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

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

Programa de doctorat: Zoologia
Bienni 2002-2004

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Barcelona, Juliol 2006



Chapter 6

Species-specific effects of ecological conditions and climate in wintering and pass areas on spring arrivals of some trans-Saharan birds

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Oecologia (submitted)

ABSTRACT

Previous bird studies have used remote sensing data to assess the effects of winter ecological conditions in Africa on some biological parameters recorded during the following breeding season in Europe. According to these studies, we expected that high winter vegetation productivity and thus resource availability should enhance spring migration of trans-Saharan birds, advancing their arrival to the European breeding areas. Variations in the first arrival date to the Iberian Peninsula between 1982 and 2001 of five species (white stork, cuckoo, common swift, barn swallow and nightingale) were examined in relation to several potential explanatory variables: ecological conditions in their African wintering grounds and pass areas, as reflected by the normalized difference vegetation index (NDVI), together to ambient temperature in their pass areas. Ecological conditions in wintering areas were important for the white stork, cuckoo and barn swallow phenology and they were able to account for between 35-56% of the variability in arrival dates in regression models. However, NDVI in the pass areas did not show any effect in all species. Temperature was important in later species (i.e., cuckoo, common swift and nightingale) although in all cases this effect should not give much importance due to the poor explanatory capacity (less than 10%) of those regression models. The nexus between African NDVI and arrival phenology can be hypothesized through increases in wintering survival rates and/or faster acquisition of pre-migratory body condition and progression through sub-Saharan areas. Therefore, the influence of ecological conditions on the wintering grounds should be taken into account when anyone wants to study long-term temporal changes in spring phenology of migratory birds in Europe.

INTRODUCTION

Trans-Saharan birds spend part of their life cycle south of the Sahara desert (Moreau, 1972; Curry-Lindahl, 1981). Despite of the spent time in these areas, winter ecology of these species is still rather poorly understood. This problem is accentuated for most of the smaller-bodied birds because basic information about their wintering distribution is still scarce or inexistent (Walther & Rahbek, 2002; Walther *et al.*, 2004). This gap in the knowledge of species biology is of interest because some species follow different ecological strategies during their breeding versus wintering seasons (Jones, 1995; Marra & Holberton, 1998; Baumann, 2000; Salewski *et al.*, 2002a; Salewski & Jones, 2006).

Environmental conditions during one part of the life cycle might not only affect that moment and may have also significant consequences in subsequent parts of the life cycle (Hogstad *et al.*, 2003; Norris *et al.*, 2004), in some cases even much later (Thomson & Ollason, 2001). In the case of trans-Saharan migrants, many studies have demonstrated that wintering conditions have detectable effects on interannual variability in their population numbers (e.g. Svensson, 1985). Changes in resource availability, weather conditions, interspecific competition, predation and/or anthropogenic habitat destruction on their wintering and migratory African areas affect directly survival of individuals (Winstanley *et al.*, 1974; Mullié *et al.*, 1995; Fasola *et al.*, 2000; van den Brink *et al.*, 2000; Sillett & Holmes, 2002; Salewski *et al.*, 2003; Bijlsma & van den Brink, 2005; Schaub *et al.*, 2005).

Nowadays, new analytical techniques offer possibilities to indirectly explore winter ecology of migratory birds (Szép & Møller, 2004; Walther *et al.*, 2004; Pettorelli *et al.*, 2005). Satellites of the U. S. National Oceanic and Atmosphere Administration (NOAA) have been measuring the daily reflected radiation of the earth surface since 1981. Based on this collection of satellite data, anyone can obtain a value of the amount and vigour of vegetation on any land surface of the globe: the Normalized Difference Vegetation Index (NDVI), which relates reflected wave-lengths to the level of photosynthetic activity (Nicholson *et al.*, 1998). Since most of trans-Saharan migrants are

insectivorous and insect abundance in turn depends on plant productivity, NDVI is likely to reflect the abundance of insect supplies (Baumann, 1999; Sanz *et al.*, 2003; Szép *et al.*, 2006).

Recently, some studies have shown that winter NDVI in Africa affects spring arrivals, sexual selection and reproductive success in some Italian and Danish populations of barn swallows (*Hirundo rustica*; Saino *et al.*, 2004a, b; Møller, 2004; Møller & Merilä, 2004; Møller & Szép, 2005). Saino *et al.* (2004a) showed that unfavourable conditions in the sub-Saharan winter quarters of barn swallows breeding in Italy resulted in delayed arrival only of individuals aged two or more years. However, Møller & Merilä (2004) showed that unfavourable conditions in Northern Africa resulted in earlier arrival dates of a population of barn swallows breeding in Denmark. Their conclusions seem to be contradictory, but two separate areas in Africa were used to study the relationship between environmental conditions in Africa and the arrival to the breeding colonies in Europe. Because these previous studies are focussed only on a single species (barn swallow) and on two concrete European populations, their conclusions could not be applicable to the rest of the trans-Saharan migrants and/or populations, which include a great idiosyncrasy of ecological strategies and migratory periods and routes.

This study aims to solve this question using five heterogeneous species of trans-Saharan birds belonging to several monitored populations from Spain. We explored whether the interannual variability in their arrival dates to the breeding grounds was related to variations in environmental conditions during their winter stay in the sub-Saharan Africa, during the previous month to their departure from there and during the migratory period over their pass areas. We expect that years with high vegetation productivity (i.e., high values of NDVI) in Africa may advance spring arrivals since best ecological conditions would favour survival and faster acquisition of pre-migratory body condition and progression through sub-Saharan areas thanks to high food availability.

MATERIAL AND METHODS

Bird phenological data

Spring migratory phenology of five trans-Saharan migrant bird species was obtained for the period of 1982 to 2000 from the phenological database of the Spanish *Intituto Nacional de Meteorología*. This database results from a phenological network constituted by volunteer observers widespread over Spain (see for details Gordo & Sanz, 2006). Observers reported the first sighted individual of the white stork *Ciconia ciconia*, common swift *Apus apus* and barn swallow *Hirundo rustica*, and the first singing male of the cuckoo *Cuculus canorus* and the nightingale *Luscinia megarhynchos* from their home towns and cities.

Records were averaged per year to obtain a single arrival date value for Spain as a whole for each species. One potential difficulty of merging so much heterogeneous data in a single time-series for a large area is the strong phenological differences in the migratory calendar among populations. These phenological differences can imply different ecological pressures acting over each population which can be difficult to assess if we joint all data in a single variable. Species with very spread arrival dates over the calendar due to the broad range of ecological conditions among their breeding Spanish grounds could benefit from a differentiation between early and late populations since better adjusted explanatory variables can be attributed. The cuckoo, common swift and barn swallow were species with a wide migratory period. In them, the distinction between early and late populations was easy thanks to the well-established geographical patterns of arrivals in these three species within the Iberian Peninsula (own unpublished data). In fact, populations from southern Spain, especially from south-western, are much earlier than those from the rest of the country. However, differences in timing of arrivals among white stork and nightingale populations are not so extreme. Therefore, in these two species, the initial purpose of a single time-series representative for the whole Spain was maintained. We finally obtained seven time-series of arrival dates (two for the cuckoo, common swift, and barn swallow, and one for the white stork and nightingale).

Annual mean phenological dates can also be seriously biased due simply to the different localities constituting the available sample each year (Häkkinen *et al.*, 1995; Linkosalo *et al.*, 1996; Schaber & Badeck, 2002). Spatial and topographical variables for each study site were used to prevent spatial gradients and to account for the observed variability in arrival dates derived from the broad latitudinal, longitudinal and altitudinal range of study localities (Legendre *et al.*, 1993), which could mask the hypothetical interannual variability in arrival dates induced by ecological conditions in wintering and pass areas. Potential spatial gradients in data were removed by means of trend surface analysis, as proposed by Legendre & Legendre (1998). Both spatial and topographical cubic polynomials were included in a multiple regression model with a forward stepwise selection procedure for each species. In the case of cuckoo, common swift and barn swallow this analysis was applied separately to early and late datasets. Residuals from the seven performed trend surface analyses were averaged per year and the seven obtained time-series used hereinafter in all analyses as dependent variables.

Selection of explanatory variables: a hypothetical framework for migratory phenology

Most of previous studies have assessed the effect of environmental changes on temporal variability in migratory phenology through climate (especially temperatures). Climate can act over migratory birds in two ways (see Fig. 6.1): directly by means of weather conditions during their migration (e.g. Ahola *et al.*, 2004) and indirectly through ecological conditions in areas previously used to the arrival site during both wintering and migration (e.g. Saino *et al.*, 2004b). These indirect effects can be difficult to detect by means of climatic variables because in many cases we do not know the key meteorological variable and/or the time on the annual calendar that determine relevant ecological conditions for certain species life cycle (Møller & Merilä, 2004; Stenseth & Mysterud, 2005). However, these indirect effects can be assessed by means of NDVI measurements because they quantify ecological conditions and offer a fully comparable value among regions and years (Pettorelli *et al.*, 2005). Moreover, changes in NDVI also assess other important

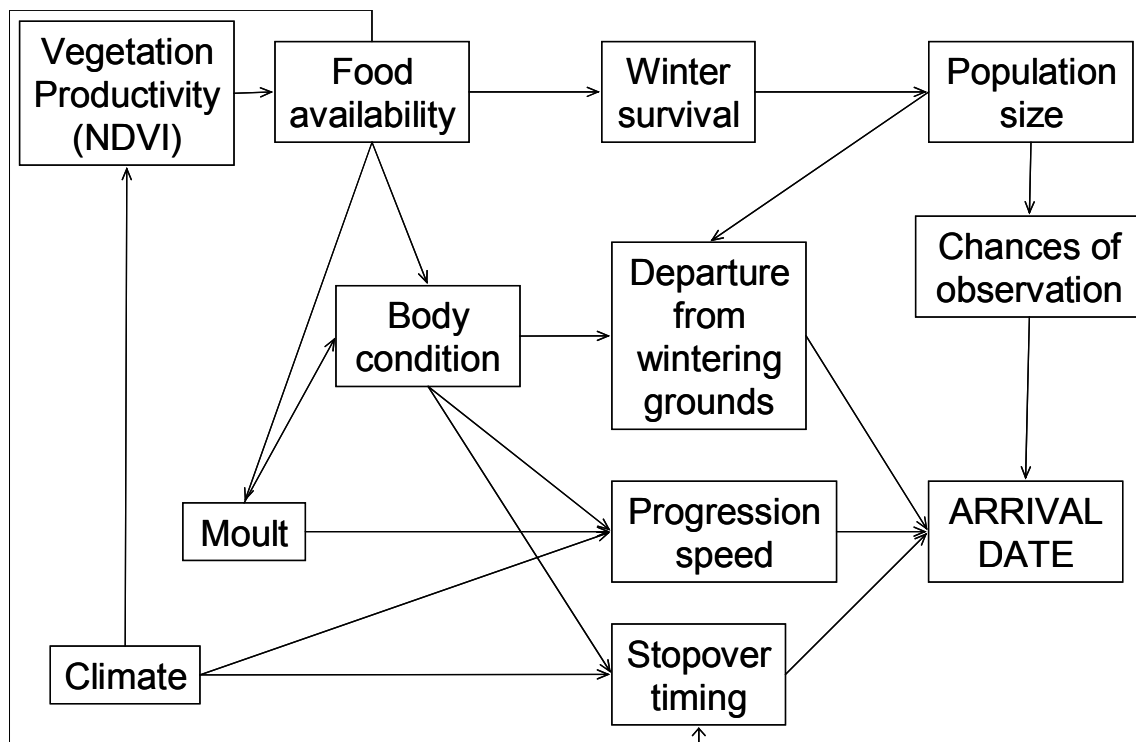


Figure 6.1 Diagram for the hypothetical framework purposed in this study about potential environmental variables that can influence arrival date phenology of a population. See text for more details.

sources of long-term variations of ecological conditions such as human transformations of ecosystems otherwise not accounted by climate fluctuations (Herrmann *et al.*, 2005).

NDVI is calculated as the normalized difference in reflectance between red (0.55–0.68 μm) and infrared (0.73–1.1 μm) channels of the Advanced Very High Resolution Radiometer (AVHRR) sensor of NOAA polar orbiting satellites. Ultimately the NDVI is determined by the degree of absorption by chlorophyll in red wavelengths, which is proportional to leaf chlorophyll density, and by reflectance of near infrared radiation, which is proportional to green leaf density (Tucker *et al.*, 1985). Therefore, NDVI correlates well with such variables as green leaf biomass, leaf area index, total dry matter accumulation and annual net primary productivity (Nicholson *et al.*, 1990). NDVI data were provided by Clark Labs as world monthly images at spatial resolution of 0.1 degree in scale values ranging from 0 to 255 covering the period from August of 1981 to

December of 2000, with exception of the period from September to December of 1994.

We gathered NDVI data for three regions: western Africa, north-western Morocco and south-western Iberia (see Fig. 6.2). Western Africa was considered as wintering area, whereas north-western Morocco and south-western Iberia as pass areas. We focussed only in western Africa because is the wintering area for Iberian populations according to the literature (Cramp & Simmons, 1977; Curry-Lindahl, 1981; Cramp, 1985; Urban *et al.*, 1986; Cramp, 1988; Fry *et al.*, 1988; Keith *et al.*, 1992) and ringing recoveries (see Fig. 6.2). Furthermore, previous studies have demonstrated yet the importance of climate from this area for phenology of some of the studied species (Dallinga & Schoenmakers, 1987; Gordo *et al.*, 2005; Gordo & Sanz, 2006). In the case of Iberia, we focussed only in the south-western quadrant because the main route of colonization of the Iberian Peninsula in all species follows a south-western to north-eastern axis (own unpublished data).

Selected areas included a great variety of habitats. Some of them are not used by the studied species to overwinter (e.g. evergreen forests; Svensson, 1985; Salewski & Jones, 2006) or are quickly crossed during migration (e.g. deserts; Moreau, 1961; Biebach *et al.*, 2000). Hence, we expect no influence of their ecological conditions on migratory phenology of birds. The USGS Global Land Use/Land Cover (http://edcdaac.usgs.gov/glcc/globe_int.html) created from 1992-93 AVHRR-NDVI at 0.1 degree of resolution was used to select only those probable wintering and pass habitat types. IDRISI32 software for Geographic Information System (Clark Labs, 2001) was employed for data managing. Excluded habitats in Western African (barren or sparsely vegetated, evergreen broadleaf forest, wooded wetland, and water bodies) were 33.82% of grid cells, while in north-western Morocco (barren or sparsely vegetated, evergreen broadleaf and needleleaf forests, and water bodies) were up to 42.27% (see Fig. 6.2).

A long- and short-term effect of the ecological conditions in wintering areas can be hypothesized (Fig. 6.1). Conditions along all the wintering stay should affect individuals' survival, which in turn affect the population size

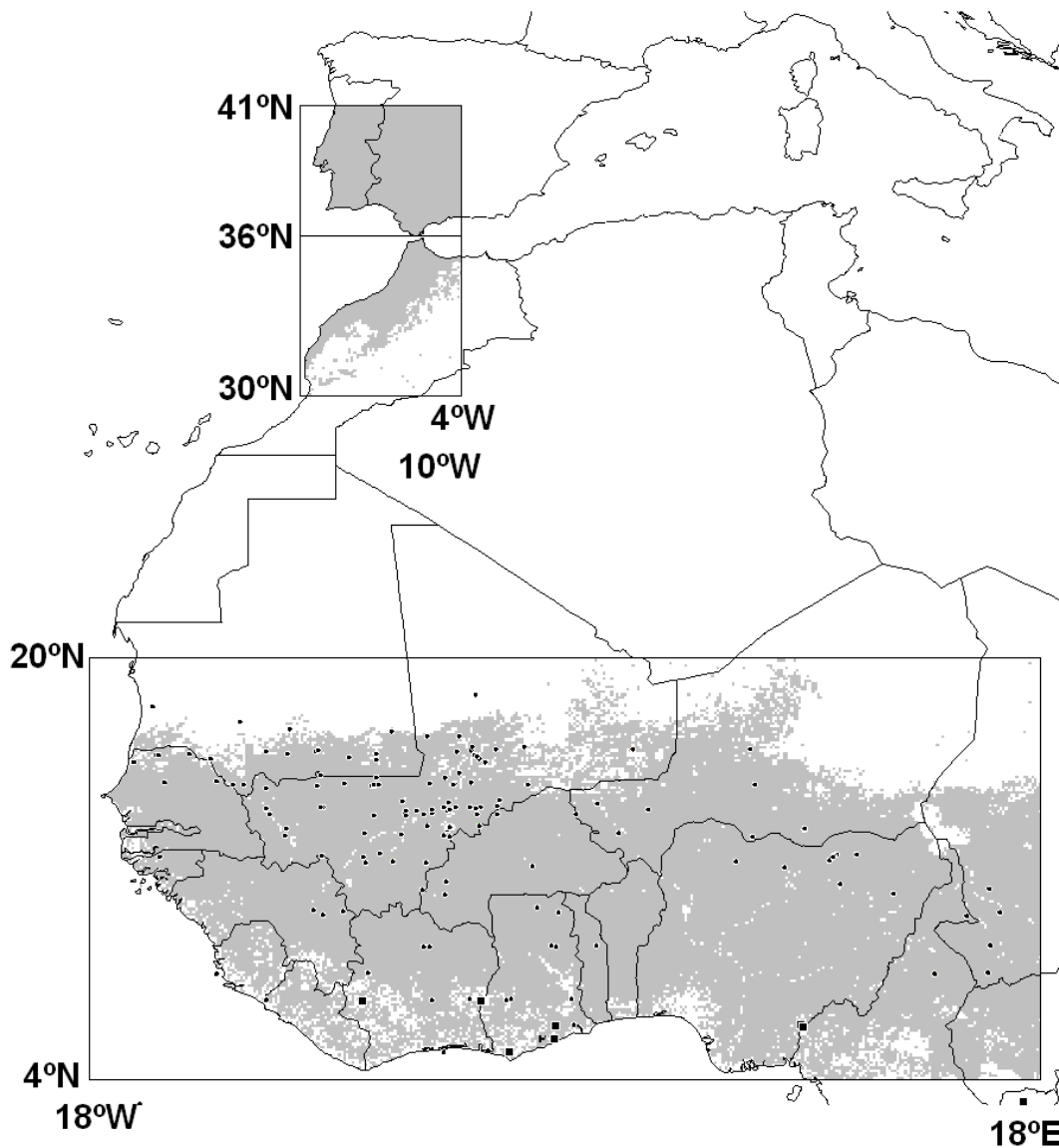


Figure 6.2 Map showing selected grid cells for calculation of NDVI explanatory variables. Exact coordinates for all areas are indicated. Black dots are recoveries of white storks and black squares of barn swallows.

returning to the breeding grounds during the next breeding season (Winstanley *et al.*, 1974; Den Held, 1981; Cavé, 1983; Szép, 1995; Foppen *et al.*, 1999; Boano *et al.*, 2004). This may affect the observational chances (Tryjanowski & Sparks, 2001; Tryjanowski *et al.*, 2005) as well as the competitiveness for earlier arrival among males to get the best breeding territories (Forstmeier, 2002; Møller, 2004) and thus the recorded arrival date to the breeding grounds. This hypothesis was evaluated including vegetation productivity (NDVI) during

those months between arrival and departure to the wintering grounds (Table 6.1).

Ecological conditions in wintering grounds can also affect individuals in a short-term through body condition in the preceding days or weeks to departures from there (see Fig 1; Loske, 1990; Salewski *et al.*, 2002b; Ottoson *et al.*, 2005). During this critical time interval migrants should accumulate necessary fat reserves to face up geographical barriers during its northwards migration as the Sahara desert and the Mediterranean Sea (Moreau 1972). It is assumed that the onset of migration is primarily controlled by endogenous rhythms (Berthold, 1996), but some plasticity in the migratory program exists to better adapt to the specific environmental conditions found by individuals (Biebach, 1985; Biebach *et al.*, 1986). On the other hand, body condition can also affect migration progress through flight performance (Lind *et al.*, 1999; Kullberg *et al.*, 2000) and stopover decisions (Biebach, 1985; Yosef *et al.*, 2005). All these potential effects were evaluated including vegetation productivity during the previous month or months to departure from wintering grounds (Table 6.1).

Pass areas play an important role both from an ecological and from a weather point of view. Ecological conditions can affect phenology throughout above mentioned body condition loop, although in this case with special regard on stopovers (Fig. 6.1). On the other hand, favourable weather conditions for migration can enhance enormously the speed of progression (Richardson, 1978, 1990; Kaňuščák *et al.*, 2004; Ahola *et al.*, 2004; Both *et al.*, 2005) avoiding forced or too prolonged stopovers. In order to evaluate the potential effects of weather on progression of spring migration, we also included monthly temperatures on pass areas (i.e. north-western Morocco and south-western Iberia). For north-western Morocco we gathered monthly data from the Global Historical Climatology Network (Peterson & Vose, 1997) for several observatories located in the same area. In the case of south-western Iberia, data was gathered for Spanish observatories located there from the Spanish *Intituto Nacional de Meteorología* archives. Temperature records for each region were averaged by months to obtain a single Moroccan and Spanish time series for the period 1982-2001.

Statistical analyses

We associated phenological time-series to a set of 6 explanatory variables: NDVI during wintering stay and at departure time in western Africa, NDVI and temperatures in north-western Morocco and NDVI and temperatures in south-western Iberia. Selected periods for each variable were adjusted to the phenology of each species (Table 6.1). In time-series for early populations of the cuckoo, common swift and barn swallow, variables for south-western Spain were not included because this is the breeding area of those populations. Multimodel inference within an information-theoretic framework was employed to determine the relative importance of each explanatory variable and for parameter estimation over arrival dates. All possible regression models (63 or 15, when 6 or 4 explanatory variables were used, respectively) were constructed and ranked according to the Akaike's information criterion (AIC) obtained with the GLZ module of STATISTICA software (StatSoft, 2001). AIC is a function of a measure of fit (maximum likelihood) and the number of parameters in the model. If more explanatory variables are used, the model fits better, but the penalty for extra variables is higher as well. The AIC provides a quantitative measure of the relative support for each competing hypothesis, i.e. each model, in a model selection framework. Since the number of observations was lesser than 40 times the number of explanatory variables a correction bias term was added to AIC values to obtain a second order criterion: AICc (Anderson *et al.*, 2000). Akaike weights for each model were calculated from AICc according to the formulation purposed by Anderson *et al.* (2000). These weights can be interpreted as approximate probabilities that a certain model is the best model in the set of models considered. The relative importance of each predictor variable was estimated by summing Akaike weights over all the models in which the predictor appears. Parameters for each explanatory variable were estimated on basis of the entire set of models using a weighted average. Model-averaged estimation has better precision and reduced bias compared to the estimation from only the best model (Anderson *et al.*, 2000). This approximation is especially recommended when no single model is overwhelming supported by data, i.e. when AIC values are nearly equal

Species Group	White Stork		Cuckoo		Swift		Swallow		Nightingale
	early	late	early	late	early	late	early	late	
NDVI during wintering	Sep-Dec	Oct-Feb	Oct-Jan	Oct-Feb	Oct-Jan	Oct-Mar	Oct-Jan	Oct-Feb	Oct-Feb
NDVI at departure time	Dec-Jan	Feb-Mar	Feb	Feb-Mar	Jan-Feb	Mar-Apr	Jan-Feb	Feb-Mar	Mar
NDVI in NW Morocco	Jan-Feb	Mar-Apr	Mar	Mar-Apr	Feb-Mar	Apr-Mai	Feb-Mar	Mar-Apr	Apr
Temp in NW Morocco	Jan-Feb	Mar-Apr	Mar	Mar-Apr	Feb-Mar	Apr-Mai	Feb-Mar	Mar-Apr	Apr
NDVI in SW Spain	Jan-Feb	Mar-Apr		Mar-Apr		Apr-Mai		Mar-Apr	Apr
Temp in SW Spain	Jan-Feb	Mar-Apr		Mar-Apr		Apr-Mai		Mar-Apr	Apr

Table 6.1 Range of months for which monthly NDVI and temperature values were averaged.

(Johnson & Omland, 2004). Parameters for all possible regression models were calculated with the GRM module of STATISTICA software (StatSoft, 2001). To have an idea of the proportion of variance accounted for by models a weighted average of the adjusted R^2 was also calculated.

RESULTS

There were not an explanatory variable that influenced clearly arrival dates in all cases (Table 6.2). Vegetation productivity in wintering area had the highest relative influence in the white stork, early cuckoo and late barn swallow. The early cuckoo and the late barn swallow were influenced by NDVI values during all the wintering stay, while the white stork was influenced mainly by NDVI at departure time. However, vegetation productivity both in Morocco and Spain were the variables with the smallest weights in all species. Temperature in north-western Morocco appeared in the overwhelming majority of the best ranked models of the early barn swallow, while temperature in south-western Spain showed a noteworthy importance in those with arrival dates in April, i.e. the late cuckoo, late swift and nightingale. In the case of the late cuckoo, the weight of NDVI at departure time from wintering grounds was also notable.

Parameters estimates from model averaging (Table 6.3) showed an overwhelming dominance of negative signs both in vegetation

Species	NDVI during wintering		NDVI at departure time		NDVI in NW Morocco		Temperature in NW Morocco		NDVI in SW Spain		Temperature in SW Spain	
	b	se	b	se	b	se	b	se	b	se	b	se
White Stork	0.443		0.675		0.243		0.337		0.354		0.218	
Cuckoo-early	0.981		0.220		0.210		0.333		-		-	
Cuckoo-late	0.408		0.543		0.237		0.257		0.272		0.665	
Common Swift-early	0.436		0.391		0.289		0.419		-		-	
Common Swift-late	0.282		0.302		0.280		0.250		0.231		0.736	
Barn Swallow-early	0.305		0.298		0.230		0.965		-		-	
Barn Swallow-late	0.779		0.371		0.198		0.381		0.195		0.354	
Nightingale	0.262		0.230		0.331		0.465		0.264		0.695	

Table 6.2 Relative importance of explanatory variables. Showed values are the sum of Akaike weights of explanatory variables over all models in which they appeared. Higher values mean that the variable appeared in the best ranked models. Early populations of the cuckoo, common swift and barn swallow did not included explanatory variables from south-western Spain.

Species	NDVI during wintering		NDVI at departure time		NDVI in NW Morocco		Temperature in NW Morocco		NDVI in SW Spain		Temperature in SW Spain		Adj R ²
	b	se	b	se	b	se	b	se	b	se	b	se	
White Stork	-0.546	0.345	-1.037	0.452	-0.022	0.065	-0.893	0.788	-0.134	0.115	0.218	0.457	0.352
Cuckoo-early	-1.142	0.287	-0.048	0.141	0.007	0.026	-0.341	0.324	-	-	-	-	0.564
Cuckoo-late	0.164	0.140	-0.409	0.218	-0.015	0.030	-0.152	0.221	0.041	0.048	-0.746	0.364	0.092
Common Swift-early	-0.196	0.200	0.175	0.213	0.005	0.057	-0.745	0.803	-	-	-	-	-0.038
Common Swift-late	-0.044	0.059	-0.065	0.076	-0.026	0.034	0.095	0.241	-0.003	0.032	-0.770	0.380	0.100
Barn Swallow-early	-0.098	0.119	-0.112	0.149	-0.016	0.033	-3.406	1.108	-	-	-	-	0.564
Barn Swallow-late	-0.602	0.210	-0.229	0.161	-0.007	0.026	-0.469	0.358	0.007	0.038	-0.294	0.223	0.421
Nightingale	-0.036	0.052	-0.016	0.054	-0.036	0.037	0.482	0.333	-0.021	0.036	-0.611	0.297	0.063

Table 6.3 Estimates of regression models parameters. Values for the slope (b), standard error (se) and explanatory capacity (Adj R²) were calculated by model averaging based on Akaike weights.

productivity (24 out 29; binomial test $P < 0.001$) and temperature (10 out 13; binomial test $P < 0.001$) variables. Therefore, elevated vegetation productivity in wintering areas and higher temperature in pass area were associated to early arrivals of trans-Saharan birds to their Spanish breeding grounds. The explanatory capacity of the models was variable according to the species. The white stork, early cuckoo and barn swallow (both early and late populations) showed a model-averaged adjusted R^2 notable. In the rest of cases, the explanatory capacity of regression models was poor which diminishes the importance of above mentioned results.

DISCUSSION

The influence of environmental conditions in the wintering area on the following parts of the individuals' life cycle is a classic objective still waiting to be tested in most of the trans-Saharan birds (Salewski & Jones, 2006). Only recently some investigators have used the available time series from satellite measurements to compare them with series of biological parameters. Even fewer studies have used NDVI in wintering quarters (Møller, 2004; Saino *et al.*, 2004a,b; Szép & Møller, 2004; Møller & Szép, 2005; Szép *et al.*, 2006), in spite of its undoubted usefulness to assess ecological conditions during this period of the life cycle of birds (Pettorelli *et al.*, 2005). To our knowledge, this is the first study to have tested the potential effect of wintering and during migration conditions, measured by the NDVI, on a large number of bird populations belonging to a broad range of conditions for several heterogeneous species. Our results show a variable effect of vegetation productivity according to species or even populations. This idiosyncrasy could be expected among species because they show absolutely different ecological requirements or between populations because they are submitted to different intrannual ecological scenarios as result of their different migratory phenology. This heterogeneity in the effects of NDVI over spring phenology suggests caution when particular results from a single species and/or population of certain species are fairly generalized (e.g. Saino *et al.*, 2004b), although our results for the late barn swallow are fully in agreement with those of Saino *et al.* (2004b).

Most of the previous studies that had tested the influence of the environmental conditions in the wintering areas on trans-Saharan migrants used meteorological variables, like precipitation (Winstanley *et al.*, 1974; Svensson, 1985; Kanyamibwa *et al.*, 1990; Peach *et al.*, 1991; Marchant, 1992; Kanyamibwa *et al.*, 1993; Møller, 1994; Barbraud *et al.*, 1999; van den Brink *et al.*, 2000; Gordo & Sanz, 2006) or temperature (Kaňuščák *et al.*, 2004; Gordo *et al.*, 2005; Chernetsov & Huettmann, 2005; Rodríguez-Teijeiro *et al.*, 2005) since these variables are the only available prior to 1980s. Their results (especially those from studies using precipitation in the Sahel) agree fully with our results. In arid regions, like the Sahel, water is the key factor to determine plant productivity and thus resource availability (Eklundh & Olsson, 2003; Herrmann *et al.*, 2005). NDVI is a well-fitted measure for the intra- and inter-annual changes in primary production as result of seasonality and annual trends in rainfalls (Nicholson *et al.*, 1990). From a long-term point of view, the Sahel is recovering slowly from a severe drought since mid-1980 (Hulme *et al.*, 2001; Nicholson, 2001). This recent increase in the amount of precipitation is closely related to an increase in NDVI (Eklundh & Olsson, 2003; Herrmann *et al.*, 2005). In this sense, improved ecological conditions in winter quarters during recent years may be partially responsible for the observed advancement in spring arrivals of some species (Gordo & Sanz, 2006; Jónzen *et al.*, 2006). Therefore, not only the increase in European temperatures would be a potential factor influencing the advancement of phenology in migrants birds, as many studies pointed out (Crick, 2004), but the improvement in precipitations in Western Africa should be also taken into account, at least for some long-distance migratory birds species and/or populations.

In our hypothetical framework (see Fig. 6.1), there are two non-exclusive paths to explain how NDVI in African wintering quarters is affecting individuals to induce changes in their migratory phenology. On the one hand, those years with better ecological conditions, individuals can enhance its body condition and moult before the beginning of pre-nuptial migration. This will affect in turn those variables that affect directly the arrival date, i.e. departure time, speed of migration and number and duration of stopovers. On the other hand, improved

ecological conditions during wintering would increase survival, and resulting larger populations would increase chances for the observation of early individuals arriving on their breeding grounds (Tryjanowski & Sparks, 2001). Furthermore, larger populations in wintering areas would increase selective pressures for earlier arrivals to breeding grounds because there would be greater competition for good territories between males (Forstmeier, 2002; Møller, 2004). In our study, two cases agree with the second path, whereas only one with the first one. This could mean strong peculiarities among species, although our species sample is too small to offer more thorough conclusions.

Interestingly, the effects of ecological conditions in pass areas over spring phenology were near to negligible (see Table 6.2). This apparent non-effect of the ecological conditions in pass areas suggests, at least in Spanish populations, a direct journey from wintering grounds without refuelling in northern Africa (Moreau, 1961; Pilastro & Spina, 1998). However, temperatures from pass areas were the most important explanatory variable in four cases. This suggests that the arrival date would be more depending on weather conditions en route (Ahola *et al.*, 2004; Both *et al.*, 2005). Better weather conditions would allow progressing quickly to those species. However, models that included temperature showed lesser explanatory capacities (expecting the early barn swallow) than those that included NDVI, stressing that variables about ecological conditions are likely better predictors than climatic variables.

Our study confirms that present performance is affected by the past life history of individuals (Marra *et al.*, 1998; Sillett & Holmes, 2002; Hogstad *et al.*, 2003; Norris *et al.*, 2004). In our case, inter-annual fluctuations in spring arrivals of migratory birds are influenced by plant productivity, and thus food availability, several months before in an area at thousand kilometres from where individuals breed. Therefore, we should consider the entire life cycle of bird species as a continuum which requires more integrative studies linking all parts of the cycle. More efforts are needed to investigate all aspects of the wintering ecology of trans-Saharan migrants in order to understand temporal population changes recorded in Europe.

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RESUM

Efectes variables segons espècies de les condicions ecològiques i el clima en les àrees d'hivernada i pas en les dates d'arribada d'algunes aus trans-Saharianes

Alguns estudis previs han emprat dades obtingudes per mitjà de satèl·lit per avaluar l'efecte de les condicions ecològiques durant el període hivernal a

l'Àfrica sobre paràmetres biològics mesurats durant el següent període reproductor a Europa. Segons aquests estudis, caldria esperar que la producció vegetal hivernal i, per tant, la disponibilitat de recursos, hauria d'afavorir la migració primaveral de les aus trans-saharianes avançant la seva arribada a les àrees de cria. Es van estudiar les variacions a les dates de primeres arribades per a la Península Ibèrica en cinc espècies (cigonya blanca, cucut, falciot negre, oreneta vulgar i rossinyol) en relació a les condicions ecològiques a les àrees africanes d'hivernada i pas (mesurades a través del *Normalized Difference Vegetation Index*, NDVI), juntament amb el clima (mesurat com a temperatura) a les àrees de pas. Les condicions ecològiques van ser importants per a la cigonya blanca, el cucut i l'oreneta. En aquestes espècies els models de regressió múltiple van ser capaços d'explicar entre el 35 i el 56 % de la variabilitat observada en les dates d'arribada. Per contra, el NDVI a les àrees de pas no va tenir cap efecte en cap de les espècies estudiades. Les temperatures van ser importants per a les espècies més tardanes (cucut, falciot, i rossinyol), tot i que no cal donar gaire importància en aquest efecte donada la pobre capacitat explicativa dels models de regressió múltiple (menys del 10 %). El vincle entre el NDVI africà i la fenologia de les arribades podria ser a través d'un increment de la supervivència hivernal i/o una adquisició més ràpida de la condició corporal pre-migratòria i de la progressió a través dels territoris sub-saharians. Per tant, la influència de les condicions ecològiques als quaters d'hivernada hauria de considerar-se quan hom vulgui estudiar canvis temporals a llarg termini de la fenologia migratòria de les aus.