Do long-distance migrants use temperature variations along the migration route in Europe to adjust the timing of their spring arrival?

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Arrival of long-distance migrants (LDMs) has been frequently linked to temperature by correlating the arrival dates with temperature from one or a few sites along the supposed migration route. We used a site-independent approach, and correlated the arrival dates of LDMs with the temperature gridded over the entire Europe to study the spatial extent of correlations. We found extensive and statistically significant spatial correlation patterns between the arrival dates and the monthly temperature during or a month preceding arrival. These correlations were in most cases strongest 500–2000 km from the sites of arrival. The correlations indicate that most of the LDMs slowed down or speeded up migration according to yearly variations in temperature or linked phenology. This adjustment of migration speed along the migration route may help LDMs match their arrival to the annual variability of phenology in their breeding grounds.

Introduction

Spring arrival of long-distance migrants (LDMs) to northern Europe is linked to temperature in mainland Europe (Hüppop and Hüppop 2003, Gordo 2007, Lehikonen and Sparks 2010). It has been suggested that birds adjust the phenology of their migration to yearly variations in spring advancement according to temperature related cues in vegetation (e.g. Tøttrup *et al.* 2008). Correct timing of arrival is important for birds since early birds can get the best territories (e.g. Newton 2008) and successful breeding can be dependent on matching the breeding cycle to temporal variations in the abundance of food sources (e.g. Both *et al.* 2006).

It is, however, less clear where along the migration route this temperature-based adjustment may take place. One way to study this is with correlation analysis using temperature at a few selected sites (e.g. Zalakevicius *et al.* 2005). One finding of such studies is that the strongest correlations are often not found at the site of arrival but in a location or set of locations at least several hundreds of kilometres in the direction where the birds are supposed to arrive from (Ahola *et al.* 2004, Sokolov 2006).

As the migration routes of passerines are typically not very well known, a good alternative to using temperatures from a few sites is to cor-

relate migration data spatially with temperatures gridded over large areas. This site-independent approach was pioneered by Hüppop and Winkel (2006) with the pied flycatcher *Ficedula hypoleuca*. In the pied flycatcher, the pattern of correlation was strongest in a southerly or southwesterly direction from the sites of arrival. Hüppop and Winkel (2006) hypothesised that individuals migrating along different routes are unequally affected by temperature changes. Bird migration data and population dynamics parameters have also been correlated with gridded vegetation indices when searching for wintering and migration areas of European LDMs (Szép *et al.* 2006), and with gridded wind data to study the effects of wind and temperature on the song thrush (*Turdus philomelos*) migration (Sinelschikova *et al.* 2007).

The use of gridded data has, however, remained an exception, probably because large gridded datasets have not been as easy to use as temperatures from a few sites (Lehikoinen and Sparks 2010). Such technical issues should now be mostly resolved as sophisticated web-based tools for correlating time series with gridded data have been available for several years. In this study, we examine the patterns of correlation between the arrival dates and gridded temperatures for 12 LDMs in Europe using the Climate Explorer of the Royal Netherlands Meteorological Institute (Oldenborgh *et al.* 2009). Our study is to our knowledge the first one where correlation patterns for a large number of species are studied with gridded temperatures.

Our hypothesis is that statistically significant correlation patterns should be indicative of the areas where birds slow down or speed up migration according to yearly variations in spring advancement. The location of the highest negative correlations should also roughly fit the migration routes indicated by ring encounters.

Our objective was to find the locations along the migration route where the timing of arrival associates with the mean monthly temperature gridded over Europe (as a proxy of phenology) during or prior to the month of arrival. The areas with the strongest associations between timing and temperature should also be those where temperature changes associated with global climate change might have most effect on the future timing of migration of long-distance migrants.

Material and methods

Arrival data

We used spring-arrival dates of ten Finnish LDMs observed at the Hanko Bird Observatory, southern Finland (59°49´N, 22°54´E) during 1979–2010: lesser black-backed gull (*Larus fuscus fuscus*), lesser whitethroat (*Sylvia curruca*), whitethroat (*S. communis*), garden warbler (*S. borin*), blackcap (*S. atricapilla*), willow warbler (*Phylloscopus trochilus*), chiffchaff (*P. collybita*), pied flycatcher (*Ficedula hypoleuca*), spotted flycatcher (*Muscicapa striata*) and common redstart (*Phoenicurus phoenicurus*). All *Sylvia* species, willow warbler and spotted flycatcher breed regularly at the observatory area, but migrants are generally much more numerous than local breeders (Lehikoinen and Vähätalo 2000). The spring migration period was considered to span the period from 20 February to 15 June (Lehikoinen and Vähätalo 2000, Vähätalo *et al.* 2004). Years of poor observation activity (the springs 1989, 1990, 1993; < 20 days of observation) or too little data (< 20 observed individuals) were excluded from the analysis. In nocturnal migrants, we used daily staging numbers, but in diurnal migrants (lesser black-backed gull) we used data of birds observed in active migration. We examined separately the arrival dates of the early and the median migrants by using the 5 and 50 percentiles, respectively, for the birds observed during the spring migratory period at the Hanko Bird Observatory (Table 1).

We also used spring migration data from four other sites in Europe: the mean arrival dates for chiffchaff in Rybachy (Baltic Russia) in 1959–2002 and in Helgoland (German North Sea coast) in 1960–2001 (Hüppop and Hüppop 2005, Sokolov 2006). The mean arrival dates for chiffchaffs passing Rybachy ranged from 17 April to 9 May with mean (± SD) on 28 April (± 6 days; *n* = 44). In Helgoland, the corresponding range for mean arrival date was from 30 April to 6 June with mean (± SD) on 16 May (± 8 days, *n* = 42). A Moravian (Czech Republic) dataset concerned the first arrival dates (FAD) of the collared flycatcher (*Ficedula albicollis*) ranging from 13 April to 30 April with mean (± SD) on 22 April (± 4 days, *n* = 30, Weidinger and Kral 2007). A Kazan (Russia) dataset concerned the FADs of the greenish war-

bler *Phylloscopus trochiloides* ranging from 3 to 29 May with the mean (± SD) on 12 May (± 5 days, $n = 40$, Askeyev *et al.* 2007).

All data were detrended before the analysis to exclude the possible effects of shared trends in temperature and migration data. If trends were not excluded, significant correlations could also be found in areas where temperature trends and the migration schedule had the same trend without relevance to migration of the species studied (Lehikoinen and Sparks 2010).

Ring encounters

Ring encounter data for birds ringed in Finland were obtained from the Ringing Centre at the Finnish Museum of Natural History. All foreign encounters from spring months were included. Encounters with inaccurate finding data were omitted, i.e. only encounters with precise finding date (± 2 weeks or less), precise finding location (± 10 minutes or less) and encounters of alive or freshly dead birds were included.

In the case of the lesser black-backed gull, only encounters of adult birds were accepted because many immature birds still linger in the non-breeding areas and are very seldom seen at the Hanko Bird Observatory during spring migration. Subsequently, only encounters of birds ringed as adults, or birds ringed as chicks but encountered as adults (> 3rd calendar-year) were included. The ring encounters were plotted on the maps using MapInfo Professional 9.5.1 (Pitney Bowes Software Inc. 2008).

Temperature data

We used mean monthly temperatures at a grid-cell resolution of 0.5° found in Global Historical Climatology Network version 2 and the Climate Anomaly Monitoring System (GHCN/CAMS; Fan and van den Dool 2008). For birds with the mean arrival date in the first half of the month, we correlated the arrival dates with the temperatures of preceding month (e.g., the arrival dates having a mean between 1 and 15 May were correlated with the mean temperature of April). If the birds arrived in the second half of the month, we used the mean temperatures of the same month. As an exception, we correlated the FAD of greenish warblers (mean on 12 May) with the May temperatures.

The use of monthly mean temperatures has been common in recent bird migration studies (Lehikoinen and Sparks 2010). It is, however, not clear if this is optimal. Ahola *et al.* (2004) studied the migration of the pied flycatcher with running 3-week periods, and found that a time window slightly longer than a month was most applicable for the population studied. Hüppop and Winkel (2006) used a two-week period as this is roughly the time that the species studied (pied flycatcher) spends on migration from the Mediterranean to Germany.

Table 1. The arrival dates of early and median migrants observed at the Hanko Bird Observatory during the spring migration periods in 1979–2010. The early and median migrants were described by 5 and 50 percentiles, respectively. The table shows the mean arrival dates and their standard deviation in days as well as the earliest and latest arrival dates for the number of seasons given by *n*.

Species	5%: mean ± SD, min–max	50%: mean ± SD, min–max	*n*
Lesser black-backed gull (*Larus fuscus*)	10 April ± 5, 1–21 April	24 April ± 6, 9 April–11 May	27
Blackcap (*Sylvia atricapillus*)	8 May ± 9, 26 April–29 May	26 May ± 8, 2 May–6 June	24
Garden warbler (*Sylvia borin*)	23 May ± 5, 13 May–3 June	1 June ± 5, 22 May–12 June	27
Lesser whitethroat (*Sylvia curruca*)	11 May ± 5, 1–29 May	25 May ± 5, 11 May–4 June	28
Whitethroat (*Sylvia communis*)	18 May ± 6, 8–31 May	1 June ± 3, 26 May–8 June	28
Chiffchaff (*Phylloscopus collybita*)	20 April ± 7, 6 April–11 May	6 May ± 6, 22 April–19 May	25
Willow warbler (*Phylloscopus trochilus*)	8 May ± 4, 30 April–16 May	24 May ± 5, 12 May–3 June	28
Spotted flycatcher (*Muscicapa striata*)	19 May ± 6, 10 May–5 June	31 May ± 4, 24 May–11 June	27
Pied flycatcher (*Ficedula hypoleuca*)	6 May ± 7, 23 April–28 May	18 May ± 8, 30 April–6 June	27
Common redstart (*Phoenicurus phoenicurus*)	7 May ± 6, 22 April–28 May	15 May ± 6, 11 May–4 June	27

We used monthly temperatures for two reasons. Firstly, yearly variations in the timing of migration were large, the mean migration date spanning almost a month in most of the species studied (Table 1). The use of a short period would have the drawback that most of the birds in a certain study year could have arrived before the time period chosen for the study. Secondly, migration timing is probably influenced much by general spring development (Strode 2003, Gordo 2007), and this is in turn largely a result of cumulated temperature sums above a certain temperature threshold (growth degree days or sums of daily mean temperature exceeding e.g. 0 °C or 5 °C).

Statistical methods

We sought negative correlations between the arrival dates and the mean monthly temperatures. Significant negative correlations indicate that birds arrived early when temperatures were high or that birds arrived late when temperatures were low, a general pattern found in bird migration studies (e.g. Lehikoinen and Sparks 2010).

We used a grid of 9600 cells, and correlations were computed separately for each of those. Coloured parts of our maps show only significant correlations ($p < 0.1$). This cut-off value is also used as default in Climate Explorer in locating correlations that are worth investigating. Significances of correlations were evaluated using a two-sided t-test, with the number of degrees of freedom equal to the number of data points (years) minus two. As the effect of low temperatures is expected *a priori* to have a delaying influence on the date of arrival, negative correlations can alternatively be interpreted as significant at $p < 0.05$ (one-sided t-test). Serial autocorrelations were taken into account whenever the lag-1 autocorrelation is significant at $p < 0.1$. In that case, the number of degrees of freedom was divided by the decorrelation length that was computed from the lag-1 autocorrelation. The routines used are described in Press *et al.* (1992), except for the reduction of the number of degrees of freedom, which was included in the routines of Climate Explorer by the Royal Netherlands Meteorological Institute.

If birds use temperature to adjust their migration speed to match yearly changes in the phenology, the correlations should be placed not very far from the site of arrivals where birds are observed. The spatial autocorrelation of temperature typically decreases with distance and is usually relatively weak at distances exceeding 1000 kilometres (Rigor *et al.* 1999). We first checked how close to the Finnish southern coast a correlation pattern should be placed to help birds to adjust their timing to yearly variability in phenology. This was done by correlating the mean monthly temperature in Helsinki (near Hanko, also on the southern coast of Finland) with monthly temperatures in Europe in 1948–2010 (Fig. 1). The area covered by spatial autocorrelations can be characterised with the correlation length scale (CLS), which is defined as the distance at which the correlation coefficient drops below $1/e$ or about 0.37 (Rigor *et al.* 1999). To be useful in adjusting migration speed according to yearly variability in phenology at the southern coast of Finland, significant correlations in a month relevant for the migration of the species (Table 1) should be found closer to the Finnish southern coast than the CLS distance. Any cut-off value for correlations is of course arbitrary, but at the CLS-distance r^2 or "explained variance" also starts to approach 10%, below which any adjustment based on temperature autocorrelation can reasonably be questioned.

Results

The spatial autocorrelation in the May temperature between Helsinki and Europe extended from high values near Helsinki to about 0.5 in the northern part of central Europe, including parts of Germany, Poland, and Ukraine (Fig. 1a). The correlation length scale-distance (CLS distance) associated with the correlation coefficient of 0.37 extended about 1200–1500 kilometres from Helsinki towards southerly directions (Fig. 1b), i.e. to the level of Hungary–Romania. The correlation between the May temperature in Helsinki and the April temperature in Europe was limited to low (< 0.37) values sporadically present in central Mediterranean (Fig. 1c). In the perspective of spring migration, these results

suggest that the temperature birds experienced at a certain location (e.g. at the southern coast of Baltic Sea) reflected the temperatures (or more generally the phenology of spring) further north within the CLS distance (e.g. in southern Finland). The correlation between temperatures was spatial, not temporal at the temporal scale studied (Fig. 1c). Therefore, birds were not able to deduce the temperatures of May based on the temperatures in April.

Correlation maps between the arrival dates in Hanko (Table 1) and other studied sites (Figs. 2–15) show the location of spatial correlations of temperature with migration data. Panels **a** show 5% migration dates and panels **b** median migration dates (Figs. 2–11). Panels **c** show the ringing encounters of ten species ringed in Finland and found in Europe–Mediterranean area outside Finland.

In the common redstart, significant negative correlations between the arrival dates and the temperatures were found mostly southwest from Hanko at the direction of ringing encounters of spring migrants (Fig. 2). The significant negative correlations between the 5% arrival dates in April and the temperature in April were mostly found southwest from Hanko and at distances mostly exceeding the CLS distance (Figs. 1b, 2a and Table 1). Later in spring, the correlations between the 50% arrival dates in May and the temperatures in May were located closer to Hanko and were included in part within the CLS-distance (Figs. 1b, 2b and Table 1). The ringing encounters of spring migrating common redstarts were located southwest from Hanko and overlapped partly the area of significant negative correlations (Fig. 2c). The negative correlations between the arrival dates and monthly temperatures indicated that common redstarts arrived early in Hanko when temperatures were high (or late when temperatures were low) in the areas of negative correlations.

The pattern of negative correlations for the pied flycatcher was similar to that for the common redstart, but the negative correlations between the 50% arrival dates in May and May temperatures were more to the east from the migratory route suggested by the ringing encounters (Fig. 3 and Table 1). Additionally, significant positive correlations between the arrival dates
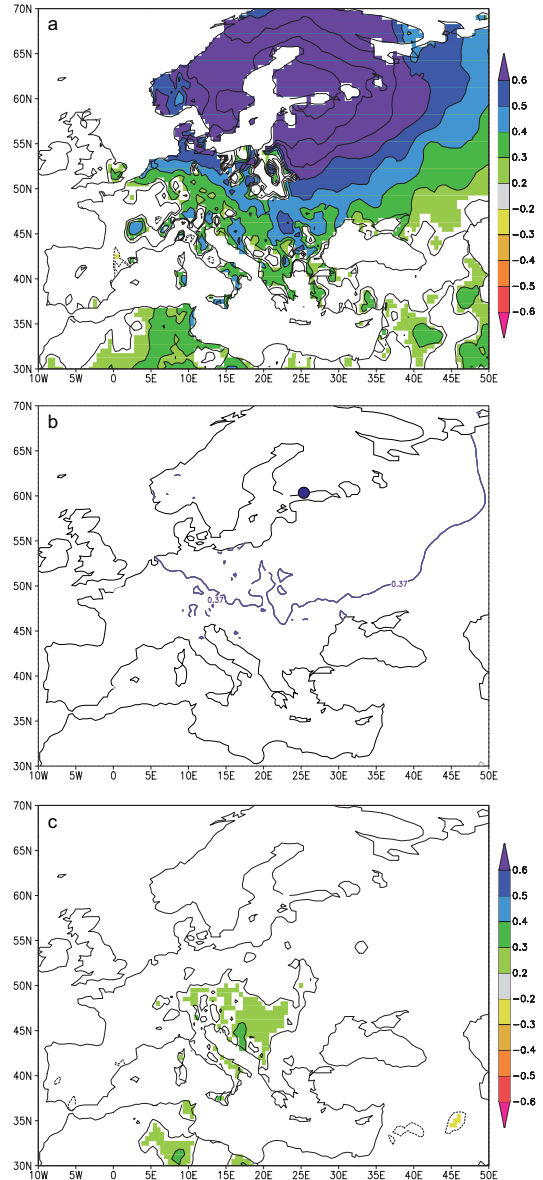

Fig. 1. The correlation between the May temperature (1948–2010) in Helsinki (blue dot) and the temperature over Europe in (**a**) May and (**c**) April, as well as (**b**) the correlation length scale-distance corresponding to the correlation coefficient of 0.37 in **a**.

and the temperatures were found in Ireland (Fig. 3a–b). Ireland is aside from the migratory route of Finnish pied flycatchers (Fig. 3c), and therefore spring-migrating pied flycatchers were not able to regulate their migration based on the Irish temperatures. Additionally, the positive correlation suggested a delayed migration with high
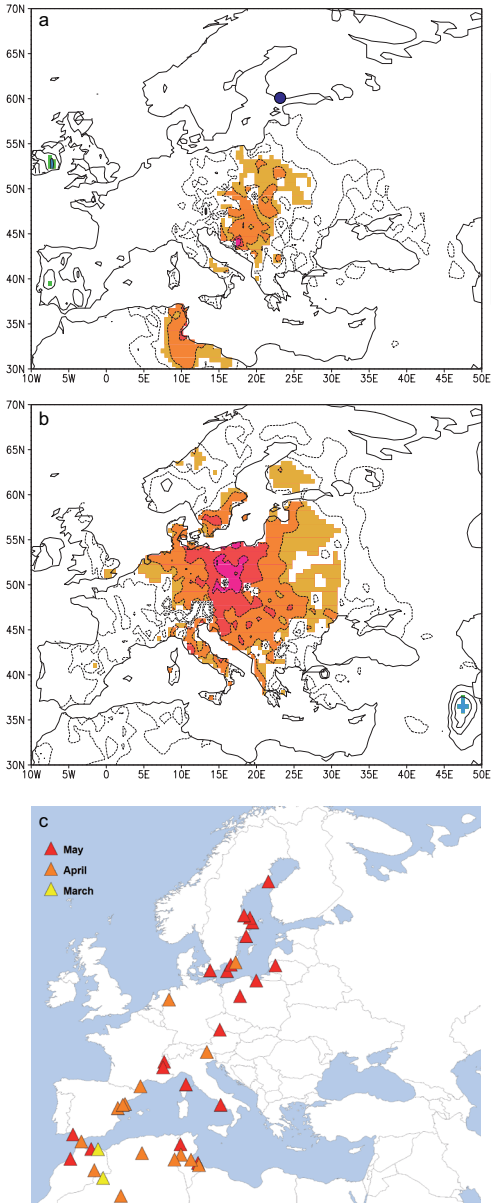
Fig. 2. (**a–b**) Correlation between the arrival dates of common redstarts in Hanko, Finland (marked with a blue dot) and the monthly GHCN/CAMS-gridded temperate, as well as (**c**) Finnish ring encounters for the species. (**a**) Early (5% of seasonal sum of migrants) arrival dates *vs*. temperature in April, (**b**) median (50%) arrival dates *vs*. temperature in May, and (**c**) ring encounters. The legends of the figures refer to correlation coefficients (negative of positive). Coloured parts of the maps show only significant correlations (two-sided *t*-test: *p* < 0.1) with the degrees of freedom equal to the number of dates minus two reported in Table 1.
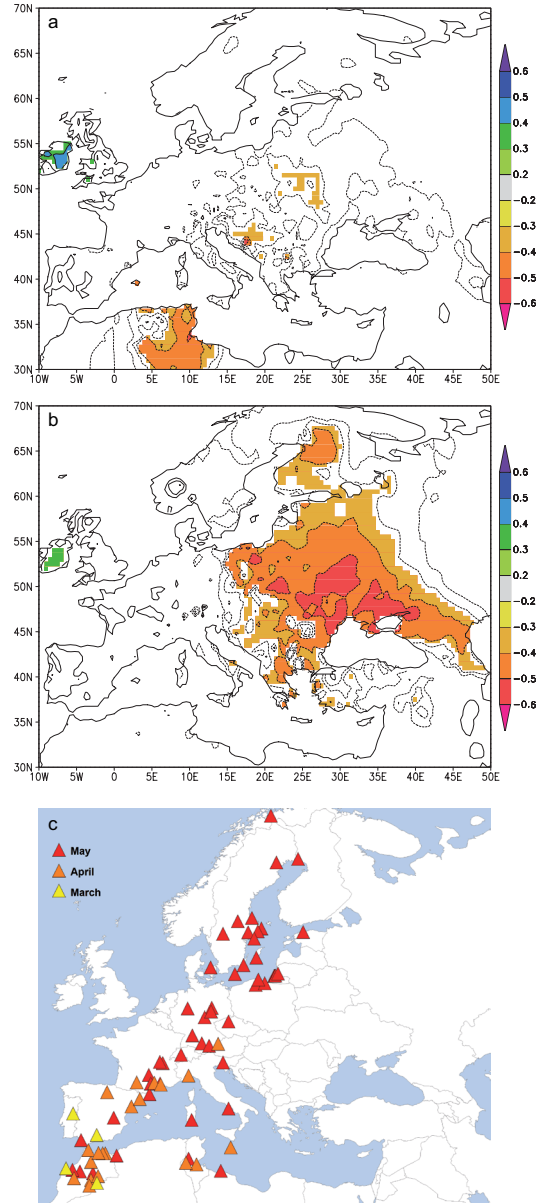
Fig. 3. Pied flycatcher; all as in Fig. 2.

temperatures. This suggestion disagrees both with a theory of optimal spring migration and the observed relationship between temperature and spring migration (Lehikoinen and Sparks 2010). Therefore, the latter part of this study focuses mainly on the biologically meaningful negative correlations.

Similar to the common redstart and pied fly-catcher, the 5% arrival dates in May were cor-
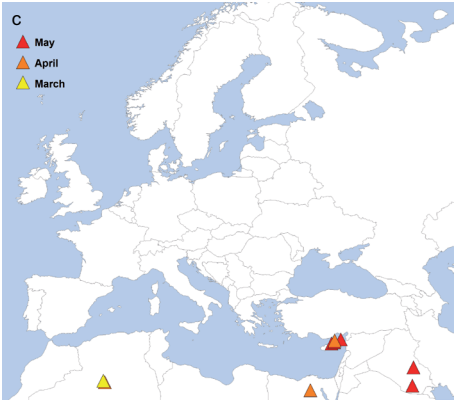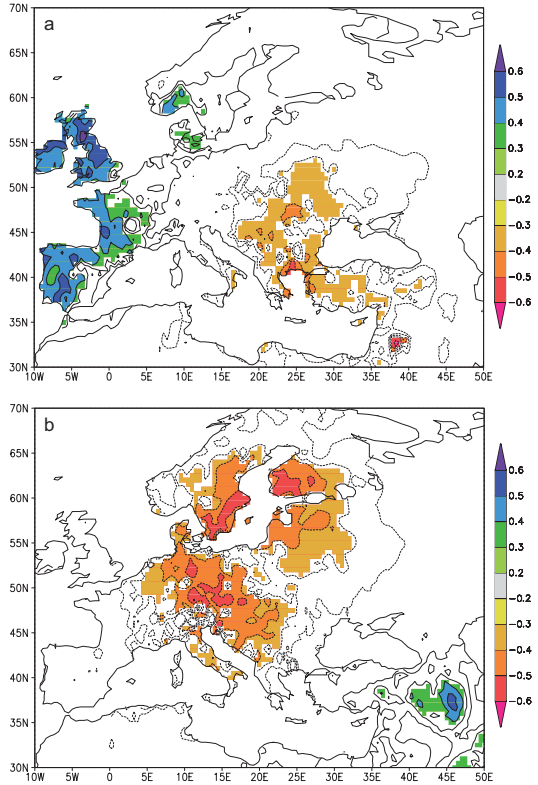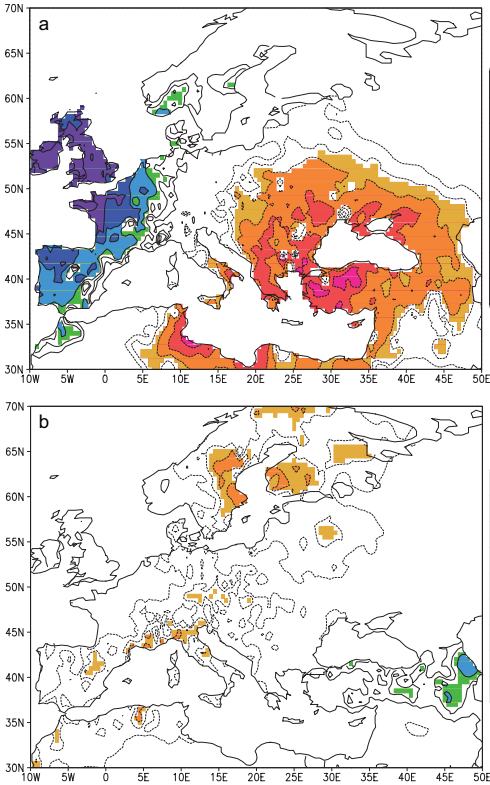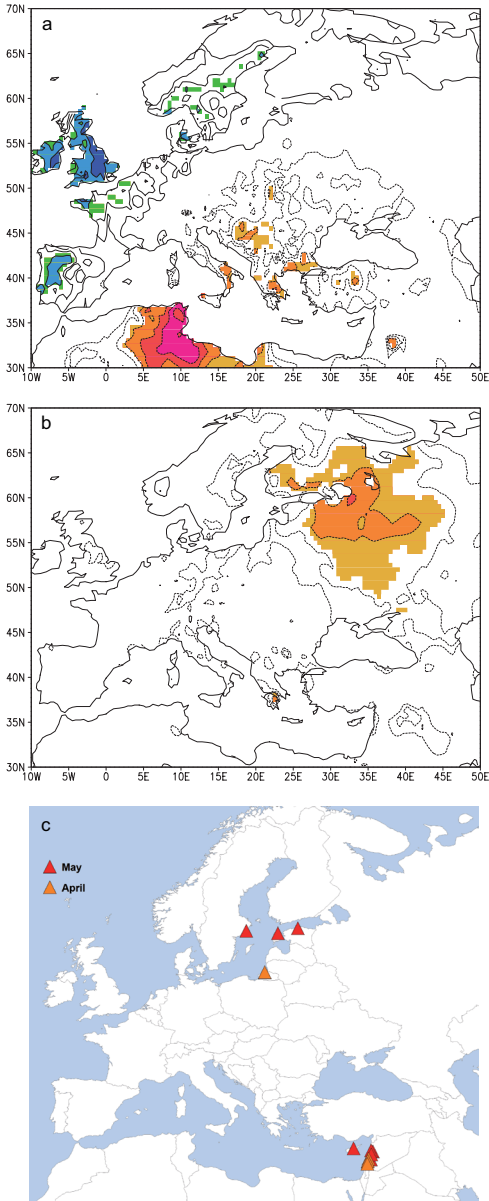
Fig. 4. Willow warbler; all as in Fig. 2 except for (**a**) 5% *vs*. April, and (**b**) 50% *vs*. May.


Fig. 5. Lesser whitethroat; all as in Fig. 2 except for (**a**) 5% *vs*. April, and (**b**) 50% *vs*. May.

related with the April temperatures and the 50% arrival dates later in May with the May temperatures for the willow warbler (Fig. 4), lesser whitethroat (Fig. 5) and blackcap (Fig. 6). In these species, the significant negative correlations were found primarily in the directions of ringing encounters. The areas of negative correlations moved northward as migratory season progressed.

In the earliest migrants — the chiffchaff and lesser black-backed gull — the significant negative correlations between the arrival dates in April and the temperatures in March or April were located along an eastern migration route beyond the CLS distance (Figs. 7 and 8). The few long-distance ringing encounters of chiffchaffs pointed to southeast roughly towards

Fig. 6. Blackcap; all as in Fig. 2 except for (**a**) 5% *vs.* April, and (**b**) 50% *vs.* May.
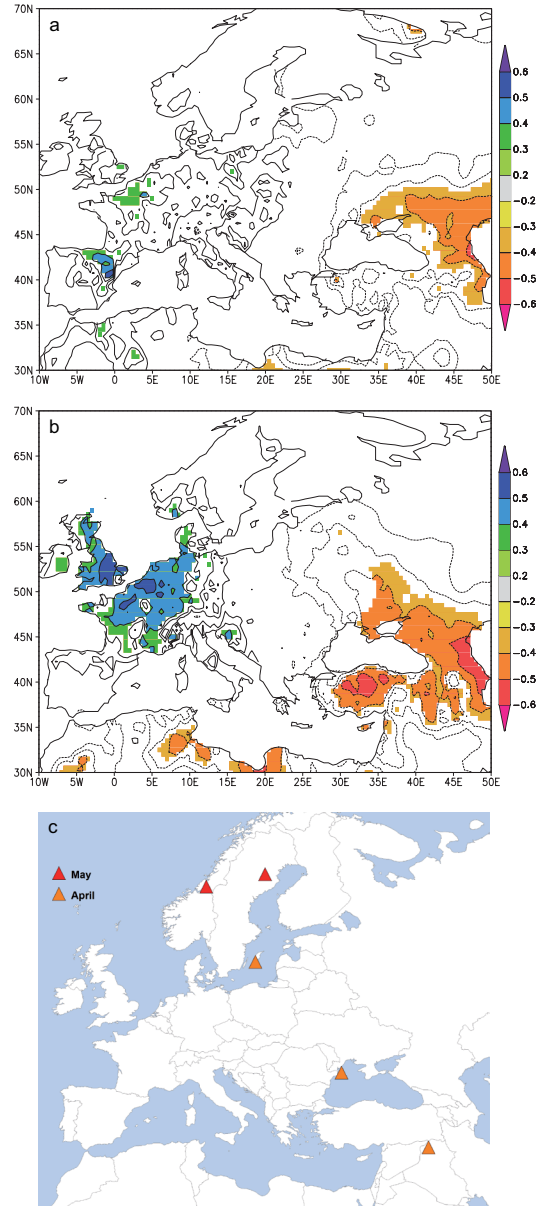
**Fig. 7**. Chiffchaff; all as in Fig. 2 except for (**a**) 5% *vs.* April, and (**b**) 50% *vs.* April.

the area of negative correlations (Fig. 7c). In the lesser black-backed gull, several ringing encounters were located in the area with negative correlations. According to satellite tracking, this area was also passed by migrating Finnish lesser black-backed gulls (Kube *et al.* 2000).

For late migrants — spotted flycatcher (Fig. 9), common whitethroat (Fig. 10), and

garden warbler (Fig. 11) — the arrival dates in May were correlated with the temperatures in May. For these species, the significant negative correlations were sometimes fragmented but primarily found within the CLS distance.

For chiffchaffs observed at the Rybachy Bird Observatory, the significant negative correlations between the mean arrival dates and the tem-
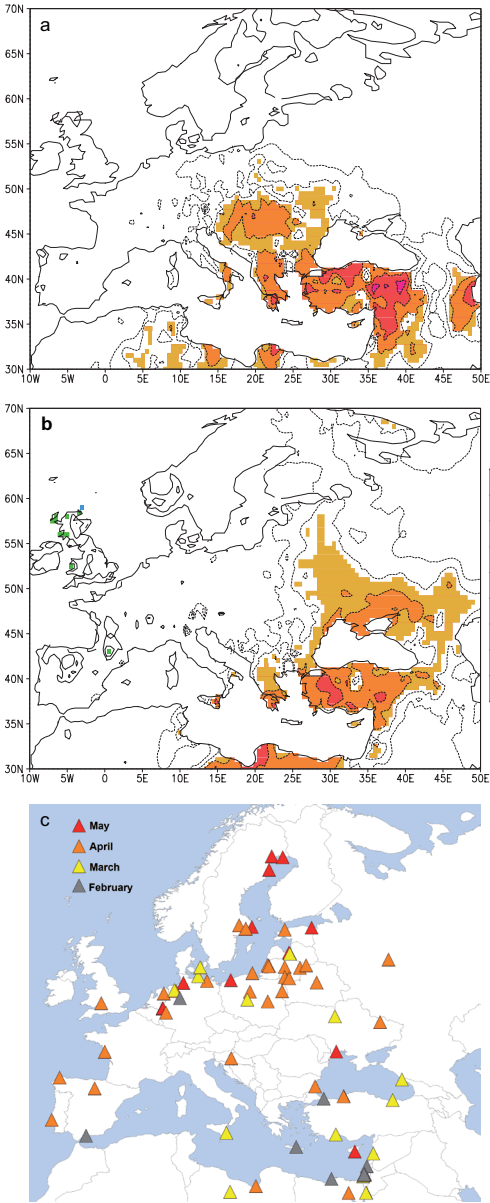
**Fig. 8**. Lesser black-backed gull; all as in Fig. 2 except for (**a**) 5% *vs*. March, and (**b**) 50% *vs*. April.
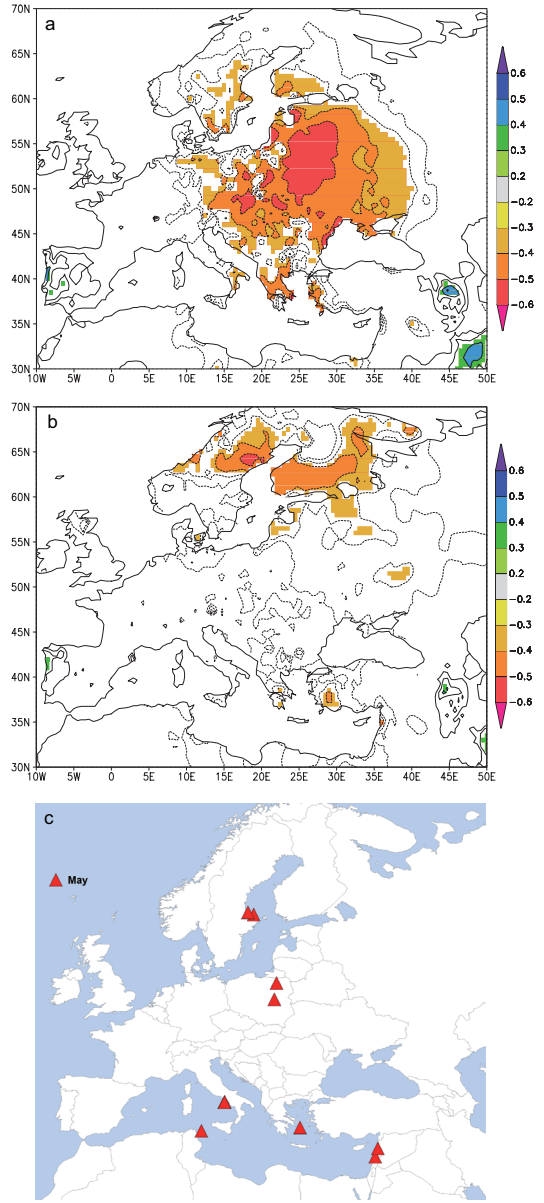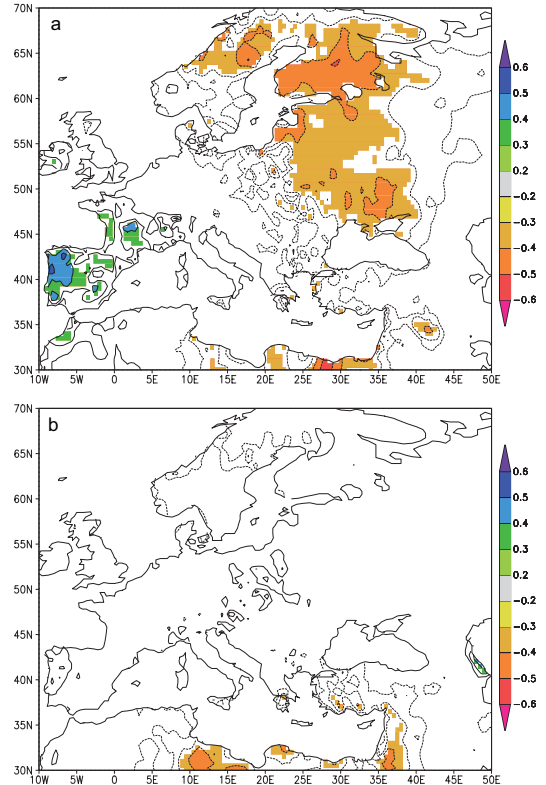

Fig. 9. Spotted flycatcher; all as in Fig. 2 except for (**a**) 5% *vs*. May, and (**b**) 50% *vs*. May.

peratures in April were located primarily towards southeast from the observatory (Fig. 12). The corresponding correlations for chiffchaffs observed in Helgoland were towards south–southwest from the observatory (Fig. 13). Collared flycatchers of Moravia showed a negative correlation pattern towards the south (Fig. 14) and greenish warblers of Kazan towards the southeast (Fig. 15).

The geographical patterns of negative correlations between the timing of migration and monthly temperatures indicated that the most species examined arrived early when temperatures were high (or late when temperatures were low) in the areas of negative correlations (Figs. 2–15). These patterns were usually situated, and in many cases elongated, along the assumed
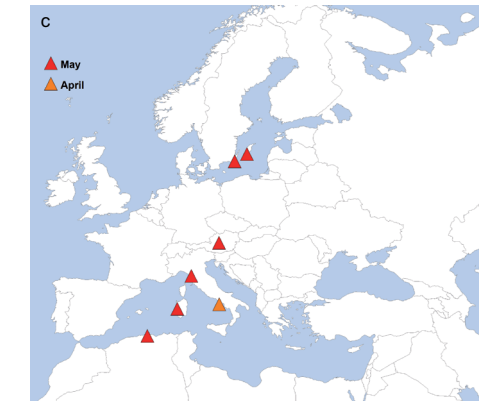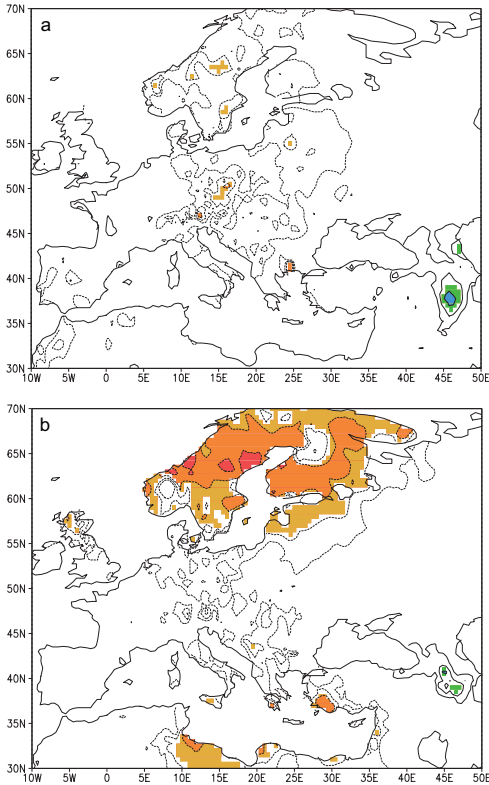
**Fig. 10**. Common whitethroat; all as in Fig. 2 except for (**a**) 5% *vs*. May, and (**b**) 50% *vs*. May.
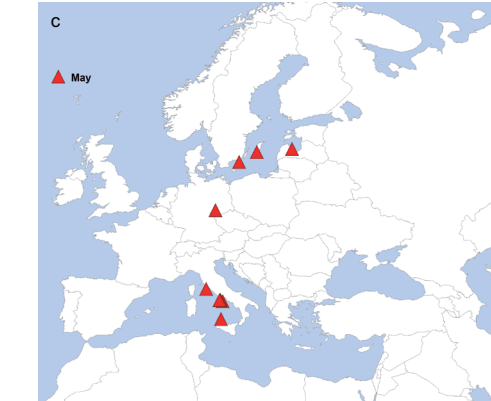
Fig. 11. Garden warbler; all as in Fig. 2 except for (**a**) 5% *vs*. May, and (**b**) 50% *vs*. May.

migration routes (e.g. common redstart, pied flycatcher, spotted flycatcher, lesser whitethroat; Figs. 2, 3, 4 and 5). For the migrants thought to follow the central or western migration route, the strongest temperature response was often found in continental Europe (500–1000 km from the Hanko Bird Observatory; Figs. 2, 3, 4, 9, 10 and

11). For the Finnish migrants crossing or passing the Mediterranean from the east (Figs. 5, 6, 7 and 8), the negative correlations were strongest close to the Mediterranean at a distance of up to 1500–2500 km, in areas that were not directly correlated with temperatures at Hanko.
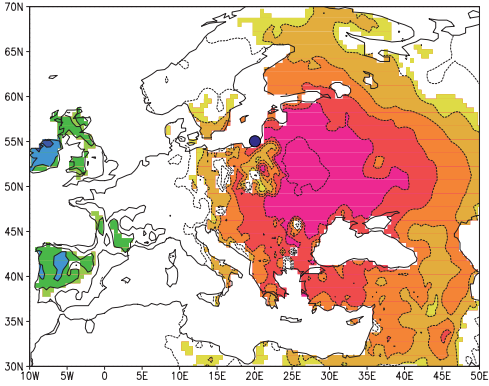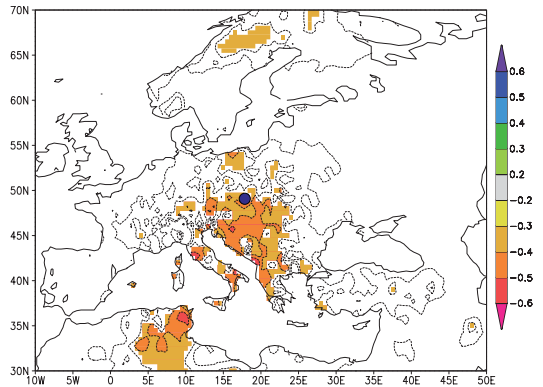
Fig. 12. Correlation between the mean arrival dates of chiffchaffs to Rybachy (dot) and April temperature.
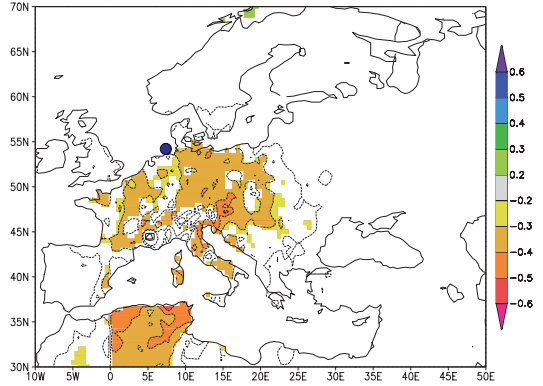
**Fig. 13**. Correlation between the mean arrival dates of chiffchaffs to Helgoland (dot) and April temperature.

Discussion

In this study, negative correlations between arrival dates and temperature are mostly placed along the assumed migration route. The areas of significant correlations found by us were often very large, stretching in the case of the spotted flycatcher from the Baltic to the Mediterranean Sea. Extended areas of significant correlations are in part due to the spatial autocorrelation of the temperature data (Rigor *et al*. 1999). However, our finding that the correlative patterns are often elongated in the direction of the migration route probably indicates that birds are continuously adjusting the timing of their migration, and

Fig. 14. Correlation between the first arrival dates of collared flycatchers to Moravia (dot) and April temperature.

Fig. 15. Correlation between the first arrival dates of greenish warblers to Kazan (dot) and May temperature.
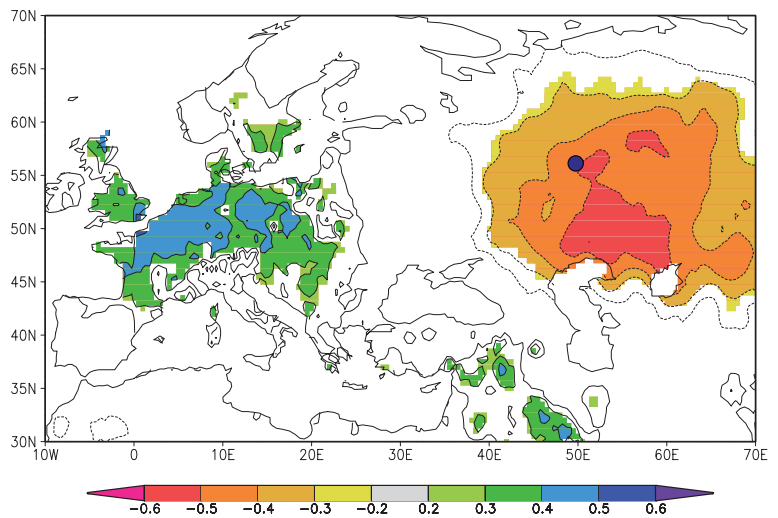
that the arrival timing is influenced by a definite area along the migration route. Our results support the idea that LDMs fine-tune their migration speed according to yearly changes in phenology en route (e.g. Tøttrup *et al.* 2010).

A comparison of the negative correlation patterns obtained from the Finnish data and Finnish ringing recoveries indicates a relatively good match between the areas of negative correlation and supposed migration routes. The correlations with the Hanko data are in accordance with the finding revealed by the ring encounter data that many Finnish and also Scandinavian LDMs (Fransson and Hall-Karlsson 2008) winter in eastern Africa and pass the Mediterranean in the eastern part of the area. For example, Finnish willow warblers represent populations belonging to the eastern side of a migratory divide; the ring encounter data has shown that Scandinavian willow warblers north of 63°00´N, and Finnish willow warblers migrate towards the southeast (Bensch *et al.* 1999).

The match between the areas of negative correlations and supposed migratory routes seems to hold also for the other observatories examined. The chiffchaff time series from the Baltic Sea coast Russian Rybachy Bird Observatory points in the same southeasterly direction as the Hanko dataset, but Helgoland shows a pattern towards the south–southwest. This is in accordance with the known migratory divide between the western and eastern populations of the species (Cramp 1992). Also the strongly southeastern pattern of the Kazan's greenish warblers is logical as the species winters in India and the Far East (Cramp 1992). The southern correlation direction of collared flycatchers in Moravia also fits the assumed migration route of the species (Cramp 1992).

Our study also includes fragmented correlations, which do not match the anticipated migratory routes of the species studied. These correlations are probably artificial; the lack of correlations along the supposed migration route can be influenced by data quality issues (Hüppop and Winkel 2006). As with generally all encounter data, the spatial distribution of ring encounters can also be biased since there are geographical differences in the encounter probability (e.g. Busse 2001, Korner-Nievergelt *et al.* 2010). The long time series of Helgoland yields more con-

sistent patterns than Hanko for additional species tested (not shown).

We also found extensive areas of positive correlations. These correlations were frequently observed but only together with negative correlations (Figs. 3a–b, 4a–b, 5a–b, 6a, 7a–b, 11a, 12 and 15). This association can be produced through a climatic teleconnection; a possible candidate is the East-Atlantic–West Russia pattern (Barnston and Livezey 1987) as it is negatively connected to temperature in eastern Europe, but positively to temperature in western Europe.

Lehikoinen and Sparks (2010) stressed that the selection of temperature data is critical in studies linking bird migration to climate. Our approach with gridded temperatures extends the study of the correlation between arrival dates and temperatures to a large geographical area. We argue that at least for multi-species studies, the use of gridded data from a large area should be favoured; migration directions of species vary so much, that many of the patterns shown here would not have been found by using temperatures from a few sites.

In this study, a part of significant negative correlations fall within the CLS distance, in particular in those cases when the arrival dates in May were correlated with the temperature of the same month. This finding agrees with numerous earlier observations that the arrival time at a certain locations depends on the temperature at that location or nearby locations (Ahola *et al.* 2004, Lehikoinen *et al.* 2004, Hüppop and Hüppop 2003, Hüppop and Hüppop 2005, Sokolov 2006, Gordo 2007, Tøttrup *et al.* 2008, Tøttrup *et al.* 2010, Lehikoinen and Sparks 2010). According to this study, the area of the highest correlation can also exceed the CLS distance, particularly in case of eastern migrants or when arrival dates were correlated with the temperatures of the preceding month. Fine-tuning with local phenology in northern Europe probably cannot explain the correlation patterns found in the Middle East; yearly temperature changes in these areas are not directly associated with temperatures in Fennoscandia.

These distant correlation patterns are present in several species and possibly linked to biological factors. A logical possibility is linked to feeding opportunities; high temperatures in the areas of negative correlations might help birds to

gain more fat in a shorter time; shorter stopover time would then speed up migration (Lehikoinen and Sparks 2010). In general, a high fat deposition rate enables fast migration (Alerstam 1990, Newton 2008). Numerous studies have also shown that birds in a good condition tend to migrate earlier; birds that rapidly restore fat levels during stopovers minimise the time spent on migration (Schaub and Jenni 2001, Moore *et al*. 2004). A good body condition of the bird, dry weather and favourable winds can speed up migration (Alerstam 1990, Åkesson *et al*. 2002, Sinelschikova *et al*. 2007, Newton 2008, Dokter *et al*. 2011).

Another possibility, which does not mutually exclude our fat deposition rate hypothesis, is that these correlations are associated with tailwind conditions, which have been shown to influence European passerine migration (Åkesson *et al*. 2002, Sinelschikova *et al*. 2007, Dokter *et al*. 2011). Southerly winds usually bring warm air, and also speed up the migration of birds. Southerly winds providing tailwinds could also be one possible explanation for temperature responses located east from the migratory route as found in some species in this study (pied flycatcher, common redstart).

Our study provides strong support to the hypothesis that temperature in Europe influences the spring migration timing of LDMs en route (e.g. Ahola *et al*. 2004, Tøttrup *et al*. 2008). Areas of significant correlations are often large. Spatial autocorrelation contributes to this, but we think that a temperature-based adjustment of long-distance bird migration probably involves a large part of the migration route. The correlative landscape would probably be extended further if multiple observation points along the same migration route could be correlated with temperature as each point would have its own correlative area.

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