Apr-Mar	Feb-Mar	May-Apr	Mar-Apr
Common Swift	May-Apr	Mar-Apr	Apr-May	Jun-May

Table 5.1 Selected temporal intervals for temperature and precipitation divided into long-term (12 months) and short-term effects (2 months) for each region.

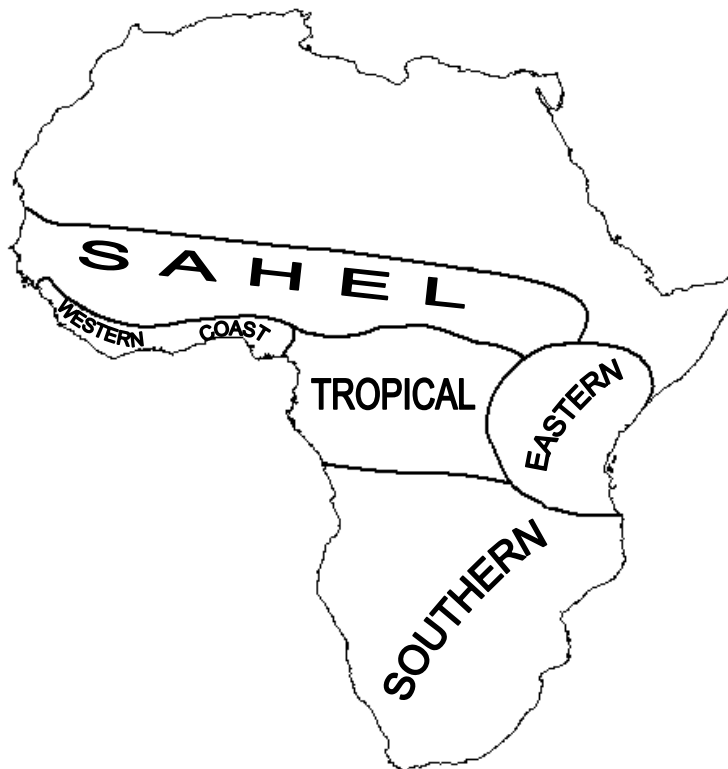


Figure 5.1 Main climatic regions of Africa. By means of combination of World Meteorological Organization stations network we calculated for each one the climatic variables used in analysis.

different regions according to broad climatic patterns prevailing in Africa, (IG-RAS, 1998; Mayaux *et al.*, 2004; Fig. 5.1). Second, for each of these selected regions, we calculated mean values for temperature and precipitation variables

using meteorological stations agreeing with the following criteria: not located in extreme environments (e.g. deserts or high mountains) where overwintering of our focal species does not occur, and covering at least 45 years of data for the period 1951-2003.

Statistical analysis

We tested for temporal trends in FADs of all species and climatic variables from each African climatic region and Cardedeu by means of regression models and judged their significance according to the *F*-test.

We used multiple regression procedures to identify the main climate variables associated with the arrival time of each species. For each species we used a total of 24 variables: long and short-term effects of temperature and precipitation from Cardedeu area (4), and from the five selected African regions (20). When wintering grounds were restricted only to part of the African continent (i.e. nightingale and hoopoe), we only used climatic regions corresponding to such areas as potential predictors of FADs. To further prevent the appearance of spurious correlations in our analyses due to high number of predictors, we ran the regression in two steps. First, we ran univariate analysis for each species and selected only those climatic variable variables with a correlation coefficient having a *P*-value lower than 0.2. Second, we used a forward stepwise multiple regression procedure with the remaining variables and eventually selected a model including only significant factors at $P < 0.05$.

RESULTS

Temporal trends in temperature and precipitation

Temperature trends showed two clearly opposite temporal patterns between regions. For Tropical Africa ($r^2 = 0.305$, $P < 0.001$), Western Coast ($r^2 = 0.455$, $P < 0.001$), Sahel ($r^2 = 0.389$, $P < 0.001$) and Cardedeu ($r^2 = 0.638$, $P < 0.001$), temperature decreased or did not show major changes until mid 1970's and since then it has shown an increasing trend (Fig. 5.2). Eastern ($r^2 = 0.390$, $P < 0.001$) and especially Southern Africa ($r^2 = 0.481$, $P < 0.001$) showed a trend towards lower temperatures in recent decades. On the other hand, precipitation did not show a significant temporal pattern for Southern ($r^2 = 0.030$,

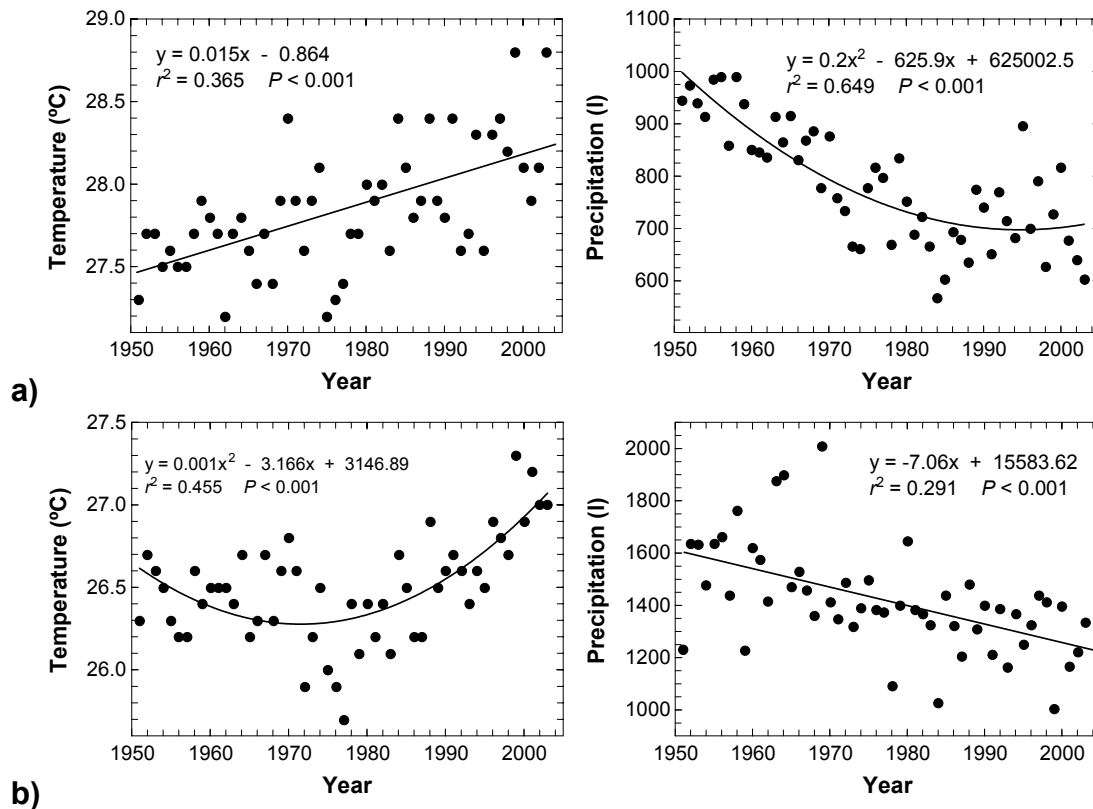


Figure 5.2 Temporal trends in annual mean temperature and total precipitation for the Sahel (a) and the Western Coast (b). Lines represent the best regression models fitted to the data. Equations, regression coefficients (r^2) and P -values are indicated in each case.

$P = 0.215$) and Eastern ($r^2 = 0.013$, $P = 0.416$) Africa or Cardedeu ($r^2 = 0.002$, $P = 0.745$). The Sahel ($r^2 = 0.649$, $P < 0.001$), Western Coast ($r^2 = 0.299$, $P < 0.001$) and Tropical Africa ($r^2 = 0.146$, $P = 0.005$), however, have suffered a dramatic decrease in rainfall at least until the 1990s (Fig. 5.2); this decline only has continued in the last decade for the Western Coast.

Temporal trends in spring arrival

Four species presented significant temporal trends in their FAD in the Cardedeu data set (Fig. 5.3). Barn swallow, cuckoo and nightingale showed a clear trend toward delayed spring arrivals. The nightingale had the highest annual rate of delay with 0.35 days per year (Fig. 5.3). On the other hand, hoopoe also delayed their spring arrivals until mid 1980's, but since then only a slight trend to advancement of arrivals was recorded.

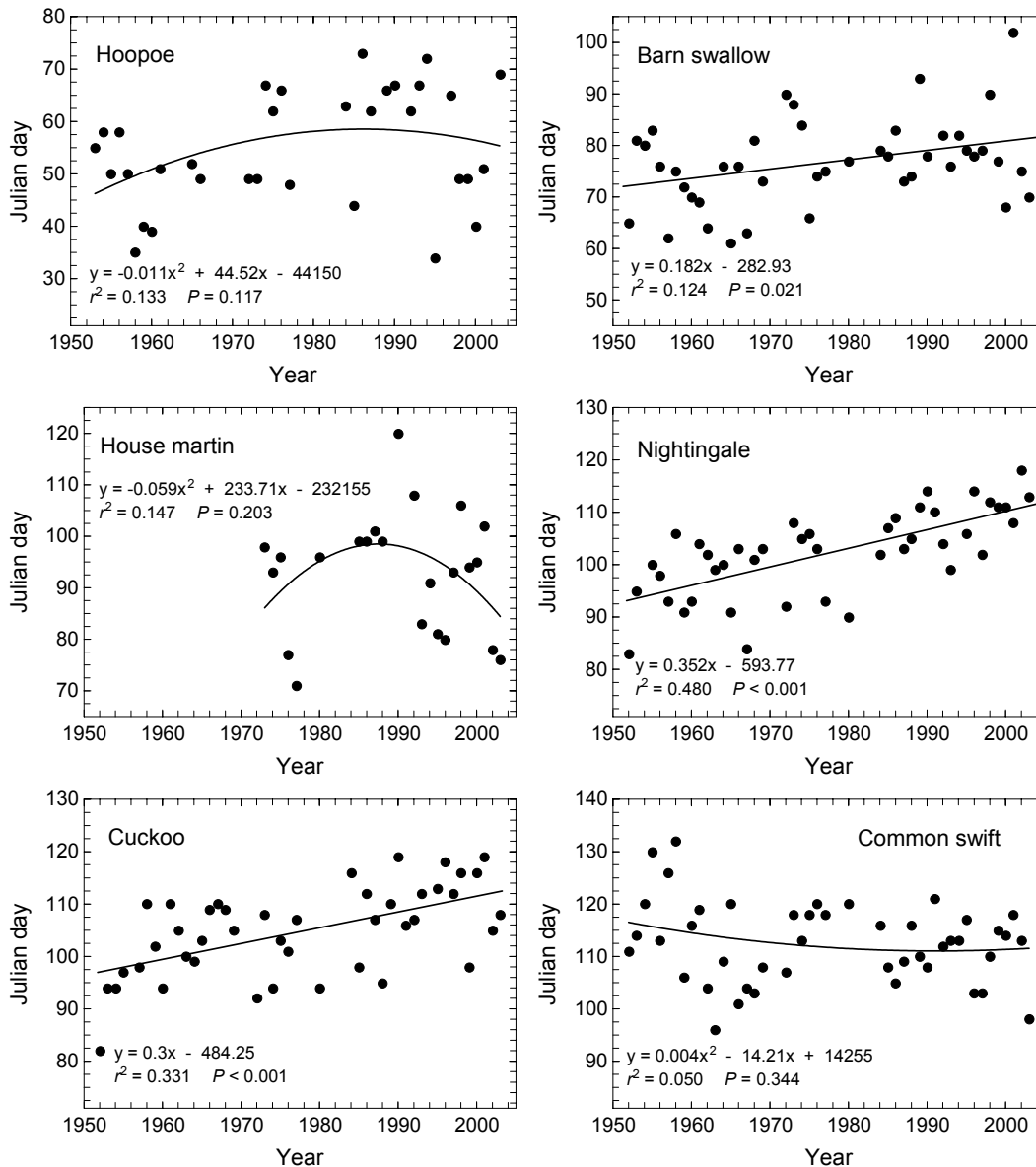


Figure 5.3 Temporal trends in FADs (first sighting or listening) of the species. Lines represent the best regressions models fitted to the data. Equations, regression coefficients (r^2) and P -values are indicated in each case. Correspondence of Julian day on axis Y: 1=1 January.

Climate correlates of spring arrival date

For all species with significant regression models, FAD was only associated with African climate variables and thus Cardedeu climatic variables never were selected (Table 5.2). For the hoopoe, barn swallow and common swift only one variable was retained, whereas there were two for the nightingale and cuckoo. The house martin was the only species without significant correlation with climatic variables.

Species	Climatic variables				Multiple regression				
				r^2	P	r^2	F	d.f.	P
Hoopoe	W	ps	-			0.215	8.47	1,31	0.007
Barn swallow	S	pl	-			0.118	5.49	1,41	0.024
Nightingale	W	tl	+	0.282	<0.001	0.411	13.60	2,39	<0.001
	S	pl	-	0.129	0.005				
Cuckoo	W	ps	-	0.306	<0.001	0.380	12.28	2,40	<0.001
	W	pl	-	0.074	0.035				
Common swift	E	pl	-			0.087	4.09	1,43	0.049

Table 5.2 Selected climatic variables and multiple regression final models for the species. Climatic variables are identified by the two first columns. The first one indicates the climatic region (E = Eastern, W = Western Coast and S = Sahel; see also Fig. 5.1) and the second one the kind variable (t = temperature or p = precipitation) and period (l = long-term or s = short-term). The third column is the sign of their effect. Variables are listed in the order they entered in the final model. Temporal periods begin at 1952 and finish at 2003.

Both precipitation and temperature variables appeared at least once in the models (Table 5.2). FADs appeared mainly associated with long-term climate variables except in the case of the hoopoe and the cuckoo where short-term precipitation accumulation appeared as significant (Table 5.2). Precipitation appeared with a clear dominance over temperature in the final regression models (6 vs 1). The association between FADs and precipitation was negative in all cases, whereas temperature showed positive relationship with FADs of nightingale. In summary, precipitation and temperature affected all species in the same way: when African temperatures were high, spring arrivals in the Mediterranean were delayed, whereas years with substantial precipitation events in Africa were associated with earlier bird arrival.

Geographical climate patterns and species arrival dates

From a geographic point of view, two regions, Sahel and Western Coast were highly dominant in final models (Table 5.2). Precipitation from the Sahel region was included in the models of the barn swallow, nightingale and cuckoo, whereas climate variables from the Western Coast were associated with FADs for the hoopoe (precipitation) and nightingale (temperature). Finally, the common swift model was the only species including a significant climatic variable from the Eastern African region (precipitation, Table 5.2) but with a

weak significance value, thus we should be cautious about the interpretation of this model.

DISCUSSION

We have shown that for migrant species arriving in spring to NE Iberia, climatic variations in sub-Saharan Africa are better predictors than local climate conditions in Europe. No climatic variables measured at the area where those species were first sighted or listened in spring was included in final regression models. Most studies of avian migratory phenology have related bird arrival patterns to the climate conditions in the breeding grounds, in particular temperature (Loxton *et al.*, 1998; Sokolov *et al.*, 1998; Loxton & Sparks, 1999; Sparks & Mason, 2001; Strode, 2003; Tryjanowski *et al.*, 2002). However, in our case the results agree with Cotton (2003) and support the hypothesis that climate variations in wintering quarters are important drivers of spring migration. Our results suggest that description of environmental conditions prevailing in areas used during winter or migration should be included in future studies or reassessed using already published data if we aim at understanding temporal variations in the timing of bird migration.

Potential factors affecting spring arrivals via climatic variation

Long-distance migrants, such as trans-Saharan birds, are obviously unable to gather direct information about the environmental conditions in their European breeding areas. Local environmental conditions in African wintering areas influencing expression of departure (Saino *et al.*, 2004) have been described as important factors in determining the onset of migration from winter quarters. Among these environmental factors, rainfall and temperature are likely to be particularly relevant as they indirectly determine changes in resource availability, which is clearly a key factor for birds (Elgood *et al.*, 1966; Alerstam, 1990; Coppack & Both, 2002; Strode, 2003).

Precipitation has not been assessed in most of the previous studies of timing of migration in birds (but see: Sparks & Carey, 1995; Huin & Sparks, 1998; Huin & Sparks, 2000). Our results indicate that this climate variable is likely to be an useful predictor of bird arrivals. Its control over resource

availability should be especially important in dry regions (e.g. Sahel) or those with a pronounced climatic seasonality (e.g. Western Coast). Rainy years often lead to a greater abundance of resources which may eventually allow species to reach their optimal fuelling conditions and new feathers at an earlier date and bring forward the onset of migration. By contrast, droughts would reduce plant productivity (Nicholson *et al.*, 1990; Gonzalez, 2001; Hulme *et al.*, 2001; Saino *et al.*, 2004) and, as a consequence, insect availability for insectivore bird species. It is important to note that although environmental factors related to climate are likely to strongly influence decisions relating the timing of departure from bird wintering sites, they may also prove important at stopover sites during migration (Ottich & Dierschke, 2003). At present, it is difficult to tell apart these two different kinds of effects. For species wintering in Africa, especially those wintering in northern regions, en route effects are likely to occur after their quick crossing of the Sahara. However, spring captures of many migrants in southern Europe point out towards a minor role of stopover African sites north of Sahara (Pilastro & Spina, 1997; Grattarola *et al.*, 1999), thus stressing the role of factors affecting timing of migration already in the wintering grounds.

We have shown that annual total precipitation has been decreasing and mean temperature has been increasing during last decades in major wintering areas of our focal species (i.e. Sahel and Western Coast; see Fig. 5.2). Furthermore climatic models for Africa seem to predict that these trends will continue in future (Hulme *et al.*, 2001). The positive correlations with temperature and the negative correlations with precipitation detected by our analyses allow us to predict greater delays in arrival in the future. On the other hand, Peñuelas *et al.* (2002) showed an advance of all phenological events in the breeding area, which may lead to a strong mismatching between timing of migration and availability of food resources. This may in turn decrease relative competitive ability of long-distance migrants relatively to residents and short-distance migrants which seem better positioned to adjust to the changes (Sokolov *et al.*, 1998; Tryjanowski *et al.* 2002; Lemoine & Böhning-Gaese, 2003; Storde, 2003).

Climate change also can endanger the habitat itself. The increased risk of desertification faced by most savannah-like habitats in sub-Saharan areas (McCarthy *et al.*, 2001; Nicholson, 2001; Gitay *et al.*, 2002) can transform the wintering grounds and endanger the fauna inhabiting such regions. The Sahara seems to be expanding, pushing the Sahel strip southwards (Gonzalez, 2001; Nicholson, 2001). In these conditions, birds would progressively overwinter more to the south where they would be exposed to a longer spring photoperiod. According to Coppack *et al.* (2003), this new photoperiod may contribute to a delay in migratory activity and thus to a delay in the arrival of migrants to European breeding quarters. This hypothesis partially agrees with the results of the present study of delayed spring arrival dates in Mediterranean areas.

Accumulative effects of climate patterns

Our results reveal the importance of including adequate, ecologically based periods of time when assessing the effects of climate on biological characters. Most previous studies have only analysed the effects of temperature and precipitation few month prior to arrivals (Mason 1995, Loxton *et al.*, 1998; Sokolov *et al.* 1998; Loxton & Sparks, 1999; Sparks & Mason, 2001; Tryjanowski *et al.*, 2002). Our results show that their long-term effects also merit further attention as hypothetical predictors of FADs in birds. The accumulative annual effect of temperature and precipitation may thus be basic to understanding the phenology of Iberian trans-Saharan birds and the mechanisms that determine the spring arrivals in this group.

Contradictory findings in migrant arrival dates within Europe

Only the hoopoe showed a slight trend to an earlier spring arrival in recent years. However, three of the studied species presented a significant trend to delayed arrivals, especially strong in cuckoo and nightingale (see Fig. 5.3). These results contradict the general pattern described by other studies in many central and northern European regions (Sokolov *et al.*, 1998; Loxton & Sparks, 1999; Sparks & Mason, 2001; Tryjanowski *et al.*, 2002; Cotton, 2003; Hüppop & Hüppop, 2003; but see: Mason, 1995; Sparks & Braslavská, 2001). Two main hypotheses may explain these apparent contradictory results in FADs

temporal trends. The first is that different European populations overwinter in different African regions under contrasting climatic constraints leading to geographic variations in the onset of migration. A second hypothesis would imply that differences in FADs between European populations occur after individuals cross the Sahara. If advanced spring conditions are to be found in the Mediterranean (Osborne *et al.*, 2000; Peñuelas *et al.*, 2002; Stefanescu *et al.*, 2003), birds may then accelerate migration rates (i.e. reduce stopover times) and arrive earlier to central and northern European breeding areas (Huin & Sparks, 1998; Coppack & Both, 2002). Furthermore, global warming probably will improve also the weather conditions, especially in early spring, in Europe ensuring better travel conditions (Sokolov *et al.*, 1998; Tryjanowski *et al.*, 2002). At present, the available data does not allow to unambiguously distinguish between the two hypotheses. More detailed information on species wintering grounds would be necessary to test the first hypothesis. On other hand, data from Huin & Sparks (1998) on the barn swallow showing that spring arrival times in England were associated to climatic variations in Spain and French Brittany gives some support to the hypothesis that differences in FADs between southern and northern Europe could originate after birds crossing of the Sahara.

Our results concerning the factors that affect the arrival times of trans-Saharan migrants indicate that the effects of climate change might be more complex than previously thought and that they might interact with species ecology, for instance by inducing opposite ecological pressures during a species life cycle (Harrington *et al.*, 1999; Inouye *et al.* 2000; Coppack & Both, 2002). We need to advance our understanding of these complex ecological interactions before we can draw conclusions about the ultimate factors affecting population biology in a context of climate change.

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RESUM

Els cicles vitals de plantes i animals estan canviant arreu del món en el sentit que prediuen les hipòtesis sobre els efectes del canvi climàtic. Fins ara, la cerca dels mecanismes ecològics responsables dels canvis observats en la fenologia dels ocells s'ha basat en l'anàlisi dels patrons climàtics a les àrees de cria de les espècies. Caldria esperar, però, que l'arribada primaveral dels migrants de llarga distància (com és el cas del ocells trans-saharians) estès més determinada per les condicions climàtiques a les àrees d'hivernada donada la influència que ha de tenir sobre el moment de sortida i durant la progressió inicial. Es va testar aquesta hipòtesi analitzant la data de primera arribada (FAD) de sis migrants trans-saharians (puput, oreneta vulgar, oreneta cuablanca, cucut, rossinyol i falciot) a una localitat catalana durant els darrers 50 anys. Mitjançant anàlisis de regressió múltiple aquestes FADs es van relacionar amb els patrons de temperatures i pluges de les cinc grans regions climàtiques africanes al sud del Sàhara on se sap que aquestes espècies hivernen, així com del lloc on es va fer el seguiment fenològic. Es van obtenir models significatius per a cinc espècies, que van explicar entre el 9 y 41 % de la variabilitat en les FADs. La interpretació dels models suggereix: 1) El clima a les àrees d'hivernada, especialment la pluja, té una influència més forta sobre les FADs que aquell de les potencials àrees de cria europees. 2) Els efectes acumulatius del clima abans de l'inici de la migració semblen tenir una considerable importància, doncs aquelles variables que servien per resumir els patrons climàtics durant els 12 mesos abans de l'inici de la migració es van seleccionar als models finals. 3) L'efecte de temperatura i pluja sobre l'inici de la migració probablement és de forma indirecta a través de la disponibilitat de recursos necessaris per a constituir les reserves energètiques i acabar la muda. Els resultats obtinguts respecte als factors que afecten el moment d'arribada dels migrants trans-saharians indiquen que els efectes del canvi climàtic són més complexes del que prèviament s'ha suggerit, i que aquests efectes poden tenir un impacte en sentit oposat en l'ecologia de les espècies durant el seu cicle vital.