



Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology

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ABSTRACT: Many studies have reported statistically significant associations between bird migratory phenology and climatic variables, and, consequently, it is mostly accepted that recent shifts in migration dates are a reaction to present climate change. Impacts of weather and climate on departure date, progression and stopover frequency and duration have been reviewed in order to explain the current knowledge of climatic mechanisms underlying such phenological shifts. Climate in departure areas can affect population phenology via the size of the returning population. In a short-term sense, ecological conditions can affect acquisition of migratory body condition during the days preceding departure. Migratory phenology can also be affected by quality and quantity of replaced feathers during moult. Adverse weather conditions en route strongly hinder the progression of individuals and even force them to land. The time spent on stopovers will greatly depend on the ecological conditions there and the opportunities for refuelling. Temperature is by far the climatic variable most frequently related to avian phenology. The use of climatic indices is spreading because they have the advantage of synthesizing weather conditions into a single variable. Remote sensing is probably the best option to explore ecological conditions in areas used by migratory species. Most of the climatic variables employed are from the arrival area, while climate from passage or departure areas is rarely assessed. The overwhelming majority of studies have used variables defined by months, while the use of periods designed ad hoc according to species' biology is almost anecdotal. It can be concluded that further research is needed to disentangle the true relevance of each type of climatic variable over avian migratory phenology during each phase of migration.

KEY WORDS: Arrival date · Bird migration · Climate change · Phenology

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1. RECENT CHANGES IN MIGRATION DATES

The alteration of climatic patterns in recent decades has already had an impact on organisms (Peñuelas & Filella 2001, IPCC 2002, Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, 2005, Parmesan 2006). One of the most evident changes has been the alteration of seasonal timing in northern latitudes (Sparks & Crick 1999, Sparks & Menzel 2002). At present, spring is beginning earlier, while autumn arrival is being delayed (Menzel et al. 2006). The potential effects of such changes on organisms' life-cycles are large and

range from ecosystem functioning to species' competitive abilities (Walther et al. 2002, Visser & Both 2005, Parmesan 2006).

In the case of migratory bird species, a growing number of studies have reported shifts in the timing of their migrations during the last decades (Sparks 1999, Sanz 2002, Root et al. 2003, Crick 2004, Lehikoinen et al. 2004, Crick & Sparks 2006, Jian-bin et al. 2006, Rubolini et al. 2007b, this issue). In most cases, a trend toward earlier spring arrival of birds has been detected at European and North American breeding grounds, especially since the 1970s. Hence, migratory birds are

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advancing their arrivals. The advancement of spring migratory phenology has been attributed to climate change, with special regard to global warming. In most cases, a negative relationship has been found between arrival dates and spring temperatures (Lehikoinen et al. 2004, Root et al. 2005, Gienapp et al. 2007, this issue), i.e. birds arrive earlier when spring temperatures are higher. Higher temperatures also advance the spring phenology of plants and insects in the European and North American passage and breeding areas (Menzel et al. 2006, Gordo & Sanz 2006b, Schwartz et al. 2006) which may improve ecological conditions for migration through these temperate regions due to increased food availability (Huin & Sparks 1998, Hüppop & Hüppop 2003, Ahola et al. 2004, Vähätalo et al. 2004, Both et al. 2005, Mitrus et al. 2005, Hüppop & Winkel 2006, Rainio et al. 2006). Warmer springs are also related to more benign weather, thus meteorological conditions for travel are improved (Forchhammer et al. 2002, Boyd 2003, Tryjanowski et al. 2002, Vähätalo et al. 2004, Marra et al. 2005, Zalakevicius et al. 2006, Sinelschikova et al. 2007).

However, those changes recorded in the arrival date at the southern fringe of the breeding distributions (such as the Mediterranean region for trans-Saharan migrants; Gordo & Sanz 2005, 2006a, Gordo et al. 2005, Rodríguez-Teijeiro et al. 2005, Jonzén et al. 2006, Rubolini et al. 2007a, Saino et al. 2007, this issue) cannot be attributed to the previously cited mechanisms. There, individuals do not pass through Europe or North America, and, consequently, they cannot be affected by conditions in temperate latitudes. Conditions during the spring in Europe and North America are overrepresented, because the overwhelming majority of studies have been conducted in northern latitudes (see Fig. 1). Individuals must fly for days or weeks through Europe or North America before reaching these northern localities (e.g. Southern 1938). In these cases, arrival dates will indeed be strongly driven by weather and climatic fluctuations occurring during the end of their travel at European and North American grounds.

The advancement of spring arrival is also expected based on the effects of climate change on the balance between the benefits and costs of the arrival date (Jonzén et

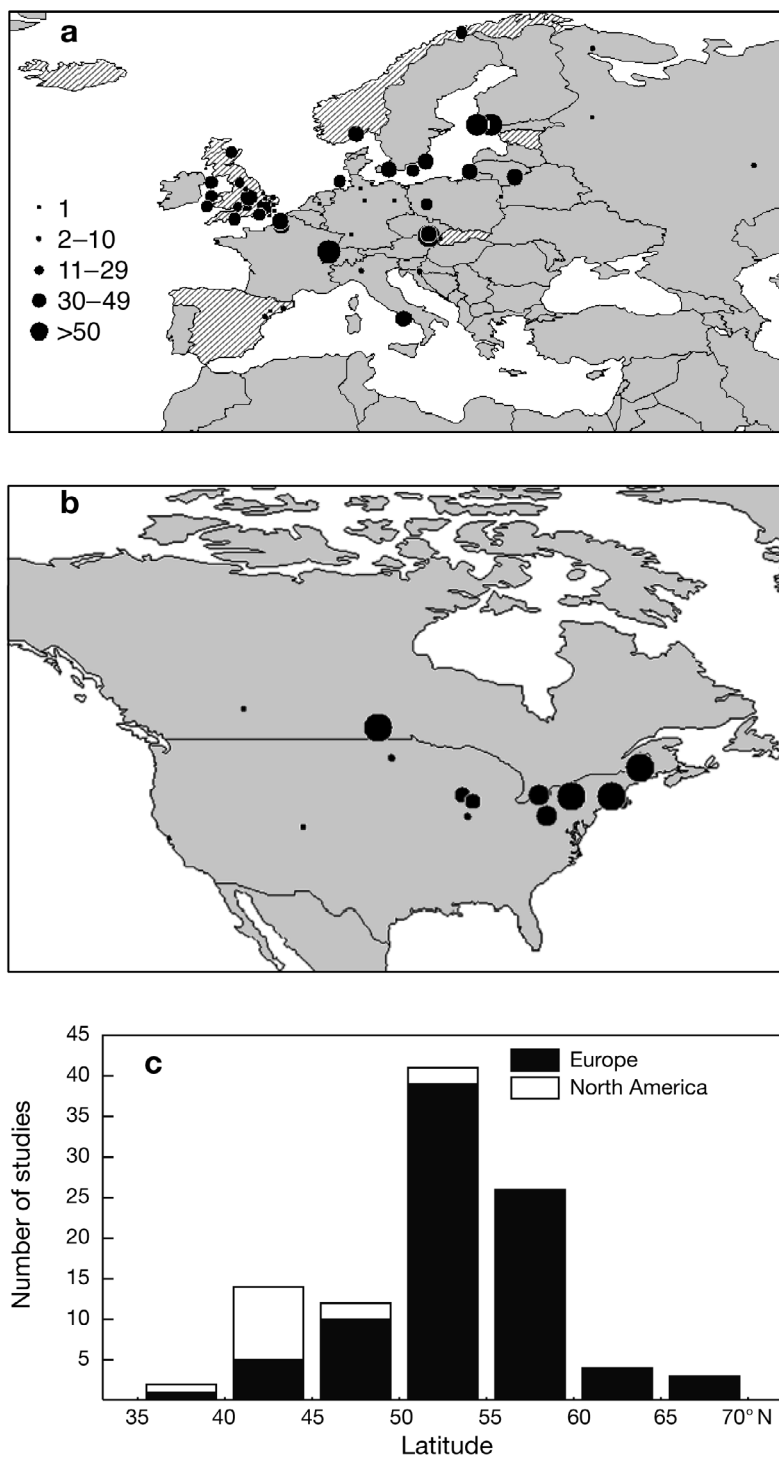


Fig. 1. Locations of recent studies on long-term changes in bird migratory phenology and climate change in Europe (a) and North America (b; see reference list). Dot size indicates the number of species analyzed at each site. Countries with diagonal shading indicate studies that used some kind of monitoring network covering several localities at a national level (Huin & Sparks 1998, 2000, Sparks & Braslavská 2001, Forchhammer et al. 2002, Boyd 2003, Gordo & Sanz 2006a). (c) Distribution of studies according to latitude (5° intervals) in the Northern Hemisphere. Solid bars: European studies; open bars: North American studies

al. 2007a). An early arrival at the breeding grounds has many benefits for individuals: best breeding territories, increased chances to obtain a mate, better quality mates, increased chances for extra clutches and higher survival rates of offspring (Møller 1994, Kokko 1999, Forstmeier 2002, Dunn 2004, Bearhop et al. 2005, Newton 2006). However, arrival date cannot be too early because of costs in terms of mortality due to the absence of suitable ecological conditions in the breeding grounds at the beginning of spring (e.g. low temperatures, food scarcity; Brown & Brown 2000, Jonzén et al. 2007a, Newton 2007). With the advancement of spring phenology, food supplies have become available at earlier dates and the mortality rate between arrival and breeding is reduced due to milder weather (Møller 2004). Therefore, advancement of arrival dates can also be interpreted as the response of individuals in order to optimize the benefits of early arrival.

Nevertheless, some populations have not changed (or have even delayed) their arrival dates during the last few decades, in spite of the favourable changes in spring climate and phenology in their breeding grounds (e.g. Inouye et al. 2000, Wilson et al. 2000, Both & Visser 2001, Strode 2003, Gordo et al. 2005, Weidinger & Král 2007). This fact would imply a maladaptive response under previous assumptions of the optimization hypothesis. However, this hypothesis is simplistic, since spring phenology at the breeding grounds cannot be the only pressure for the best adjustment of arrival dates. Migratory birds spread out their annual cycles over different geographical areas and, consequently, suffer several environmental changes in each of these areas (Coppack & Both 2002). Therefore, it is necessary to examine other environmental pressures apart from those, such as the increase of temperature, recorded in the breeding grounds (Inouye et al. 2000, Saino et al. 2004b, 2007, Gordo et al. 2005, Both et al. 2006, Gordo & Sanz 2006a, Sinelschikova et al. 2007, Sparks & Tryjanowski 2007, this issue). Furthermore, the timing of life-cycle events of migratory birds is under the control of endogenous rhythms (Berthold 1996, Gwinner 1996), which could constrain the plasticity of responses of some species to climatic changes (Both & Visser 2001). Finally, a population decline can override the advancement of spring migration due to a decrease in the likelihood of the first individuals' detection (Sparks et al. 2001, Tryjanowski et al. 2005, Croxton et al. 2006, Sparks et al. 2007).

There is a third mechanism by which spring arrival can be advanced. Individuals can change the locations of the wintering grounds. In Spain, the white stork *Ciconia ciconia* has advanced its arrival by 1 mo since the 1980s (Gordo & Sanz 2006a), while the number of wintering individuals on the Iberian Peninsula has

increased sharply since then (Molina & Del Moral 2005). Bearhop et al. (2005) showed that blackcap *Sylvia atricapilla* males overwintering in Britain arrive earlier at their German breeding grounds than their conspecifics overwintering in Iberia. Indoor experiments with 3 trans-Saharan species (garden warbler *Sylvia borin*, common redstart *Phoenicurus phoenicurus* and pied flycatcher *Ficedula hypoleuca*) have demonstrated that phenotypic plasticity in response to novel photoperiodic conditions from northern wintering grounds could be the cause of such advancement (Coppack et al. 2003; see also Coppack & Both 2002, Coppack & Pulido 2004).

In the case of autumn migratory phenology, there has been evidence of delays and advances (Gatter 1992, Bezzel & Jetz 1995, Sokolov et al. 1999, Bairlein & Winkel 2001, Sparks & Braslavská 2001, Sparks & Mason 2001, Gilyazov & Sparks 2002, Cotton 2003, Jenni & Kéry 2003, Witt 2004, Hüppop & Hüppop 2005, Mills 2005, Gordo & Sanz 2006a, Tøttrup et al. 2006b, MacMynowski & Root 2007, Peron et al. 2007, this issue Sparks et al. 2007). In contrast to spring arrival dates there is no clear picture, as temporal trends of autumn migratory dates are strongly species specific. The optimal migratory strategy would fall under different pressures between long- and short-distance migrants during autumn migration (Jenni & Kéry 2003). Long-distance migrants should depart as early as possible to profit from the abundance peak of resources at the end of the summer and the beginning of the autumn in some of their tropical passage and/or wintering areas (e.g. the Sahel; Morel 1973). In the case of single-brood species with earlier spring arrivals and/or earlier breeding dates, an advancement of departures should be expected as a result of a shift in the whole annual cycle (Fig. 2; Ellegren 1990, Sokolov 2000, Bojarinova et al. 2002). However, the advancement of spring arrivals and/or breeding dates could paradoxically delay autumn departures in multiple-brood species, because they could profit from this shift in the annual cycle by increasing the proportion of pairs that can lay second or third clutches (Fig. 2; Møller 2002).

Short-distance migrants are under different evolutionary pressures as a result of the ecological characteristics of their wintering areas. Ecological conditions of wintering areas of short-distance migrants (e.g. Mediterranean basin for European species) improve throughout autumn thanks to abundant rainfall during this season and the consequent end of summer drought conditions. Therefore, an overly early arrival to the wintering grounds could be constrained by the poor ecological conditions at the end of the summer and their potential costs in terms of survival. However, costs of remaining at the breeding grounds increase as

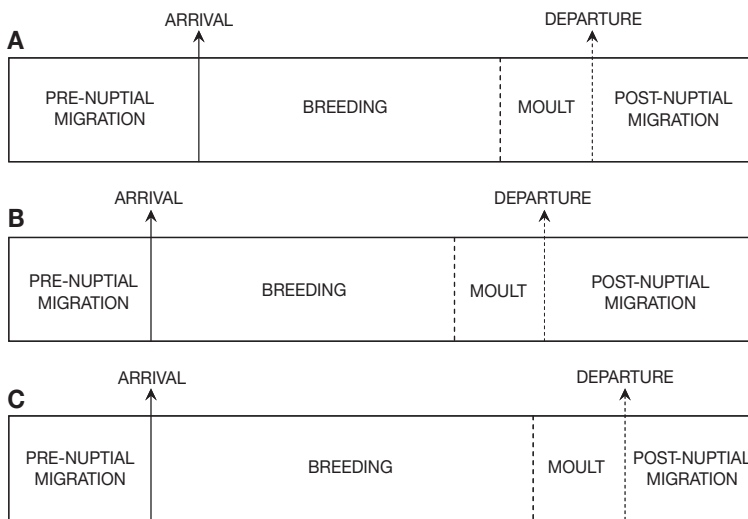


Fig. 2. (a) Main events in the life cycle of a migratory bird between pre- and post-nuptial migration. (b) An advancement of arrival date could advance departure date in single-brood, long-distance migrants. (c) However, in a multiple-brood, long-distance migrant, the advancement of arrival could extend breeding period through extra clutches and this fact could, in turn, delay departure

autumn progresses, because of unexpected adverse weather conditions (Newton 2007). Future climatic scenarios predict milder conditions in northern latitudes. Therefore, short-distance migrants could postpone (or even suppress) departure from their breeding grounds in order to profit from milder conditions in northern latitudes resulting from climate change (Bezzel & Jetz 1995, Jenni & Kéry 2003).

Other characteristics of autumn migration could mask temporal patterns on departure dates. In many species autumn departures are furtive, which hinders the precise detection of this phenomenon through observation. Observational records of autumn migration are also unprotected against the stronger mixture of individuals of different ages (juveniles and adults), sexes (males do not precede females) and natal origin (common in the southern areas of species' distribution) during autumn than during spring migration. Finally, the increase in temperatures is not homogeneous throughout the year, being especially slight or even non-existent in autumn (Karl et al. 1993, Easterling et al. 1997, Klein Tank et al. 2005). Hence, if autumn migration is affected by climate, but autumnal climate has not changed, then there are no climatic pressures to shift post-nuptial migratory phenology.

In summary, there is irrefutable evidence that avian migratory phenology has shifted during recent decades, but is climate change the true cause for such shifts? In spite of a consensus answering this question affirmatively (Sparks & Crick 1999, Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, Crick 2004, Root et al. 2005, Crick & Sparks 2006), there is a lack

of consensus regarding the mechanisms by which climatic changes can induce such shifts (Both 2007, Jonzén et al. 2007b), maybe as a result of the complex evolutionary pressures involved in the optimization of the arrival date together with geographical variability and a strong species-specific component of reported responses (Both & te Marvelde 2007 this issue, Rubolini et al. 2007b). The aim of this paper is to review the potential climatic and weather mechanisms underlying the recently detected shifts in migratory dates. I pursue this objective in 2 steps in the present paper. First, I review direct and indirect effects of climate and weather from departure and passage areas on avian migratory phenology. Second, I review the use of climatic variables in recent studies of bird migratory phenology and climate change. By means of a quantitative assessment I want to highlight what we know and what we need to address in future research. I also identify the main advantages and pitfalls related to each type of climatic variable. The temporal patterns of advancements and delays are already well described (e.g. Lehikoinen et al. 2004); now is the time to delve into the underlying mechanisms for these patterns, especially those regarding climate and weather.

2. EFFECTS OF CLIMATE AND WEATHER ON MIGRATORY PHENOLOGY

The arrival date of a migrant bird will depend on what happens between individual departure from its origin to individual arrival at its destination. Therefore, arrival date will be a function of both the moment of departure and the time spent moving from its origin to its destination. The later the departure and the longer the time spent moving, the later the birds arrive. The time necessary to move between one place and another will, in turn, depend on: (1) the speed of progression through passage areas and (2) the total time spent at stopovers. Therefore, if we want to know what affects the arrival date of a migratory bird recorded at a certain place, we should examine those environmental elements that can potentially influence departure date from the origin, speed of progression (i.e. average movement rate between consecutive stopping places) and frequency (i.e. the number of stops during the whole journey) and length (i.e. the average duration of the stay in each refuelling site) of stopovers (Fig. 3).

Conditions at the end of the migratory journey, i.e. the goal area, have not been taken into account in this

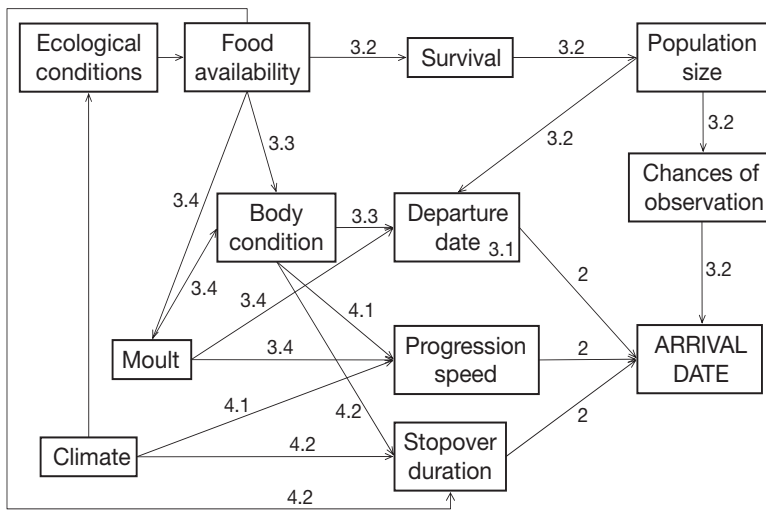


Fig. 3. Potential impacts of climate on the arrival date of a migratory bird species. This would be valid both for spring and autumn migration. In the latter case, breeding phenology should be included. Numbers indicate text sections for further details

sketch of migration (Fig. 3). However, the overwhelming majority of studies included some kind of climatic variable from the same site where arrivals are recorded (Mason 1995, Loxton et al. 1998, Sokolov et al. 1998, Ahas 1999, Loxton & Sparks 1999, Sparks & Mason 2001, Sueur & Triplet 2001, Barrett 2002, Tryjanowski et al. 2002, Dolenc 2003, Lane & Pearman 2003, Ptaszky et al. 2003, Murphy-Klassen et al. 2005, Askeyev et al. 2007, Sparks & Tryjanowski 2007). Birds depart from sites at 100s or 1000s of kilometres away from their goal areas (e.g. their wintering grounds in the tropics), and, thus, it is unlikely that they can accurately assess the climatic conditions at their destination sites (e.g. breeding grounds in temperate latitudes). The high number of significant relationships reported between the arrival at a certain place and the climate there can be attributed to the strong spatial autocorrelation of climatic variables, especially temperatures (Huin & Sparks 1998, Ahola et al. 2004, Mitrus et al. 2005, Murphy-Klassen et al. 2005, Zalakevicius et al. 2006, Sparks et al. 2007). For example, in the case of spring arrivals, warmer springs at the breeding site are also related to warmer springs in the nearby passage areas that are traversed by individuals during the preceding days. Weather is governed by large-scale atmospheric circulatory systems, which can influence areas of 100s of kilometres. Therefore, climatic conditions at the study site are a surrogate for climatic conditions in a broader surrounding area. Relationships between arrivals and local climate at the study site can consequently be interpreted as effects of climate on progression speed or time spent at stopovers during the previous days of the migratory journey.

The huge number of significant relationships reported between climatic variables and arrival dates reflect complex underlying mechanisms rather than a single cause-effect relationship between 1 response variable (i.e. arrival) and 1 predictor variable (i.e. climate; see Fig. 3). Indeed, climate is the ultimate cause of arrival date variability, but there are several non-exclusionary ways to mediate climatic effects on avian migratory phenology. These ways (arrows in Fig. 3) can be classified as direct or indirect effects. Direct effects refer to those direct impacts of weather on departure decisions, progression speed, or stopover duration. Indirect effects refer to the cascade of effects derived from changes in the ecological conditions driven by interannual climatic fluctuations. Harsh climatic conditions (e.g. drought in arid regions or low temperature during winter in temperate regions) are associated with

poor and restrictive ecological conditions. If ecological conditions are poor and restrictive, food resources will be scarce, and this will have negative repercussions on the survival and physiology of individuals.

The sketch proposed in Fig. 3 would be valid for both the arrival at the breeding grounds as well as at the wintering grounds, although, in the latter case, the effects of breeding phenology over departure must be included (Ellegren 1990, Sokolov 2000, Bojarinova et al. 2002). Nevertheless, there is little empirical evidence on the arrival dates at the wintering grounds (Sparks & Mason 2004, Gordo & Sanz 2005), and climate impacts over these dates have rarely been assessed (Sparks & Mason 2004, see also Shamoun-Baranes et al. 2006). For this reason, I will focus examples mainly on spring arrivals at breeding grounds.

Climatic impacts on departure phenology from both breeding and wintering grounds can be evaluated following Fig. 3. In fact, departure and arrival should be considered as the beginning and end, respectively, of the same phenomenon: migration. Therefore, a comprehensive search of the climatic mechanisms underlying arrival date variability must include an assessment of climatic effects on departures because departures are a key piece of the migratory puzzle. Unfortunately, there is little knowledge about departure dates from wintering grounds (Kok et al. 1991, Sparks & Mason 2004, Gordo & Sanz 2005) in comparison to their coupled arrivals at the breeding grounds. However, the opposite situation is found for autumn migration: many studies have analysed departures from breeding grounds, but few have assessed the arrivals at the wintering areas (Kok et al. 1991, Sparks & Mason 2004, Gordo & Sanz 2005).

3. EFFECTS OF CLIMATE AND WEATHER IN DEPARTURE AREAS

This section will be focussed on the direct and indirect ways in which climate and weather affect the departure date from a certain area (i.e. all arrows and boxes between climate and departure date in Fig. 3). Since the final aim is to assess the effect of departure date on arrival date, and primarily the latter is available for the breeding grounds, most of this discussion will be focussed on spring pre-nuptial migration.

3.1. Plasticity of migration onset

Photoperiod is the most reliable calendar, and for this reason birds use it to trigger their migration (Berthold 1996, Gwinner 1996). However, environmental conditions encountered by individuals in departure areas are different each year at the same date (i.e. interannual variability), and, consequently, they should be flexible in their responses (i.e. departure dates) in order to make the best decision. The evidence about internal clocks and the relevance of photoperiod as a trigger of migration are irrefutable (Berthold 1996). Nevertheless, such evidence has been obtained only for a few songbird species and under captive conditions. These experimental conditions are far from the complex situation found by migrant birds in the wild. In nature, individuals must evaluate many other environmental cues (e.g. weather, food supplies) before choosing a well-balanced response. For example, autumn departure dates can show large differences from year to year related to weather, which suggests a fine tuning of endogenous rhythms according to the particular environmental conditions (see Shamoun-Baranes et al. 2006). Furthermore, interannual climatic fluctuations could indirectly affect departure decisions of individuals due to food supplies (Fig. 3), which affect individuals' physiological status (Bairlein 1985, Biebach 1985, Biebach et al. 1986, Gwinner et al. 1988). Endogenous rhythms would trigger migratory restlessness, but migratory onset should not be effective until the individual's body condition is sufficiently prepared. Leaner individuals would delay departure to obtain all the necessary fuel reserves to ensure their survival during migratory flight. Therefore, the potential effect of climate at wintering grounds on migratory onset through ecological conditions and food availability should be taken into account (Studds & Marra 2007, this issue).

Recent studies have reported evidence in favour of a certain phenotypic plasticity in migratory phenology, in response to variable ecological conditions in the wintering quarters. The arrival date of barn swallows *Hirundo rustica* in northern Italy between 1993 and

2001 was earlier after winters with favourable ecological conditions in their African wintering grounds, as was reflected by higher values of the normalized difference vegetation index (NDVI; Saino et al. 2004b). Interestingly, this effect was only detected in old individuals (i.e. individuals of 2 or more years). The arrival of 1 yr old individuals was not related to wintering conditions, due to the time taken to choose a colony in their first breeding season, which is independent of conditions in Africa. In turn, arrival dates had an effect on breeding success, and, consequently, ecological conditions during winter showed an indirect effect on individuals' fitness (see also Dallinga & Schoenmakers 1987, Marra et al. 1998, Hötter 2002, Norris et al. 2004a). In a locality from north-eastern Spain, 6 common trans-Saharan bird species delayed their arrival dates between 1953 and 2004 (Gordo et al. 2005). This delay was unexpected, since all spring phenological events (e.g. leaf unfolding, flowering and insect appearance) were advanced (Peñuelas et al. 2002). In 5 out of 6 species, rainy years in Africa, especially in the Sahel region, were linked to an earlier arrival. Since precipitation has decreased in that region, as a result of the persistent droughts during the last decades (Zeng 2003, Dai et al. 2004), individuals arrive later in response to impaired ecological conditions there. Results for this single population have been confirmed in 100s of localities spread throughout Spain for several species (Gordo & Sanz 2006a). In the case of the barn swallow, the effect of conditions in wintering grounds was even greater than that of Spanish temperatures (Fig. 4). Dallinga & Schoenmakers (1987) drew similar conclusions from the negative relationship between white stork *Ciconia ciconia* arrivals in Alsace (France) and the discharge of the Niger and Senegal Rivers dur-

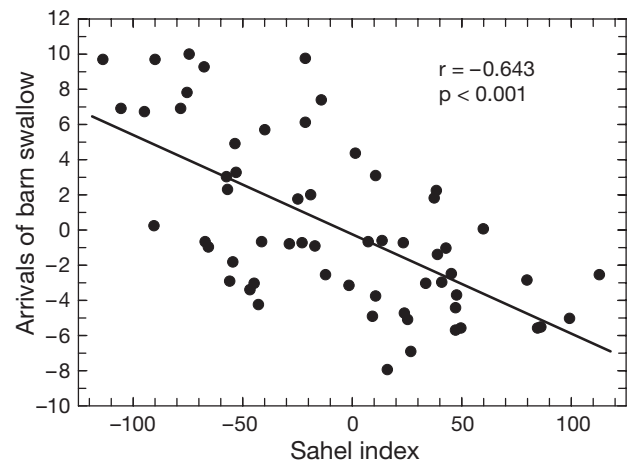


Fig. 4. *Hirundo rustica*. Effect of the Sahel index during the rainy season on barn swallow arrivals in Spain in the following spring. Annual arrival of barn swallows is the annual average of resids of first arrival dates from a model to account for spatial variability (see Gordo & Sanz 2006a for more details)

ing the preceding rainy season. Flows of these rivers are a good proxy for the amount of rainfall in the Sahel region (the wintering region of western white storks; Fiedler 2001) and, thus, of the ecological conditions there. In an arid region, such as the Sahel, wet years are benign years, while dry years are restrictive. Forchhammer et al. (2002) found a negative relationship between the NAO index and the arrival of 2 long-distance migrants, the cuckoo *Cuculus canorus* and the barn swallow *Hirundo rustica*, to Norway. Since high NAO values are related to increased vegetation productivity in southern Africa (the wintering quarter of these populations), the authors suggest that improved foraging conditions would allow individuals to depart earlier from Africa as a result of an improved body condition.

3.2. Population numbers

Food availability could affect departure date in 2 non-exclusionary ways, which can be designated long- and short-term effects (Fig. 3). The long-term effects refer to the ecological conditions during the period that individuals remain in a certain area. Such ecological conditions can affect population numbers through survival. Poor ecological conditions can increase both inter- and intraspecific competition for resources and, consequently, increase the mortality risk due to starvation. A large number of studies have demonstrated the connection between poor environmental conditions in wintering grounds and the low survival rates of individuals in the following breeding season (Winstanley et al. 1974, Den Held 1981, Cavé 1983, Svensson 1985, Dallinga & Schoenmakers 1987, Kanyamibwa et al. 1990, Peach et al. 1991, Marchant 1992, Kanyamibwa et al. 1993, Møller 1994, Szép 1995, Barbraud et al. 1999, Foppen et al. 1999, Sillett et al. 2000, Boano et al. 2004, Newton 2004, Sæther et al. 2006). Population size can directly affect the recorded arrival date through a methodological artefact. Migrant individuals can be recorded earlier in larger populations simply due to the increased opportunities to detect an individual. This kind of bias would be especially probable when arrival dates of populations are quantified by the individuals that arrive first (Tryjanowski et al. 2005). Tryjanowski & Sparks (2001) showed for a red-backed shrike *Lanius collurio* population from western Poland that the advancement of the arrival date during the period from 1983 to 2000 was related to the increase of the studied breeding population. The authors proposed 2 potential factors acting simultaneously: (1) the higher probability of observing an early individual in a larger population and (2) the increased singing activity in denser populations. Similar effects of population

size over arrivals have been found for the turtle dove *Streptopelia decaocto* (Sparks 1999, but see Browne & Aebischer 2003), the nightingale *Luscinia megarhynchos* (Huin & Sparks 2000), the blackcap (Sparks et al. 2001) and many other migrants (Croxtton et al. 2006, Sparks et al. 2007) from Britain. This bias due to population size could be especially serious for those more cryptic and skulking species for which chances of observation are even more strongly constrained by species behaviour. Unfortunately, population number trends are rarely available to test this potential effect.

Wintering population size could also directly affect departure date from wintering grounds through competitiveness among males for an early return in protandry species (Morbey & Ydenberg 2001). It could be predicted that competition for a breeding territory, as well as sexual selection, become more marked the higher the number of males (e.g. due to high wintering survival; Kokko 1999, Møller 2004, Coppack et al. 2006, Kokko et al. 2006, Jonzén et al. 2007a, Møller 2007, Rainio et al. 2007, this issue). Since important features for individual fitness, such as mate quality, resource availability during breeding season, or the number of offspring, rely largely on the acquisition of breeding territory and its characteristics, selection pressures over this parameter should be very strong and will be stronger as competition increases for territory acquisition. On the other hand, Spottiswoode et al. (2006) demonstrated that those species under the strongest sexual selection show the steepest advancement in their arrival dates (but see Rainio et al. 2007). Therefore, the mating system could also help to explain the variability in the adaptive responses of migratory bird species to climate change, since stronger responses should be expected in those species under stronger sexual selection.

3.3. Physiological condition

The short-term climatic effect refers to the hypothetical effect of food availability on individual body condition in departure areas during the days or weeks preceding migration onset (Fig. 3). Individuals undergo surprising behavioural and physiological changes before migration (Berthold 1996). The time required for the acquisition of the necessary pre-migratory body condition (i.e. fuel stores) will depend on the foraging opportunities offered by the occupied habitat as well as the foraging abilities of each individual. In an environment with scarce food supply, individuals will need more time to store the necessary fuel reserves to guarantee the onset of the migratory journey. Marra et al. (1998) demonstrated that winter habitat may be limiting for breeding success and fitness of migrants (see

also Sherry & Holmes 1996, Norris et al. 2004a). Individuals' migratory schedule and physiological status in the American redstart *Setophaga ruticilla* was determined by the habitat occupied during the winter (Studds & Marra 2007). In the Jamaican wintering grounds, those individuals from scrub habitat (i.e. poor environment) showed several deteriorating physical features (e.g. loss of body mass during winter, elevated plasma corticosterone; see also Marra & Holberton 1998) and departed significantly later than those individuals from forest habitat (i.e. rich environment). In the breeding grounds of central New Hampshire (USA), individuals that arrived earlier showed isotopic signatures related to wetter tropical habitats (i.e. rich), which suggests that earlier individuals occupy better wintering habitats. Similar conclusions were obtained for individuals on passage through the Caribbean of another neotropical migrant species, the black-throated blue warbler *Dendroica caerulescens* (Bearhop et al. 2004). Those migrant individuals with better body condition showed isotopic signatures belonging to moist forest habitats, i.e. good habitats. However, those individuals overwintering in poor, xeric environments returned to the breeding grounds in poorer physical condition, which could be detrimental to their fitness by means of later arrivals and increased risk of mortality during migration. In Iceland, the arrival date of individuals of the black-tailed godwit *Limosa limosa islandica* was strongly dependent on the population trend detected at the site selected to overwinter (Gill et al. 2001). Those individuals from increasing wintering populations arrive later than those from stable populations, because food intake rates previous to migration were lower in the increasing populations. A later arrival date has negative impacts on breeding success, because late individuals are relegated to lower quality territories (Gunnarsson et al. 2005, 2006).

3.4. Molt

Food availability in departure areas could have indirect effects on arrival dates through moulting (Fig. 3). Birds replace their feathers during molt, a costly process (Dietz et al. 1992, Schieltz & Murphy 1995, Portugal et al. 2007) that takes place before pre- and post-nuptial migration. Molt can be affected by resource availability, which, in turn, depends on climatic variability (Fig. 3). Van den Brink et al. (2000) showed that the rate of primary and tail molt in barn swallows was closely related to environmental conditions encountered by this species in their African wintering grounds. The rate of molt was higher in those years with higher amounts of rainfall during winter. Wet years were associated with a greater abundance of

insects and, by implication, to an improvement in foraging conditions of insectivorous birds, such as barn swallows. Furthermore, in this species, the availability of roosting habitat (i.e. reedbeds), which depends on river discharge (which, in turn, depends on rainfall), affects the density of individuals and the distance to reach the foraging areas. In dry years, roosting habitat is scarce, and barn swallows are forced to concentrate in a few places. This fact implies a higher competition for aerial insects and a necessity to move further to forage.

Molt can affect migratory phenology through: (1) time constraints and (2) quality of replaced feathers. Time constraints refer to potential delay of departure until the molt is complete. Due to the costs of molt (Dietz et al. 1992, Schieltz & Murphy 1995, Portugal et al. 2007), individuals avoid overlapping this process with breeding (Hemborg et al. 1998, Hall & Fransson 2000, Morales et al. 2007) or migration (Gorney & Yom-Tov 2001, Pérez-Tris et al. 2001, Norris et al. 2004b). However, this is not always possible. At high latitudes, summer is too short and imposes a trade-off on the time allocation for breeding, molt and preparation for autumn migration (Hemborg et al. 1998, 2001). Late individuals in the breeding season are also affected by this trade-off (Svensson & Nilsson 1997, Hall & Fransson 2000). Nevertheless, time constraints can be dealt with by overlapping molt and breeding (Underhill et al. 1992, Svensson & Nilsson 1997, Hemborg et al. 1998, 2001), accelerating feather growth (Hall & Fransson 2000), suppressing molt before migration onset (Hall & Fransson 2001), or overlapping molt and migration (Norris et al. 2004b). Therefore, individuals have mechanisms to avoid the time constraints that molt imposes on autumn departure date. In the case of pre-nuptial molt, individuals are relatively free of time constraints, and it may be for this reason that replacement of the same feathers takes more time in the pre-nuptial molt in some species (Underhill et al. 1992).

The quality of replaced feathers depends on the molt rate (Dawson et al. 2000) and food availability (Van den Brink et al. 2000, Saino et al. 2004a; but see Salewski et al. 2004). The quality of feathers affects the manoeuvrability and flying performance of individuals (Swaddle et al. 1996, Gorney & Yom-Tov 2001), as well as the resistance to abrasion, thermoregulatory capacity and coloration (Serra et al. 2007). In aerial feeders, like the barn swallow, this could have serious repercussions on its foraging ability and thus on body condition (Fig. 3; Pérez-Tris et al. 2001, Rubolini et al. 2002).

Moreover, consequences of molt through phenology can go beyond the level of individual success. When feathers constitute a sexual character, they undergo strong selective pressures. Saino et al. (2004a) demonstrated that the length of the tail ornament in barn swallow males from northern Italy was longer after winters with good ecological conditions in Africa.

Since male sexual attractiveness depends on tail ornaments (Møller 1988), ecological conditions in wintering quarters affect an individual's fitness through sexual selection during the following breeding season. In species with sexual selection, the sex under selection must develop high-quality ornaments to attract mates. When feathers are a sexual trait, the development of such traits requires time (i.e. moulting period). The longer the moulting period, the better, potentially, the feather quality (Dawson et al. 2000, Hall & Fransson 2000) and, consequently, the better the sexual character phenotype (Serra et al. 2007). Therefore, it is interesting to note the potential existence of a trade-off between moulting and departure time, which merits further attention (Saino et al. 2004a, Serra et al. 2007).

4. EFFECTS OF CLIMATE AND WEATHER EN ROUTE

4.1. Progression speed

En route, climatic effects can act on the progression speed as well as on the frequency and duration of the stopovers, both directly and indirectly (Fig. 3). In the case of progression speed, a direct effect would be the weather conditions during travel, which can reduce or increase the flying speed under unfavourable (e.g. rainfall) or favourable (e.g. tailwinds) conditions, respectively (reviewed in Richardson 1978, Richardson 1990; see also Bernis 1966, Alerstam 1990, Newton 2007). The median date of spring passage of the song thrush *Turdus philomelos* has advanced by 10 d during the last 4 decades in the south-eastern Baltic region (Sinelschikova & Sokolov 2004). The main factor controlling the number of trapped song thrushes at the ringing station of Rybachy (SE Baltic) was the frequency and speed of tailwinds from France to the Baltic region during the spring (Sinelschikova et al. 2007). Interestingly, frequency and speed of tailwinds over central Europe have increased during the last 40 yr. Therefore, flight conditions have been improved. This fact has allowed an increase in the progression speed of song thrushes and, subsequently, an advancement of arrival dates. In Norway, arrivals of the song thrush, as well as the skylark *Alauda arvensis* and the starling *Sturnus vulgaris* (both short-distance migrants), were affected by the NAO (Forchhammer et al. 2002)—the higher the NAO, the earlier the arrival date. The effect of the NAO index would also be through wind and, consequently, progression speed en route, since high values of the NAO are related to favourable wind conditions for northward migration.

An individual's progression speed could also be affected indirectly by climate through body condition and quality of replaced feathers (see Sections 3.3 and

3.4). Lean individuals can better avoid predation (Lind et al. 1999, Kullberg et al. 2000, Cimprich & Moore 2006), but a lighter body mass would be penalized with a shorter flight autonomy. Therefore, lean individuals must stop to replenish their fuel reserves more frequently (Bairlein 1985, Biebach 1985, Biebach et al. 1986, Yosef et al. 2006).

4.2. Stopover frequency and duration

Stopovers are key periods for migrant birds in spite of their short duration within the annual schedule. Indeed, success of the migratory journey depends greatly on what happens during stopover periods and at stopover sites (Newton 2006). The greater amount of time spent at stopovers, the greater the delay in the arrival date, with all else being equal. Climate can impact the number and duration of stopovers directly through en route weather conditions. Bad weather conditions can force individuals to land without physiological necessity (i.e. without empty fuel reserves) and to remain stopped until weather becomes suitable for flying (Zalakevicius 2001, Barriocanal et al. 2002, Gordo 2006). Weather conditions can also be important in take-off decisions. Nocturnal migrant passerines that stopped at Ottenby (Sweden) preferably resumed their migration on those days with tailwinds (Åkesson & Hedenström 2000).

Climate can affect the time spent at a stopover through the ecological conditions imposed at the stopover site (Fig. 3). Refuelling opportunities can be determined by the amount of food supplies, which, in turn, depends on ecological conditions. Food supplies at stopover sites can vary greatly both inter- and intrannually. An example of the interannual variation effect is provided by rufous hummingbirds *Selasphorus rufus* during their autumn migration in North America (Russell et al. 1994). The density of nectar-providing flowers was low in dry years. During those years, the stopover duration of rufous hummingbirds in the Sierra Nevada (California, USA) was longer as a result of the impaired refuelling opportunities and low body mass of incoming birds. At temperate latitudes, interannual variability can also be due to the degree of phenological development of the ecological conditions at stopover sites. An advanced year as a result of a warmer spring can notably improve foraging opportunities, especially in insectivorous birds, because arthropod abundance is higher during dry and warm days, which could enhance feeding rates (Schaub & Jenni 2001). Intrannual variation refers to changes in food supplies within the course of migration. Several studies have reported a depletion of resources by the first arriving migrants (Ottich & Dierschke 2003). This

fact imposes poor conditions for late migrants, which will spend more time in efforts to replenish their fuel reserves as a consequence of food scarcity (Russell et al. 1994, Nolet & Drent 1998).

4.3. Northern versus southern populations

Ecological and weather conditions during the spring at northern latitudes have improved in recent decades thanks to recent climatic changes. Progression through these areas is faster due to increased flight speed as a consequence of more favourable weather (Sinelschikova et al. 2007) and reduced time spent at the stop-over sites as a consequence of improved foraging conditions due to advanced spring phenology (e.g. Huin & Sparks 1998). However, most of the studied populations were located at high (or very high) latitudes (Barrett 2002, Forchhammer et al. 2002, Gilyazov & Sparks 2002, Vähätalo et al. 2004, Stervander et al. 2005, Rainio et al. 2006; see Fig. 1), where en route climate conditions have greater opportunities to impact migratory phenology in the later stages of migration through Europe or North America. For example, if we consider pre-nuptial migration of a widespread trans-Saharan migrant such as the barn swallow, a Scandinavian individual is just at the halfway point of its migratory journey when it reaches the breeding area of the Moroccan individuals (Southern 1938). Therefore, we should expect a greater impact of climate from temperate regions as we analyse arrival dates from northern populations. In this sense, the study of southern populations (Dolenec 2003, Gordo & Sanz 2005, Gordo et al. 2005, Rodríguez-Teijeiro et al. 2005, Gordo & Sanz 2006a, Rubolini et al. 2007a) becomes a good alternative to determine the relative importance of climatic changes in temperate passage regions versus climatic changes in departure areas on migratory phenology of populations from northern latitudes.

5. VARIABLES EMPLOYED TO ASSESS CLIMATE CHANGE EFFECTS ON MIGRATORY PHENOLOGY

5.1. A quantitative analysis of a difficult choice

In facing the challenge of the assessment of climate change effects on avian migratory phenology, the first pitfall is the plethora of variables that quantify climatic fluctuations. Climatologists have developed a huge number of variables to quantify the complexities of the atmosphere, but which variables should ecologists select? In general, climate variables show a strong collinearity because they summarize the same phenomenon: weather. Weather results from a complex and

unique combination of physical atmospheric features at a certain time and place. Nevertheless, all of these features always covary in the same way. A simple example: temperature is usually lower when it is raining. Therefore, it is not surprising to find significant relationships between a single time series of arrival dates and several climatic variables. All of these relationships indicate the same thing: arrivals are affected by climate and are earlier (or later) under certain weather conditions. Therefore, large numbers of climatic explanatory variables, which are usually characterized by their high collinearity, should be summarized by applying multivariate techniques, such as principal component analysis or partial least squares regression (Gordo et al. 2005, Saino et al. 2007). Climatic indices, such as the NAO, are also a good summary of weather conditions in a single value. Multiple regression would also be a preferable alternative to many simple correlations in order to account simultaneously for the effects of several explanatory variables, especially in those cases where the geographical and temporal identity of key climate variables is unknown. Furthermore, some kind of selection procedure of the best subset of explanatory variables in multiple regression models can help us to reveal the most relevant climatic variables for the analysed arrival dates.

An overview of the studies dealing with temporal shifts in arrival date reveals that temperature is by far the most often employed explanatory variable (Fig. 5a; see also Appendix 1). Indeed, the main mechanism suggested for the advancement of arrival dates is global warming (see Section 1). In a minority of studies, other meteorological variables, such as precipitation (Sparks & Carey 1995, Huin & Sparks 1998, 2000, Boyd 2003, Sokolov & Kosarev 2003, Kaňuščák et al. 2004, Chambers 2005, Gordo et al. 2005, Gordo & Sanz 2006a, Sokolov 2006, Zalakevicius et al. 2006, Beaumont et al. 2007, Rubolini et al. 2007a, Saino et al. 2007, Sinelschikova et al. 2007, Studds & Marra 2007) or wind (Boyd 2003, Sinelschikova et al. 2007) have been assessed in addition to temperature. The use of wind has been almost anecdotal (Boyd 2003, Sinelschikova et al. 2007), in spite of the fact that it is traditionally recognized as one of the most important drivers of migratory progression (Richardson 1978, 1990; see also Ball 1983). Only Boyd (2003) assessed the effects of all 3 types of variables in the arrival dates of 4 migratory birds to Iceland during the 20th century. In fact, this is probably the study with the most comprehensive examination of potential climatic influences on arrival dates, since he also evaluated the effects of NAO, snowmelt date, atmospheric pressure at sea level and plant growth as other potential explanatory variables. Furthermore, he used variables from departure, passage and breeding areas. Interest-

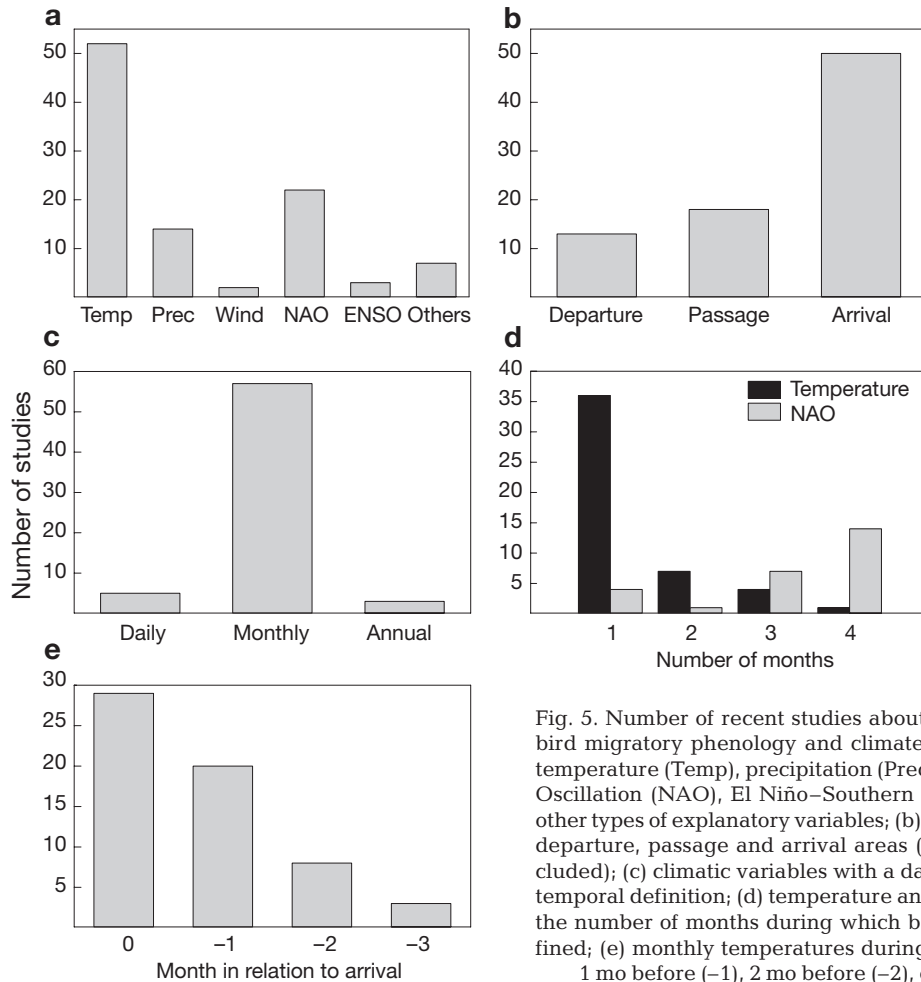


Fig. 5. Number of recent studies about long-term changes in bird migratory phenology and climate change that used: (a) temperature (Temp), precipitation (Prec), wind, North Atlantic Oscillation (NAO), El Niño–Southern Oscillation (ENSO), or other types of explanatory variables; (b) climatic variables from departure, passage and arrival areas (climate indices not included); (c) climatic variables with a daily, monthly, or annual temporal definition; (d) temperature and/or NAO according to the number of months during which both variables were defined; (e) monthly temperatures during the arrival month (0), 1 mo before (–1), 2 mo before (–2), or 3 mo before (–3)

ingly, the only goal of some studies was the detection of temporal trends of bird arrivals (Wilson et al. 2000, Witt 2004, Mills 2005, Reichholf 2005, Tøttrup et al. 2006a), and thus the effect of climate in these time series remains to be assessed. In other studies, temporal trends of climatic variables were assessed, but there were no explicit relationships between phenological variables and climatic ones (Jenkins & Watson 2000, Butler 2003, Gordo & Sanz 2005, Beaumont et al. 2006).

Climatic indices, such as the NAO or El Niño–Southern Oscillation (ENSO), have been used in a noteworthy number of studies (Fig. 5a). This is meaningful because climatic indices as explanatory variables of long-term trends in bird migratory phenology were applied for the first time only a few years ago (Forchhammer et al. 2002). Only 3 studies have evaluated the ENSO (Cotton 2003, Barbraud & Weimerskirch 2006, MacMynowski & Root 2007), in comparison to 22 that have used the NAO, due to the fact that the overwhelming majority of studies have been conducted in the Northern Hemisphere (see Fig. 1), where

the NAO is probably the most important large-scale climate driver (Hurrell & Van Loon 1997, Ottersen et al. 2001, Stenseth et al. 2003). Interestingly, none of the 3 studies found significant effects of the ENSO on arrival dates. The NAO has been evaluated in addition to other variables, such as temperature and precipitation, with only 8 studies exclusively using the NAO (Forchhammer et al. 2002, Hubálek 2003, 2004, Vähätalo et al. 2004, Stervander et al. 2005, Ahas & Aasa 2006, Jonzén et al. 2006, Rainio et al. 2006). Only Barbraud & Weimerskirch (2006) used another climatic index, the Southern Annular Mode, which did not have effects on the arrival of Antarctic birds.

Finally, I have found only 7 studies in which other types of variables have been used to assess the mechanisms underlying long-term trends in migratory phenology. These variables were related to atmospheric pressure (Boyd 2003, Zalakevicius et al. 2006), snow melting (Inouye et al. 2000, Boyd 2003), plant phenology (Boyd 2003, Marra et al. 2005, Sokolov 2006), vegetation productivity (Saino et al. 2004b) and sea ice extent (Barbraud & Weimerskirch 2006).

In summary, the assessment of climate on bird arrivals is strongly focussed on temperatures and the NAO (e.g. Gienapp et al. 2007). One reason for this prevalence could be the availability and ease of interpretation of both variables. Another non-exclusionary reason could be the geographical location of the study sites (see Fig. 1). Most of the studies have been conducted at northern latitudes, especially in the Atlantic and Baltic regions of Europe, where both temperature and the NAO are very important drivers for ecosystem functioning. More research is urgently needed in populations from southern latitudes, as well as studies employing several types of climatic explanatory variables (Boyd 2003, Kaňuščák et al. 2004, Sokolov 2006, Zalakevicius et al. 2006).

5.2. Temperature

High values of temperature in tropical departure areas can be linked to an impairment of ecological conditions as a result of an increase in aridity. However, high temperatures are linked to advancement of spring course (Menzel et al. 2006) and improved weather for progression (Zalakevicius et al. 2006) at temperate latitudes. Therefore, global warming could have the opposite effect on arrival dates, depending on the area considered: in tropical arid areas, it could delay departure or progression (but see Saino et al. 2007), while, in temperate regions, global warming could favour faster passage.

Significant relationships between arrival dates and temperature at the study locality do indeed reflect the effect of temperatures in the previously traversed passage areas due to the strong spatial autocorrelation of temperature. Zalakevicius et al. (2006) related the first arrival date of 40 species in areas around Vilnius (Lithuania) between 1971 and 2004 with temperature records from several European and North African cities. The overwhelming majority of species affected by temperatures showed simultaneously significant relationships with several cities. Does this mean that migrant individuals pass through all of them? No, it does not. This trend is simply due to the fact that temperature patterns from closely situated cities are quite similar (i.e. strong spatial autocorrelation). Hüppop & Winkel (2006) related the arrival of several central European populations of pied flycatchers and temperature patterns throughout Europe. They found significant correlations between arrivals and many of the $2.5^\circ \times 2.5^\circ$ European grids. This massive effect of temperature is due simply to the climatic resemblance between neighbouring grids, because they are under a common pattern of climatic variability. Sparks et al. (2007) showed that the arrival of 10 common species to

6 different areas of the United Kingdom was related to March temperatures in both England and Spain. However, temperatures in both places had quite similar interannual variations ($r = 0.76$).

Temperatures also suffer from temporal autocorrelation (i.e. temperatures between 2 consecutive moments are not fully independent). This would explain why species phenology is usually affected by several months (Loxton et al. 1998, Sokolov et al. 1998, 1999, Loxton & Sparks 1999, Sokolov 2000, Tryjanowski et al. 2002, Sokolov & Kosarev 2003, Zalakevicius et al. 2006, Croxton et al. 2006, Sparks et al. 2007). Does this mean that migrant individuals are migrating over the period of several months? No, it does not. This is simply because interannual fluctuations in temperatures for 2 consecutive months are usually similar. Ahola et al. (2004) studied the effect of climate along the migratory route and at the breeding grounds in the migration and breeding dates of pied flycatchers from south-western Finland for the period from 1970 to 2002. According to ringing recoveries, they selected 8 European cities along the migratory route and calculated mean temperatures during a time window of 3 wk. The authors made an accurate selection of the key period of temperatures for arrivals (i.e. highest correlation) by moving this time window in 3 d steps from 1 March onwards. Consecutive time windows showed very similar correlation coefficients with arrival dates of pied flycatchers. This similarity was maintained even between time windows with few overlapped days. This study stresses the strong temporal autocorrelation of temperatures and the necessity of an accurate selection of the time window of the climatic variables.

5.3. Precipitation

The direct and immediate effect of rainfall is to hinder individuals' flight and force them to land even when precipitation is scarce (Bernis 1966, Richardson 1978, 1990, Gordo 2006, Newton 2007). Therefore, rainfall slows migratory progression and could delay arrival date. Precipitation can also impact migratory phenology through indirect effects on ecological conditions (Fig. 3). In arid regions (e.g. the Sahel or Mediterranean region), a higher amount of rainfall improves ecological conditions, since water is a restrictive element for ecosystem productivity (Vicente-Serrano & Heredia-Laclaustra 2004, Herrmann et al. 2005). Nevertheless, ecosystem response to rainfall is not immediate (i.e. plants need time to grow). Time is also needed before primary production leads to an increase in arthropod populations. Furthermore, ecosystem response can be maintained even well after the occurrence of rainfall, e.g. by means of soil moisture.

Hence, lag effects could be especially relevant in the study of this variable.

One interesting feature of precipitation is the latitudinal change in its ecological significance. Birds coming from the equator must face a minimum rainfall gradient around the tropics (Jones 1995, Salewski & Jones 2006). As a result, rainfall becomes crucial in tropical environments, especially those that are more arid such as the African Sahel, where the alternation of dry and wet seasons is the most important determinant of intrannual variations in ecological conditions (Herrmann et al. 2005). However, it can become a nuisance for progression at northern latitudes where water is not a restrictive element.

5.4. North Atlantic Oscillation

Climatic indices, such as the NAO or ENSO, have received much attention due to their ability to assess general climatic conditions over large areas (Holmgren et al. 2001, Ottersen et al. 2001, Blenckner & Hillebrand 2002, Hallett et al. 2002, Stenseth et al. 2003, Forchhammer & Post 2004, Stenseth & Mysterud 2005). Indeed, they avoid redundancy and spatial autocorrelation of meteorological variables because they summarize climatic conditions into a single value.

Many studies have shown that migrants advance their spring arrivals after winters with a positive phase of the NAO (Forchhammer et al. 2002, Boyd 2003, Hubálek 2003, 2004, Hüppop & Hüppop 2003, Sokolov & Kosarev 2003, Ahola et al. 2004, Kaňuščák et al. 2004, Vähätalo et al. 2004, Sparks et al. 2005, Stervander et al. 2005, Ahas & Aasa 2006, Gunnarsson et al. 2006, Jonzén et al. 2006, Rainio et al. 2006, Zalakevicius et al. 2006, MacMynowski & Root 2007; see a meta-analysis in Gienapp et al. 2007). Positive values of the NAO are linked to increased temperatures and precipitation in northern Europe and south-eastern North America and dry anomalies in the Mediterranean basin (Hurrell 1995, Hurrell & Van Loon 1997). Therefore, a positive NAO index means ecologically improved conditions at northern latitudes, such as in central and northern Europe, as a result of advanced spring phenology (Aasa et al. 2004, Menzel et al. 2005). Migratory birds would progress quickly through European areas during those years with a positive NAO and would consequently arrive at their destinations earlier. Furthermore, a positive NAO is also associated with westerly and southerly tailwinds in western Europe, which favours northward flight of migrants (Forchhammer et al. 2002, Zalakevicius et al. 2006, Sinelchikova et al. 2007). Therefore, the advance of arrival dates observed during recent decades could be due to the prevalence of the positive mode of the NAO from

1980 onwards, especially during the winter (Visbeck et al. 2001, Osborn 2006).

In the case of North American migrants, only 2 studies have assessed the effects of the NAO on migration dates (Marra et al. 2005, MacMynowski & Root 2007). Marra et al. (2005) found few relationships between the NAO and migration dates at both the Powdermill ringing station (Pennsylvania, USA) and the Long Point Bird Observatory (Ontario, Canada). However, MacMynowski & Root (2007) found that the early phase of migration of 73% of long-distance migrants and 18% of short-distance migrants had a significantly negative correlation ($p < 0.1$) with NAO values at McCormick (near Chicago, USA). Nonetheless, more studies are necessary in order to draw conclusions about the effect of the NAO on American migrants.

5.5. Normalized difference vegetation index

At present, new analytical techniques offer possibilities to indirectly explore ecology of migratory birds (Pettorelli et al. 2005, Szép & Møller 2005). Satellites of the U.S. National Oceanic and Atmosphere Administration (NOAA) have been measuring the daily reflected radiation of the earth's 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, expressed as the normalized difference vegetation index (NDVI), which relates reflected wave-lengths to the level of photosynthetic activity (Nicholson et al. 1998).

Satellite measurements are especially suitable for isolated and sparsely populated areas, such as most tropical wintering quarters of migratory birds, where ground climatic measures are scarce or even nonexistent. Another advantage of the NDVI is the fact that precise knowledge about the functioning of ecosystems is unnecessary. High values of NDVI are related to higher photosynthetic activity and, consequently, primary productivity (Nicholson et al. 1998, Nemani et al. 2003, Vicente-Serrano & Heredia-Laclaustra 2004, Herrmann et al. 2005). Higher primary productivity can, in turn, increase food abundance in higher trophic levels, such as arthropods, the main food supply for most migratory birds. Therefore, high NDVI values will be related to improved ecological conditions and this can be related to earlier arrival (Fig. 3; see also previous sections). Unfortunately, NDVI data have only been available since 1981, which constrains the analysis of time series over a longer time span or ending before this decade.

Recent studies have demonstrated the huge potential of remote sensing to assess the effect of ecological conditions in wintering areas on biological features,

such as arrivals, sexual selection and reproductive success of migratory birds (Saino et al. 2004a,b, Møller 2004, Møller & Merilä 2004, Møller & Szép 2005). Szép et al. (2006) employed NDVI data to predict wintering areas of Danish barn swallows on the basis of survival rate observed at the breeding grounds. Wintering mortality of the studied population was strongly related to NDVI values in some areas in South Africa. Authors suggest using this result as a guide to focus ringing efforts on concrete areas of wintering grounds. Both et al. (2006) showed that NDVI in wintering (western Africa) and passage (northern Africa) areas have effects on the laying phenology of the pied flycatcher. Nevertheless, the effect of NDVI in Africa was only significant for early European populations. These populations advanced their laying dates in those years with more vegetation productivity in Africa, maybe as a result of an earlier migratory onset and faster progression.

Nevertheless, there are still few studies that have employed remote sensing, and only two have related arrival dates to NDVI (Saino et al. 2004b, Gordo & Sanz 2008). Furthermore, most studies are focussed on a few Danish and Italian populations of a single species (the barn swallow). Hence, further studies would be necessary to generalize the usefulness of the NDVI.

6. SPATIAL AND TEMPORAL DEFINITIONS OF PREDICTORS TO ASSESS CLIMATIC EFFECTS

6.1. Quantitative analysis according to spatial criterion

Explanatory variables used for the assessment of climate change impacts over bird migratory phenology can be classified in 3 groups according to their geographical origin: variables from departure area, variables from passage areas and variables from the arrival area. As shown in Fig. 5b, I have quantified the number of occurrences, i.e. the number of studies, for each geographical origin (see also Appendix 1). I have only considered studies dealing with spring arrivals, and I have not included climatic indices because of their large-scale influence. Variables from the arrival area (i.e. breeding grounds) are by far the most frequently employed. Moreover, they have been the only type of explanatory variable employed in 29 out of 46 studies that use variables from the arrival area. However, the effects found for climate from arrival area would be better attributed to climate from passage areas (see Section 4.3). This would be especially valid for those studies that used regional instead of local data from the study area (Marra et al. 2005, Hüppop & Winkel 2006, MacMynowski & Root 2007). MacMynowski & Root (2007) used monthly temperatures

calculated for a $5^\circ \times 5^\circ$ grid, because they considered local temperatures to be too strongly influenced by Lake Michigan and unrepresentative of spring conditions at about 42° latitude in North America.

The number of studies that have explicitly included variables from passage areas are few (Fig. 5b; Huin & Sparks 1998, 2000, Boyd 2003, Sokolov & Kosarev 2003, Strode 2003, Ahola et al. 2004, Both et al. 2005, Chambers 2005, Mitrus et al. 2005, Rodríguez-Teijeiro et al. 2005, Croxton et al. 2006, Hüppop & Winkel 2006, Sokolov 2006, Zalakevicius et al. 2006, Sinelschikova et al. 2007, Sparks & Tryjanowski 2007, Sparks et al. 2007, Weidinger & Král 2007) and all of them also included variables from the arrival area. Few studies have used variables from the departure area (i.e. wintering grounds; Boyd 2003, Cotton 2003, Kaňuščák et al. 2004, Saino et al. 2004b, Gordo et al. 2005, Mitrus et al. 2005, Rodríguez-Teijeiro et al. 2005, Gordo & Sanz 2006a, Sokolov 2006, Zalakevicius et al. 2006, Saino et al. 2007, Sinelschikova et al. 2007, Weidinger & Král 2007). Most of them also included variables from passage and arrival areas (exception Saino et al. 2004b). In summary, there is a strong bias toward the use of climate from arrival areas, probably because these are the variables most easily available to researchers. More research is needed to clarify the true extent of the relevance of climate at departure and passage areas on arrival dates.

6.2. Quantitative analysis according to temporal criteria

According to the temporal interval during which climatic variables are measured, I have identified 3 categories: daily, monthly and annual. In the case of spring migration, the overwhelming majority of studies have used variables calculated over months (Fig. 5c). Within this category there are diverse criteria to select the best temporal interval according to the type of variable (Fig. 5d). If we focus on temperature, most studies examined temperature only during a 1 mo period, especially the month of bird arrivals (Fig. 5e). Only a few studies have averaged monthly temperatures over several months to evaluate conditions during a longer temporal interval (2 mo: Loxton et al. 1998, Loxton & Sparks 1999, Ptaszyk et al. 2003, Ledneva et al. 2004, Gordo et al. 2005, Marra et al. 2005, Gordo & Sanz 2006a; 3 mo: Sparks & Mason 2001, Dolenc 2003, Beaumont et al. 2006; or 4 mo: Kaňuščák et al. 2004). However, in the case of the NAO, there is an opposite trend (i.e. most studies use NAO values averaged over several months; see Fig. 5d). Studies that used the NAO during 4 mo are those that used the winter NAO (from December to March). The winter NAO is an especially important measure for climatic and ecological conditions during

the spring in the Northern Hemisphere (Ottersen et al. 2001, Stenseth et al. 2003). Only a few studies have evaluated the NAO for different periods and intervals (1 mo: Boyd 2003, Sokolov & Kosarev 2003, Ahas & Aasa 2006, MacMynowski & Root 2007; 2 mo: Sokolov 2006; or 3 mo: Cotton 2003, Hubálek 2003, Sokolov & Kosarev 2003, Hubálek 2004, Ahas & Aasa 2006, Zalakevicius et al. 2006, Rubolini et al. 2007a).

Only a few studies have used climatic data on a daily basis (Hüppop & Hüppop 2003, 2005, Strode 2003, Ahola et al. 2004, Hüppop & Winkel 2006). Daily data are preferable to any other kind of temporal interval because they allow climate conditions to be defined during precise periods of biological relevance (Hüppop & Hüppop 2003, 2005, Ahola et al. 2004).

Climatic conditions during a complete annual cycle have been reported in some studies (Sparks & Carey 1995, Chambers 2005, Gordo et al. 2005). However, an entire year seems to be too long a period for migratory birds (Fig. 3), as they spend only part of the year in the same place.

In summary, there is a strong bias toward the use of variables within a monthly time frame, probably because variables are typically reported in climatic databases by monthly averages. However, the month is a temporal interval imposed by the human calendar, but without any biological relevance. More research with daily values averaged over periods designed ad hoc (e.g. Ahola et al. 2004) is needed for a precise assessment of sensitive periods. It can be concluded that the existence of a strong bias in the spatial and temporal definition of variables presents serious concerns about the reported magnitudes of climate over arrival dates.

6.3. Problems with the spatial and temporal definition of variables

The correct selection of the type of explanatory variables, as well as a precise definition of their geographical and temporal range, is essential for the correct assessment of climate impacts (Stenseth & Mysterud 2005). It is expected that climate will affect individuals just during a certain time period in a certain place, i.e. birds become sensitive to particular meteorological conditions (Shamoun-Baranes et al. 2006). In the case of the spring migration, it is expected *a priori* that there will be an effect of climate in wintering and passage areas during wintering and passage times because these are sites where and moments when individuals can be affected. Unfortunately, in most species there is no precise knowledge about the wintering and passage areas used during migration or about the period for each population. This is especially evident in most

European long-distance migrants (Walther & Rahbek 2002, Kaňuščák et al. 2004, Walther et al. 2004). Furthermore, some climatic variables can affect migrants through lag effects (e.g. precipitation or winter NAO), and, consequently, their effects could occur beyond wintering or passage dates.

Another added difficulty is the apparently low fidelity to the wintering grounds shown by many migratory species. In the case of the Palaearctic-African migratory system, recurrence of migratory species at African wintering grounds has been reported for only 60 species (Salewski et al. 2000a). This low fidelity at the species level is much lower at the individual level. Salewski et al. (2000a,b) found that just 4 out of 16 ringed species in the Comoé National Park (Ivory Coast) recurred in successive winters in the same ringed area. Individual recurrence ranged from 1 to 40% within these 4 species. In fact, most migrant species in sub-Saharan Africa show itinerancy within the wintering areas (Moreau 1972, Jones 1995), in some cases even performing well-defined intra-African migrations during winter. Such movements would be promoted by the progression of the dry season and a subsequent decline in the available resources (Jones 1995). This could be the reason for the low repeatability detected in the arrival dates of individuals for some species (Potti 1998, Hötter 2002, Berthold et al. 2004; but see Battley 2006). Since individuals overwinter in different areas each year, they would be affected by different conditions (Berthold et al. 2004).

If we do not know the precise wintering location of the studied population or we are studying a species with low wintering ground fidelity, 2 alternative methods can be used. Gordo et al. (2005) applied a conservative approach and considered all wintering ranges defined for the species, since they did not know the precise wintering area for their studied populations. For those species with broader wintering distribution, wintering range was divided into several climatic subregions to avoid the potentially confounding effect of the different intra- and interannual patterns of climatic variability. This approximation could also be useful to determine wintering areas. If we assume that interannual variability of arrival dates can be partially due to the variability in the departure date (Fig. 3, see Section 3.1), then those wintering areas with the strongest relationship to climatic patterns would be potential wintering area for the species (Rodríguez-Teijeiro et al. 2005, see also Szép et al. 2006). The same argument could be applied to determine the most important passage areas through the degree of association between arrivals and climatic patterns at those locations (Huin & Sparks 1998, 2000, Sokolov & Kosarev 2003, Ahola et al. 2004, Croxton et al. 2006, Hüppop & Winkel 2006, Sokolov 2006, Zalakevicius et al. 2006).

A second method would be the use of measures of arrival dates beyond 1 population (e.g. average for several populations; Gordo & Sanz 2006a) or the first sighted individual (e.g. total distribution of arrivals; Knudsen et al. 2007, this issue). Such measures would summarize the interannual variability for a bulk of populations or individuals, which offers a much better suited measure of migratory phenology. Furthermore, since these measures are a summary of migratory behaviour of many individuals, they would be more comparable to regional climatic measures (e.g. gridded or country data), because both variables would be working on a macroscale.

Acknowledgements. Three anonymous reviewers provided valuable comments that notably improved the first draft of this manuscript.

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Appendix 1. List of studies used for the quantitative assessment of climatic variables classified in each of the categories defined for Figs. 5a to e. In the case of Fig. 5d, the exact number of months used in each study is shown

Source	Type of explanatory variable (Fig. 5a)						Geographical origin (Fig. 5b)			Temporal definition (Fig. 5c)			No. of months (Fig. 5d)		Month (Fig. 5e)			
	Temp	Prec	Wind	NAO	ENSO	Others	Depart	Passage	Arrival	Daily	Month	Annual	Temp	NAO	0	-1	-2	-3
Ahas & Aasa (2006)				X						X			1, 3					
Ahola et al. (2004)	X			X				X	X	X			4					
Askeyev et al. (2007)	X								X	X			1		X	X		
Barbraud & Weimerskirch (2006)	X				X	X			X	X			1		X			
Barrett (2002)	X								X	X			1		X			
Beaumont et al. (2006)	X	X							X	X			3					
Both & Visser (2001)	X								X	X			1		X			
Both et al. (2005)	X							X	X	X			1			X		
Boyd (2003)	X	X	X	X		X	X	X	X	X			1	1, 4				
Bradley et al. (1999)	X								X	X			1					
Browne & Aebischer (2003)	X								X	X			1		X	X		
Butler (2003)	X								X	X			1					
Chambers (2005)	X	X					X	X			X							
Cotton (2003)	X			X	X		X			X			3	3				
Croxton et al. (2006)	X							X	X	X			1		X	X	X	X
Dolenec (2003)	X								X	X			3					
Forchhammer et al. (2002)				X						X				4				
Gordo & Sanz (2006a)	X	X					X		X	X			2		X	X		
Gordo et al. (2005)	X	X					X		X	X	X		2		X	X		
Hubálek (2003)				X							X			3				
Hubálek (2004)				X							X			3, 4				
Huin & Sparks (1998)	X	X						X	X		X		1		X			
Huin & Sparks (2000)	X	X						X	X		X		1		X			
Hüppop & Hüppop (2003)	X			X					X	X				4				
Hüppop & Hüppop (2005)	X			X					X	X				4				
Hüppop & Winkel (2006)	X							X	X	X								
Inouye et al. (2000)						X												
Jenkins & Watson (2000)	X								X									
Jonzén et al. (2006)				X						X				4				
Kaňuščák et al. (2004)	X	X		X			X	X	X	X			1, 4	4	X			
Lane & Pearman (2003)	X								X	X			1		X			
Ledneva et al. (2004)	X								X	X			2		X	X		
Lehikoinen et al. (2004)	X								X	X			1		X	X		
Loxton & Sparks (1999)	X								X	X			1, 2		X	X	X	
Loxton et al. (1998)	X								X	X			1, 2		X	X	X	
MacMynowski & Root (2007)	X			X	X				X	X			1	1	X	X		
Marra et al. (2005)	X			X		X			X	X			2	4	X	X	X	
Mason (1995)	X								X	X			1		X	X		
Mitrus et al. (2005)	X						X	X	X	X			1		X			
Murphy-Klassen et al. (2005)	X								X	X			1		X			
Ptaszyk et al. (2003)	X								X	X			2		X	X		
Rainio et al. (2006)				X						X				4				
Rodríguez-Teijeiro et al. (2005)	X						X	X	X	X			1		X	X		
Rubolini et al. (2007a)	X	X		X					X	X			1	3	X			
Saino et al. (2004b)						X	X			X								
Sinelschikova et al. (2007)	X	X	X				X	X		X			1		X	X	X	X
Sokolov & Kosarev (2003)	X	X		X			X	X	X	X			1	1, 3	X	X	X	X
Sokolov (2000)	X								X	X			1		X	X		
Sokolov (2006)	X	X		X	X		X	X	X	X			1	2	X	X		
Sokolov et al. (1998)	X								X	X			1		X	X		
Sparks & Braslavská (2001)	X								X	X			1		X			
Sparks & Carey (1995)	X	X							X	X	X		1		X	X	X	X
Sparks & Mason (2001)	X								X	X			3					
Sparks et al. (2005)	X			X					X	X			1	4	X	X	X	
Sparks et al. (2007)	X						X	X		X			1		X	X	X	
Stervander et al. (2005)				X						X				4				
Strode (2003)	X							X	X	X								
Sueur & Triplet (2001)	X								X	X			1		X			
Tryjanowski et al. (2002)	X								X	X			1		X	X	X	
Vähätalo et al. (2004)				X						X				4				
Weidinger & Král (2007)	X			X			X	X	X	X			1	4	X			
Zalakevicius et al. (2006)	X	X		X		X	X	X	X	X			1	3	X	X		