



# Climate change and timing of avian breeding and migration throughout Europe

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**ABSTRACT:** Bird breeding and spring migration phenology have advanced in response to climate change, but the effects differ between sites. Here, we examine the geographical variation in laying-date trends in a short-distance migrant, the European starling *Sturnus vulgaris*, and a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. We model the trend in laying date for these 2 species—between 1980 and 2004 for most of their European breeding areas—by combining geographical variation in mean laying date, the effect of temperature on laying date, and spatial variation in temperature change. Starlings are predicted to have advanced breeding over most of their range, with the greatest advance in north-eastern Europe. In contrast, pied flycatchers have delayed their laying in northern Europe, but have advanced their laying in western and central Europe. The species differ because pied flycatchers lay their eggs 25 d later at each site than starlings, and temperatures during these 2 periods show different trends. Temperatures during migration have also changed differently for populations heading to different breeding areas. This was most pronounced for pied flycatchers; northern populations experience an increase in temperatures during migration, while more southern populations presently still migrate at temperatures similar to those experienced 25 yr ago. As a consequence the southern population may be constrained in adapting to climate change by low temperatures during migration. There is a large contrast in how circumstances during migration and at the breeding grounds have changed: populations that advanced breeding most were subjected to the lowest temperature increases during migration. The temporal and spatial variation in temperature change has important consequences on how migrants adapt to ongoing climate change.

**KEY WORDS:** Laying date · Timing · Migration · Phenotypic plasticity · Temperature · *Ficedula hypoleuca* · *Sturnus vulgaris*

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## 1. INTRODUCTION

Migrant birds time their migration to make use of the profitable parts of the year in highly seasonal ecosystems, and escape to other areas when circumstances become hostile. A common migratory strategy is to breed in the short, but productive spring periods of arctic and temperate ecosystems and leave those areas to improve survival during the non-breeding season (Alerstam & Högstedt 1982). The most productive periods in such ecosystems occur during a short burst when vegetation grows at the start of spring (Lack 1968, Perrins 1970, van Balen 1973). Matching breeding time with this food peak enhances fitness, and tim-

ing of arrival should be closely matched with the food peak. The timing of this food peak differs between years depending on, e.g., spring temperatures (Visser et al. 2006), but especially long-distance migrants may not be able to match their arrival dates accordingly. At their wintering grounds these birds have probably little or no cues that predict the timing of peak food availability at their breeding grounds, 1000s of kilometres away (Coppack & Both 2002, Both et al. 2006b). Furthermore, long-distance migration generally takes a couple of weeks between start and arrival, reducing the opportunity for adjusting migration timing to annual variation in timing of the food peak in the breeding areas. As a result birds have evolved timing

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mechanisms based on circannual clocks, which are synchronised with day length variation during a particular part of the year (Gwinner 1996, Gwinner & Helm 2003). These clocks most likely evolved so that birds arrive in the breeding area at an optimal time for breeding in most years. Costs of early arrival under cold conditions (Møller 1994, Brown & Brown 1998, 2000) prevent evolution towards arriving too early.

Migration time has evolved to allow breeding at the optimal time, but recently the phenology at breeding areas has become progressively earlier as a result of climate change (Visser et al. 1998, 2006, Cresswell & McCleery 2003), and hence the optimal breeding date has changed (Visser et al. 1998, 2004, Both & Visser 2001). Many bird species, including migrants, breed earlier during warmer years (Dunn 2004), and, over the past decades, breeding times have become progressively earlier in many bird species (Crick et al. 1997, Winkel & Hudde 1997, Crick & Sparks 1999). The advance in breeding dates differs across geographic areas (Winkler et al. 2002), being strongest in areas where spring temperatures have increased most (Both et al. 2004). Long-distance migrants have advanced their breeding date, partly by reducing the interval between an unchanged arrival date and the start of breeding (Both & Visser 2001, Hüppop & Winkel 2006), but advances in arrival date are also commonly observed (for review see Lehikoinen et al. 2004, Gordo 2007, this issue, Rubolini et al. 2007). Generally the advance in arrival date was stronger for short- than for long-distance migrants (but see Jonzén et al. 2006), fitting the idea that short-distance migrants may be more flexible in reacting to changes at the breeding sites (Coppack & Both 2002, Hötker 2002). The observed change in arrival date in long-distance migrants may be at variance with the notion of rather inflexible timing mechanisms described above, but these changes may be the result of improved conditions en route, allowing faster migration rather than an earlier onset of migration (Huin & Sparks 1998, Coppack & Both 2002, Ahola et al. 2004, Bairlein & Hüppop 2004, Both et al. 2005, Gordo & Sanz 2005, Hüppop & Winkel 2006, Gordo 2007). Migration dates may also change because of changed conditions at the wintering grounds, allowing birds to start migration earlier (Cotton 2003, Saino et al. 2004, 2007, this issue, Sparks & Tryjanowski 2007, Studds & Marra 2007, this issue), although these circumstances may be unrelated to phenological conditions at the breeding grounds.

An earlier onset of migration probably requires a genetic change in timing mechanisms, and some evidence exists for such genetic variation of migration in the laboratory (Pulido et al. 1996, 2001) and in the field (Møller 2001), although it is not universal (Potti 1998; see also Pulido 2007, this issue). The increased selec-

tion for early breeding (and probably for early arrival date) in a Dutch pied flycatcher *Ficedula hypoleuca* population, without an actual change in arrival date, suggests that in this population either no genetic variation exists or that selection in other parts of the year prevent an evolutionary response (Both & Visser 2001). In contrast, it was recently shown that several long-distance migrants, including the pied flycatcher, have progressively advanced their spring migration date throughout the Mediterranean between 1980 and 2004 (Jonzén et al. 2006). Because this is halfway along the migratory route, and conditions at the African wintering grounds and along part of the migration route were assumed to be stable, Jonzén et al. (2006) surmised that the observed advance was an evolutionary response to climate change (see Both 2007 for discussion). Problems in the interpretation of these results are that the breeding destination of these migrating birds is not known in all cases, and that their breeding dates may not have advanced at all, because of the spatial variation in temperature changes (Both et al. 2004). If the phenology with regard to the breeding area has not advanced, selection is unlikely to have led to an evolutionary response; this is supported by the fact that large proportions of the long-distance migrants analysed by Jonzén et al. (2006) breed in Scandinavia where laying dates have not advanced strongly (see Table 1). In this study we aim to show how laying dates for a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*, and a short-distance migrant, the European starling *Sturnus vulgaris*, have changed over their European breeding grounds during the last 25 yr.

Global climate change has the connotation of rising temperatures at all places and during the whole year. We want to stress that this is not the case (IPCC 2001), and hence different bird species are affected differently by climate change, depending on where and when they breed and where and when they migrate (Sparks & Tryjanowski 2007). Also within species, populations differ in their response, because they breed at different places and during different periods of the year. The spatial-temporal variation in temperature change not only affects breeding time, but also migration time in complicated ways. Migrants take-off at higher temperatures during migration (Cochran & Wikelski 2005), and, if temperatures en route increase, they increase their migration speed (Schaub & Jenni 2001b, Gordo 2007). Migrants that experience increased temperatures en route as a result of climate change may arrive earlier at the breeding grounds, but the circumstances there may not have changed; thus, climate change could result in birds progressively arriving too early (Ahola et al. 2004) and during even colder conditions than in the past. We explore the effects of this spatial-

Table 1. Proportion of breeding population of species studied by Jonzén et al. (2006) passing through Italy and going to areas with and without spring warming. We assumed that birds passing through Italy were heading to the following countries that have experienced warming: Belarus, Belgium, Croatia, Czech Republic, Denmark, Germany, Hungary, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Netherlands, Poland, Slovakia, Slovenia, Switzerland, and to Estonia, Finland, Norway and Sweden that have not shown clear warming (Fig. 3A). Although the most southerly parts of these countries have some warming, quantitative data on bird numbers are only available for whole countries. Many birds probably also go to Russia, and in large parts of northern Russia there is no apparent warming, so the figures below are probably underestimates (see Fig. 3A). Data are from Birdlife International (2004). If the advance in migration date were the result of stronger selection for early arrival because of climate change, we would expect that species with a higher proportion of birds breeding in areas with spring warming would also show a stronger advance in migration date, for which we found no unequivocal evidence (correlation between the trend in 50th percentile in Italy with year and proportion breeding in areas with warming — Pearson's correlation:  $-0.28$ ,  $N = 9$ ,  $p = 0.54$ )

Common name	Scientific name	Total flyway population	Areas with spring warming	
			Population size	Proportion
Tree pipit	<i>Anthus trivialis</i>	13 609 545	4 984 545	0.37
Common redstart	<i>Phoenicurus phoenicurus</i>	1 929 915	609 915	0.32
Whinchat	<i>Saxicola rubetra</i>	2 801 157	1 876 157	0.67
Icterine warbler	<i>Hippolais icterina</i>	1 356 676	1 064 176	0.78
Common whitethroat	<i>Sylvia communis</i>	6 823 001	5 423 001	0.79
Garden warbler	<i>Sylvia borin</i>	7 976 055	4 226 055	0.53
Willow warbler	<i>Phylloscopus trochi</i>	37 665 870	8 265 870	0.22
Spotted flycatcher	<i>Muscicapa striata</i>	5 453 150	2 653 150	0.49
Pied flycatcher	<i>Ficedula hypoleuca</i>	4 303 922	1 378 922	0.32

temporal variation in temperature changes during the last 25 yr on migration and breeding in both a long-distance and a short-distance migrant.

## 2. METHODS

### 2.1. Study species

Pied flycatchers are small insectivorous passerines that breed in large areas of Europe and West Asia, and winter in West Africa at around  $10^{\circ}\text{N}$  (Lundberg & Alatalo 1992). The species breeds readily in nest boxes, and therefore large numbers of young are ringed in several European countries. The breeding ecology of the species is well known (Sanz 1997, Both et al. 2004), and it is one of the long-distance migrants for which detailed knowledge is available on its response to climate change (Both & Visser 2001, Sanz et al. 2003, Both et al. 2006a). Starlings were chosen because they are also cavity nesting species for which data on laying dates are available over a large part of their range. This species has also been ringed extensively, and good data are available on the timing of spring migration for populations breeding in different European countries (Fliege 1984).

### 2.2. Bird data selection and analysis

Breeding dates of pied flycatchers were taken from the review by Sanz (1997), supplemented with some data from Russia (Both et al. 2004). Only data from

latitudes higher than  $48^{\circ}\text{N}$  were used, because we had no recovery data from more southerly populations, and pied flycatchers at the Iberian Peninsula breed at high altitudes and comparatively late (Sanz 1997). The effect of temperature on laying date was analysed using 16 time series of pied flycatchers (21 878 nests) between 1980 and 2001 (see Both et al. 2006b for data selection), by means of GLMs (generalised linear model), with annual median laying date for each year–site combination as a dependent variable ( $N = 296$ ), and area (factor), local spring temperature (see below) and their interaction as explanatory variables.

In order to estimate how circumstances changed during spring migration, we need to know when migrants of different populations migrate and how fast they migrate. For this reason, we used recovery data on pied flycatchers provided by the national ringing centres of Denmark, Finland, Germany, the Netherlands, Norway, Sweden and the United Kingdom via the EURING office; most of these data will be presented elsewhere (C. Both unpubl. data). Here, we give a brief summary of methods and results, which were used as input for a model to analyse changes in temperature during the migratory journey. We selected individuals that were ringed as nestlings and were recovered between  $30$  and  $38^{\circ}\text{N}$  in the period from 1 March to 3 June; we only excluded cases for which too little information was available to assign a recovery date ( $N = 245$ ). Data on migration date from the more southerly wintering areas are not available, so we consider only the journey from northern Africa to the breeding grounds. We calculated the median recovery date of birds hatched in blocks of  $3^{\circ}$  latitude

by longitude, in order to have a reasonable estimate for local breeding populations. Only if there were >10 recoveries did we use the data for that particular block; in other cases, we took the data from 2 or 3 neighbouring blocks to have at least 10 recoveries ( $N = 9$ ). We analysed the effect of birth latitude by regressing the median recovery date for each block against the median latitude of birth.

The relationships between latitude of breeding ground and mean population arrival dates of pied flycatchers at the breeding grounds will be presented in a forthcoming study. In short, data from the literature (Curio 1959, Lundberg & Alatalo 1992, Sandberg 1996) were supplemented with data we collected at the Hoge Veluwe from 2003 to 2004, and data provided from a population at 64° N by J. T. Seppanen (see Forsman et al. 2002). We only included data for which arrival was scored for a large proportion of the population, and for males and females separately. From these data, we calculated that arrival date was, on average, 20 d prior to mean laying date for populations at 52° N, 15 d at 60° N and 10 d at 68° N.

For starling breeding and migration data, we used only data from the literature. The breeding data were taken from the handbooks by Glutz von Blotzheim et al. (1993) and Cramp & Perrins (1994); in addition, literature on starlings was scanned for data on laying dates (Kluyver 1933, Ojanen et al. 1979, Lundberg & Silverin 1986, Kallander & Karlsson 1993, Reid et al. 1999, Feare & Forrester 2002, Reid et al. 2002). Sources differed in whether data for single years were given or for several years combined. In 3 cases, we found time series of 7 yr or more; in these cases we analysed whether laying dates were correlated with spring temperature (see below). Data on timing of migration was taken from Fliege (1984), who plotted the mean recovery position from birds ringed as nestlings in the Netherlands, Germany, former Czechoslovakia, Denmark, Sweden, Switzerland and Finland, for each month, for both first year and older birds. We took the longitudes and latitudes from these maps, and calculated the mean values for young and old birds combined, for each month from January to the month of arrival at the breeding area.

### 2.3. Temperature data

Daily temperature data were taken from 155 weather stations across Europe obtained from <http://eca.knmi.nl/dailydata/index.php> (Klein Tank et al. 2002). We selected those stations that supplied daily temperature data from 1980 to at least 2000 and at most 2005. If stations were closer than 1° in distance, we selected 1 of them, because temperature data are

strongly spatially correlated. For some stations, data were not available for the whole period from 1980 to 2005, and we excluded stations for which <21 yr of data were available.

### 2.4. Spatial models of local temperature change on breeding dates

In our breeding date model our aim was to investigate the spatial variation in predicted laying-date change between 1980 and 2004, for both pied flycatchers and starlings. We do not know whether birds react directly to temperatures, food availability (which most likely is related to temperature), or to the phenological states they encounter upon arrival at the breeding grounds, but we know that laying dates are strongly correlated to temperatures in almost all bird species (Dunn 2004). We do not know either exactly over which time window we have to average the temperatures to capture the biological processes underlying the effects of temperature on breeding dates. Here, we use as a time window the 30 d preceeding the average laying dates for each latitude from the data provided in Figs. 1A & 2A, since annual mean laying dates within populations are strongly correlated with annual mean temperatures during this time window for both tit *Parus* species (Visser et al. 2003) and flycatchers (Both et al. 2004). Both et al. (2004) showed that the change in temperature in this period strongly predicts the change in laying date.

The predicted change in breeding date was calculated for each site by the following steps: (1) for each weather station, we calculated the predicted site-specific mean laying date for the latitude, longitude and altitude using the relationships between population laying date and these explanatory variables (including the interaction longitude  $\times$  latitude, which did not explain more variance), and the time window for temperatures was set as the 30 d before this calculated laying date; (2) for each year we calculated the average temperature at that site for this time window; (3) we calculated the slope of the least-squares regression of the annual temperatures on year, multiplied by 25 for the 25 yr period; and (4) this temperature change was converted into a predicted laying-date change, by multiplying it with the species-specific slope of laying date on temperature, giving the predicted change in laying-date for 1980 to 2004. (5) The weather station-specific predicted laying-date changes were used to produce isocline maps with the kriging procedure in ArcGIS to cover the European breeding range of pied flycatchers and starlings (excluding south-eastern Europe). Isocline maps of laying date and temperature trends were calculated for each of 12 weather stations, using uni-

versal kriging with a circular semivariogram model in ArcGIS software, v. 9.2. This interpolation method gives weight to the distance of a point to the measured points based on spatial correlation, rather than giving weight only based on the distance to the measured points (inverse distance interpolation). The standard error (SE) of the interpolation normally increases with distance to the measured points. For the final map, we selected only the depicted estimates for the areas with reasonable values with respect to the SEs.

### 2.5. Spatial models of local temperature change on migration environments

In the migration model, our aim was to show how the temperatures during the migratory journey changed

for populations at different breeding latitudes between 1980 and 2004. We developed different models for starlings and pied flycatchers, because information about the timing of migration differs between species, and the speed of migration is much higher for long-distance migrants than for short-distance migrants. For migration, we had to guess about the time window that is important to capture the biological processes determining migration decisions. Migratory take-off in individual long-distance migrants was found to occur only in nights after days with certain minimal temperatures in North American thrushes (Cochran & Wikelski 2005), and stop-over time is also related to local temperatures (Schaub & Jenni 2001a,b). To capture both this immediate effect of temperature on take-off and a longer term effect covering both the phenological state (i.e. food availability) and the fuelling rate (i.e.

food intake and energy expenditure), we chose to take average temperatures during a 10 d window before the calculated average migration date at each site in our pied flycatcher migration model. This model was calculated for the migratory journey throughout Europe for populations breeding at 3 latitudes: 52, 60 and 68°N. The calculations for each breeding latitude consisted of the following steps: (1) migration date in North Africa was calculated as well as arrival date at the breeding grounds; (2) travel speed was calculated in latitudinal degrees per day, and, for each weather station, we calculated the mean passage time using the latitude of the site; (3) we calculated the annual mean temperatures for the 10 d period before this average passage time; (4) from this, we calculated the slope of the least-squares regression of the annual temperatures on year; and (5) the weather station-specific temperature changes were used to produce maps with the kriging procedure in ArcGIS.

The model for temperature changes during migration of starlings was made in an essentially similar manner, but we calculated monthly mean temperatures for each month between January and breeding for the mean recovery site for starlings ringed in 6 European countries (Switzerland, former Czechoslovakia, the Netherlands, Germany, Sweden and Finland).

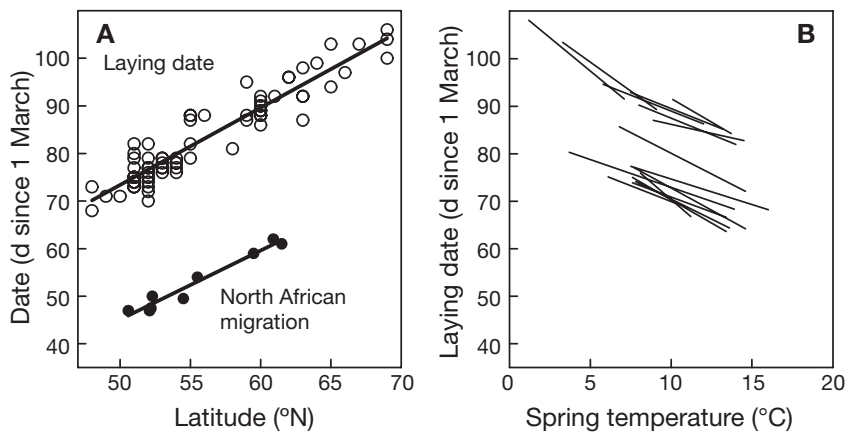


Fig. 1. *Ficedula hypoleuca*. (A) Effect of breeding latitude on mean laying date of pied flycatchers across Europe and their median recovery date in North Africa. (B) Effect of local spring temperature on annual median laying dates between 1980 and 2001 for 16 populations across Europe. Each line is the least-squares regression line for the regression of temperature on laying date for the observed variation in local spring temperatures

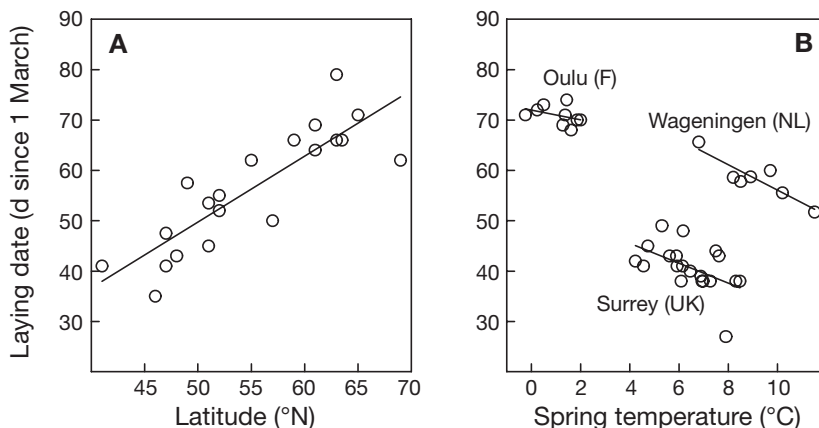


Fig. 2. *Sturnus vulgaris*. (A) Effect of breeding latitude on mean laying date of European starling across Europe. (B) Effect of mean annual spring temperature on annual mean laying date for 3 populations of starlings for which >7 yr of data were available. F: Finland; NL: The Netherlands; UK: United Kingdom

These populations winter in different parts of Europe and migrate via different routes to their breeding areas. In January starlings are still at their wintering sites, but from February onwards they start to migrate back to their breeding sites. The mean monthly location of recoveries for both first year and older birds was taken from Fliege (1984), and weather stations closer than 1.5° of latitude or longitude were selected to average monthly temperature for each migration site. We calculated the change in temperature for each month–site combination during migration, by calculating the least-squares regression coefficient of monthly temperature on year for 1980 to 2004, and multiplying this annual change by 25 to cover the whole period.

### 3. RESULTS

#### 3.1. Breeding data

Pied flycatchers *Ficedula hypoleuca* breed later at higher latitudes (see Fig. 1A), more easterly longitudes and higher altitudes [GLM (means are presented with SE): laying date = 0.022 (4.13) + 1.42 (0.08) × latitude + 0.15 (0.06) × longitude + 0.0085 (0.0021) × altitude; latitude:  $F_{1,67} = 301.02$ ,  $p < 0.0001$ ; longitude:  $F_{1,67} = 7.51$ ,  $p = 0.008$ ; altitude:  $F_{1,67} = 16.40$ ,  $p = 0.0001$ ; total  $R^2 = 0.91$ ]. For 16 populations for which laying-date time series were available between 1980 and 2001, there was a strong negative effect of spring temperature on the annual median laying date; this temperature effect did not differ significantly between populations (Fig. 1B; GLM: area:  $F_{15,275} = 147.9$ ,  $p < 0.0001$ ; spring temperature:  $F_{1,275} = 173.8$ ,  $p < 0.0001$ ; interaction area × temperature:  $F_{15,260} = 1.40$ ,  $p = 0.15$ ). Flycatchers advanced laying date by 1.57 d (0.12) for each degree temperature (°C) increase.

Starlings *Sturnus vulgaris* also breed later at higher latitudes (see Fig. 2A) and more easterly longitudes [GLM (SE): laying date = -0.95 (10.59) + 0.96 (0.21) × latitude + 0.43 (0.16) × longitude; latitude:  $F_{1,17} = 20.34$ ,  $p = 0.003$ ; longitude:  $F_{1,17} = 6.92$ ,  $p = 0.017$ ; total  $R^2 = 0.78$ ]. We had no data on the altitudes of the sites and, therefore, could not analyse the altitudinal effect. Annual mean laying dates (MLD) were earlier in years with higher temperatures for the Dutch population in Wageningen (MLD = 50.24 - 2.52 × temp;  $F_{1,5} = 21.31$ ,  $p = 0.006$ ), for the British population in Surrey [MLD = 22.34 - 1.97 (0.77) × temp;  $F_{1,18} = 6.56$ ,  $p = 0.02$ ], but we found no significant effect for the Finnish population in Oulu [MLD = 71.96 - 0.96 (0.86) × temp;  $F_{1,7} = 1.26$ ,  $p = 0.30$ ]. The effect of spring temperature did not differ across populations and was on average a 2.03 d (0.49) advance for each degree temperature (°C) increase

(ANCOVA: area:  $F_{2,32} = 173.5$ ,  $p < 0.001$ ; temperature:  $F_{1,32} = 17.48$ ,  $p < 0.001$ ; area × temperature:  $F_{2,30} = 0.39$ ,  $p = 0.68$ ).

#### 3.2. Spatial variation in laying-date trends across Europe

In reaction to recent climate change, pied flycatchers were predicted to have advanced their laying dates at mid-latitudes (45 to ca. 60° N) throughout Europe, but at the same time more northerly populations delayed their laying date between 1980 and 2004 (Fig. 3A). At mid-latitudes, there was also a tendency towards stronger advance in laying date at more easterly longitudes.

Starlings were also predicted to have advanced their laying date in response to climate change in large parts of Europe (Fig. 3B), but there are strong spatial differences compared to the pied flycatcher. In the area in central Europe where pied flycatchers were predicted to have advanced most, starlings most likely have not advanced their breeding dates (as calculated on the basis of temperature changes). In contrast, the strongest predicted advance in laying date was found in northeastern Europe, an area where pied flycatchers have not advanced their laying date.

#### 3.3. Spatial variation in changes in migration environments

Pied flycatchers hatched at more northern and eastern breeding areas migrated later through northern Africa compared to more southern and western breeding populations [recovery date (SE) = -16.14 + 1.22 (0.12) × latitude + 0.15 (0.06) × longitude; latitude:  $F_{1,6} = 99.60$ ,  $p < 0.001$ ; longitude:  $F_{1,6} = 7.18$ ,  $p < 0.037$ ;  $R^2 = 0.97$  (all in days since 1 March)].

We found large variations in temperature changes between 1984 and 2004 for pied flycatcher migrating to different breeding latitudes (Fig. 4). Birds breeding at 52° N experience relatively small changes in temperature during migration over most of the route through Europe (Fig. 4A). In contrast, flycatchers heading to breeding areas at 60° N profit from a general warming over most of their migratory trajectory through Europe, but, when approaching the breeding grounds, this warming changes to even slightly colder conditions (Fig. 4B). Pied flycatchers breeding at 68° N experience warmer conditions in the southern part of Europe, but cooler conditions during the second half of their journey through Europe (Fig. 4C).

Starlings from Switzerland and former Czechoslovakia overwinter in Spain, where January and February tem-

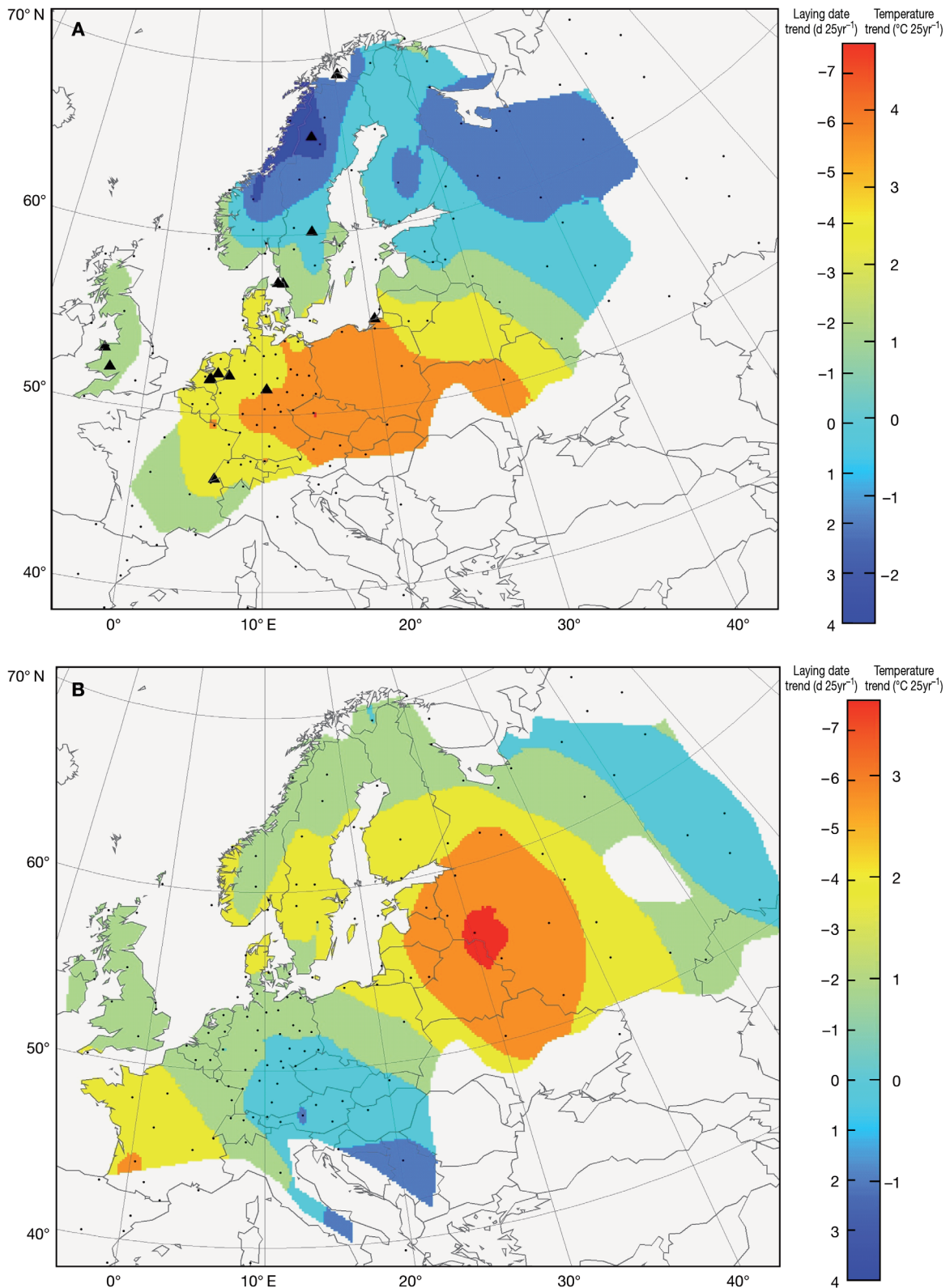


Fig. 3. *Ficedula hypoleuca* and *Sturnus vulgaris*. Spatial variation in predicted laying-date trend (1980 to 2004) in: (A) pied flycatchers and (B) European starlings. Dots: weather stations used to calculate local laying-date trend (derived from temperature data); triangles: source of pied flycatcher laying-date time series. Scale: 25 yr interpolated temperature trends on which laying-date trends were based

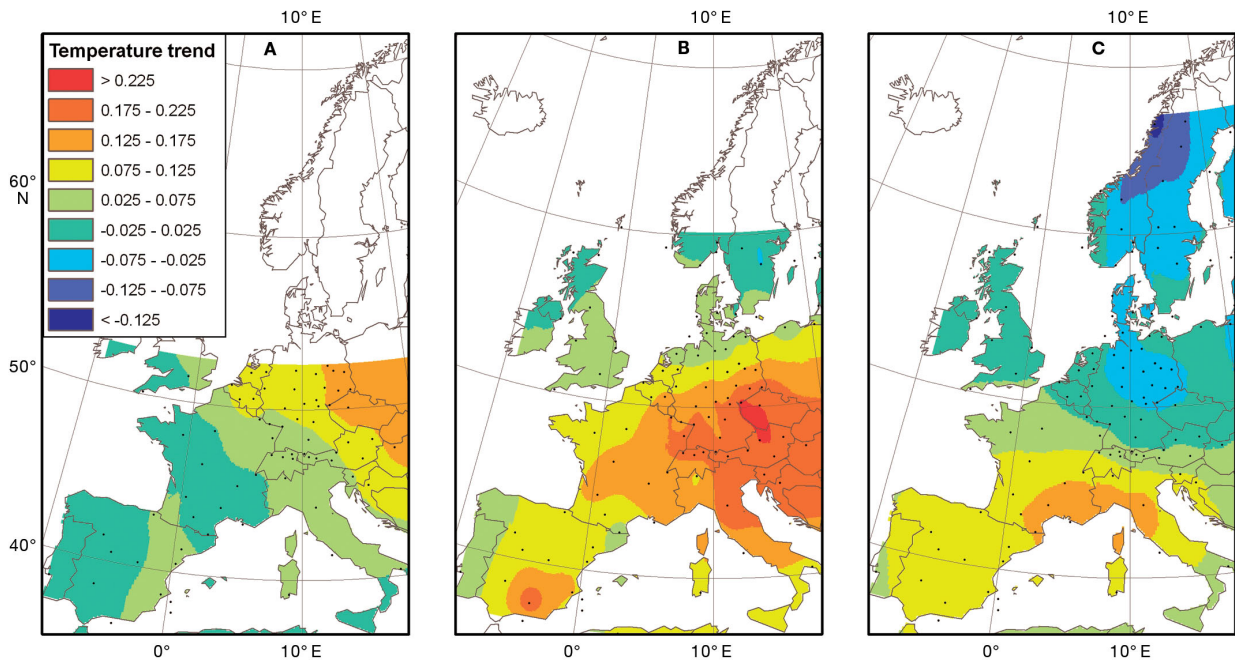


Fig. 4. *Ficedula hypoleuca*. Trends in temperature ( $^{\circ}\text{C yr}^{-1}$ , 1980 to 2004) at the time of migratory passage of pied flycatchers breeding at: (A)  $52^{\circ}\text{N}$ , (B)  $60^{\circ}\text{N}$  and (C)  $68^{\circ}\text{N}$ . Dots: weather stations used to calculate the temperature trend

peratures have shown no significant increase (Fig. 5). During migration in March and April, temperatures have increased along their migration routes for both populations. Starlings from the Dutch, German, Swedish and Finnish populations overwinter in north-western Europe; for all of these populations, the temperatures have increased at their wintering sites (January) and along most of their migratory route (February to April; Fig. 5).

#### 4. DISCUSSION

During the last decades global mean temperatures have increased (IPCC 2001), but strong geographical and temporal variation exists in temperature changes, which must be important for long-distance migrants during their annual movements. In this study we show that the predicted change in breeding dates over time

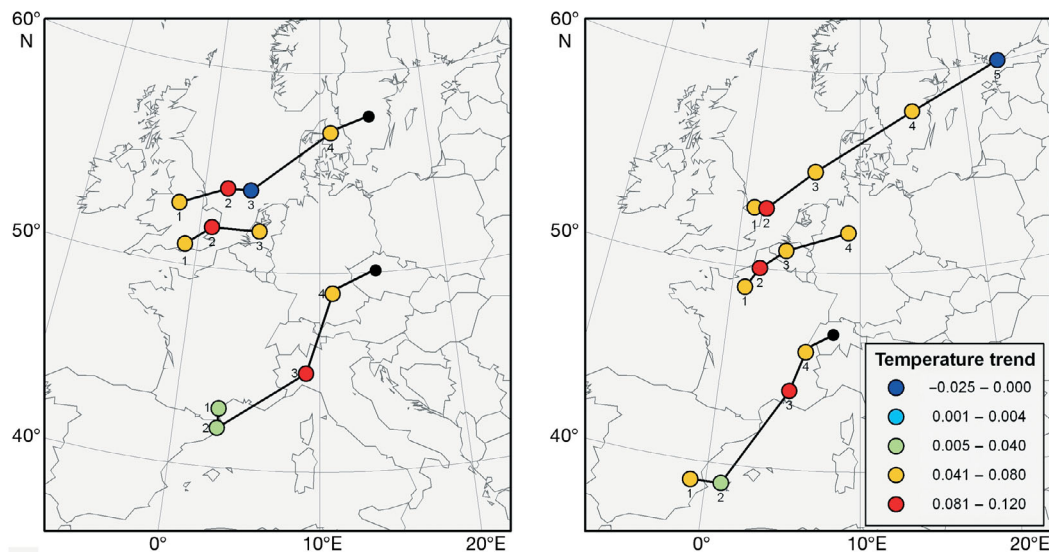


Fig. 5. *Sturnus vulgaris*. Trends in temperature ( $^{\circ}\text{C yr}^{-1}$ , 1980 to 2004) during late winter and migration of European starlings breeding in: (A) former Czechoslovakia, the Netherlands and Sweden and (B) Switzerland, Germany and Finland. Each point is the mean recovery position for a given month, and numbers refer to the month



differs strongly between species and geographical locations, because the 2 examined species breed at different times of the year and there is strong spatio-temporal variation in temperature change. Not only do temperature changes differ in breeding areas, but also in the areas that these migrants pass through during their migratory journey. We showed that, for the long-distance migratory pied flycatcher *Ficedula hypoleuca*, the population with the strongest predicted (and observed; Winkel & Hudde 1997, Both & Visser 2001) change in breeding dates (48 to 54°N) experience the least change in temperatures during spring migration, and these populations have not advanced their spring arrival date (Both & Visser 2001, Both et al. 2005, Hüppop & Winkel 2006). In contrast, more northern populations breeding in areas without increased temperatures (>60°N) are now encountering much better circumstances en route, and their spring arrival has advanced in the last decades (Hüppop & Hüppop 2003, Ahola et al. 2004, Jonzén et al. 2006). Migrants are thus faced with different rates of temperature change in different parts of their annual cycle, and this must affect their capability to adapt to climate change.

#### 4.1. Climate change and laying-date changes

We believe that our laying-date results for the 2 species will be applicable to other species with similar breeding phenology. Our model on the change in breeding date across Europe was well parameterized for the pied flycatcher, but less so for the European starling. The predicted trend in pied flycatcher laying dates over the years was in close agreement with the observed change at many sites (Winkel & Hudde 1997, Slater 1999, Sokolov 2000, Both et al. 2004), the correlation between the predicted change between 1980 and 2004 and the observed change (1980 to 2000) being 0.80 (Pearson's  $r$ ,  $n = 16$ ), which is not surprising because these data were used as input for the laying date–temperature relationship. Note that the observed quantitative trend in laying date was stronger than that predicted (thus more delay in areas that got cooler, and more advance in areas that got warmer), because the between-population response of laying-date change to temperature change (Fig. 1 in Both et al. 2004) was steeper than the within-population response (our Fig. 1B) used in this model ( $-3.09 \pm 0.34$  vs.  $-1.57 \pm 0.12$  d °C<sup>-1</sup>), but we do not understand these differences yet. For European starlings, time series of laying dates were only available from 3 populations, and the within-population response of annual laying date to local temperature did not differ between populations. It may, however, be the case

that in northern populations the relationship is weaker (see Fig. 2B), which would make a qualitative difference in the geographical pattern of laying-date changes, with probably weaker changes towards the far north.

The geographic difference in predicted laying date changes between starlings and pied flycatchers is the result of temperatures changing at different rates during different periods in the spring and at different locations. In the early spring, when starlings start to breed, temperatures have increased over most of Europe, with the strongest change in northeastern Europe and the least change in central Europe. Pied flycatchers breed, on average, 25 d later, and at their breeding time temperatures have increased at latitudes <60°N, but decreased mostly at more northerly latitudes. This difference between latitudes for predicted breeding time trends in flycatchers is partly due to a date difference: during the last decades there has been a sharp increase in temperatures in western and central Europe at the end of April and the beginning of May (see e.g. Visser et al. 1998, Ahola et al. 2004), which 'disappears' later in spring when the flycatchers start breeding in northern Europe. This temporal and spatial variation in temperature trends may have a negative effect on the birds' breeding success: starlings that start to breed earlier in northern Europe will hatch their eggs at about the moment when pied flycatchers start to breed, a period when it got colder instead of warmer. Consequently, if they indeed have advanced their breeding dates in reaction to the temperature increase during the pre-breeding period, they now raise their offspring under increasingly colder conditions, with potentially less food. Temperature increases before laying may, therefore, lead to a general advance in laying date, but the declines in temperatures after laying will lead to increased selection for later laying (Visser et al. 2004). A full prediction of the impact of climate change on avian breeding dates and their fitness consequences requires knowledge on whether temperatures continue to change at these different rates at different times and places.

#### 4.2. Temperatures trends during migration

We know little about the actual migration times of passerine populations heading for different breeding areas and the speed of their migration, but, in general, more northerly populations migrate later in spring than do southerly populations (Fransson 1995, Bell 1996). As a consequence of variation in migration time and the within-year variation in temperature trends over the years, different populations experience different temperature changes during their migratory journey.

Although additional environmental factors like wind speed and direction also affect migration speed (Jenni & Schaub 2003, Schaub et al. 2004, Gordo 2007, Sinelshikova et al. 2007), we focus here just on temperature change for the sake of simplicity and because high temperatures are often affected by southerly (and hence tail-) winds.

There is a strong latitudinal trend in the dates of pied flycatcher migration through northern Africa (Fig. 1A), and the early migrating western and central European pied flycatchers do not experience increased temperatures during their migratory journey throughout Europe. These populations have advanced their breeding date most strongly (Both et al. 2004; and Fig. 3), but have not arrived earlier in the spring in all populations for which arrival dates have been published (Both et al. 2005, Hüppop & Winkel 2006), probably because circumstances in the European part of migration were unchanged (see also Hüppop & Winkel 2006). In contrast, late-migrating, more northerly breeding populations have not advanced their breeding dates, but conditions during their migration have changed considerably during the last decades, leading to earlier arrival in Fennoscandia (Hüppop & Hüppop 2003, Ahola et al. 2004, Jonzén et al. 2006). This most likely means that these populations now arrive under colder conditions than in the past, which may entail increased mortality costs, especially for early arrivals (Møller 1994, Brown & Brown 2000).

Increasing migration speed under high temperatures (Cochran & Wikelski 2005, Marra et al. 2005, Saino et al. 2007, Sparks & Tryjanowski 2007) may seem an important adaptation to track climatic variability, because it allows birds to arrive and breed earlier in warm years. However, if the temperatures en route do not have high predictive power for the circumstances at the breeding grounds, this strategy fails, and may even lead to individuals arriving too early if they do not halt their migration when encountering adverse circumstances (Brown & Brown 1998, Jonzén et al. 2007). We think that long-distance migrants in particular face the problem of adapting to climate change, because of the different temperature trends at different places and times of the year as observed during the last 25 yr.

There is some debate on whether short-distance migrants react more or less strongly to climate change with respect to their migration dates than do long-distance migrants (Lehikoinen et al. 2004, Jonzén et al. 2006, Rubolini et al. 2007). Our analyses show that the difference between long- and short-distance migrants may vary geographically, depending on when a species migrates and how strongly the temperatures during the migratory flight path have changed. In western Europe short-distance migrants are, for example, expected to advance their arrival more than long-

distance migrants, but in northern Europe the reverse is expected. These expectations are based on the assumption that most of the trends observed are the result of phenotypic, rather than genetic changes in migration time; thus, we also need to address the potential for evolutionary responses (Gienapp & Merila 2007).

#### 4.3. Evolution of migration and breeding dates

Until now most trends in avian laying dates in response to climate change were reported as phenotypic adjustments to increased temperatures, rather than evolutionary responses resulting in changing gene frequencies (Przybylo et al. 2000, Both & Visser 2001). It is unclear why, so far, no reports exist of evolutionary responses in laying dates, because selection for early laying has increased in several species (Visser et al. 1998, Both & Visser 2001; but see Reale et al. 2003). Although several studies have shown that spring migration dates are also related to environmental variables at the wintering grounds or en route (Huin & Sparks 1998, Coppack & Both 2002, Ahola et al. 2004, Bairlein & Hüppop 2004, Saino et al. 2004, 2007, Both et al. 2005, Gordo & Sanz 2006, Hüppop & Winkel 2006, Sparks & Tryjanowski 2007), changes in spring migration have recently been claimed to be an evolutionary response to climate change (Jonzén et al. 2006). This reasoning was based on the fact that many migrants have advanced their passage through the Mediterranean (measured at an Italian study site) during the last decades, and that ecological circumstances south of this area had not improved. Furthermore, it was assumed that climate change leads to increased selection for early breeding and arrival in all these birds, favouring the early migrating genotypes. There are, however, several problems with this reasoning, making the claim of an evolutionary response at least premature at this moment (Both 2007). The most prominent problem is that several species with an advanced migration date in the Mediterranean have a high proportion of their breeding population in areas with little or no spring warming (see Table 1, Fig. 3A), and (contrary to expectations) no correlation was found between the proportion of the population breeding in areas with clear spring warming and the advance of migration date (Table 1). Furthermore, there may even be increased selection for later, instead of earlier, arrival at more northern sites. We know that migration speed is strongly related to climatic effects at the wintering grounds and en route (Cotton 2003, Ahola et al. 2004, Cochran & Wikelski 2005, Gordo et al. 2005, Marra et al. 2005, Hüppop & Winkel 2006, Gordo 2007), and the advanced progress made at the

midway point during the migratory route from the African wintering grounds to the European breeding grounds is most likely a phenotypic response to changed environmental conditions, although an advance was still found after including African climatic variables (Saino et al. 2007).

An evolutionary response to climate change may not just be a change in the frequencies of the local gene pool; rather we expect that genetic exchange between populations will play an important role (Møller & Merila 2004). If birds do adjust their arrival date insufficiently to the optimal breeding period of their natal area, they may extend their migratory journey to the north (or uphill) until they reach a place where they can breed at the optimal time (Coppack & Both 2002). These movements of locally maladapted individuals can speed up an evolutionary response to climate change, because new genotypes with earlier migration dates are introduced into the population, on which selection can act. The success of such a process depends strongly on the relative reproductive success of these immigrants compared with the native birds. The spatial variation in laying-date trends across Europe means that maladapted central European birds are expected to move to the north, but that they settle in areas without spring warming where their genotypes for earlier migration may not be an advantage at all.

Variation in temperature trends in space and time are an important aspect of climate change, which has been mostly ignored so far in the study of adaptation to climate change. Migrant birds in particular have to face this variability, because they rely on a whole series of sites during the year, and therefore changes during the entire annual cycle should be considered (Hedenström et al. 2007, this issue). To understand the impact of climate change we need to study movements of individual birds during their life time and the effects climatic factors have on them. Small-scale devices to track birds may become feasible for small passerines in the near future, enabling researchers to address these questions. We need to realise that the essential studies on the link between migration and breeding ecology should not be concentrated on a single population, because populations may differ to a large extent on when and where their timing is constrained by environmental factors.

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