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Avian migrants adjust migration in response to environmental conditions *en route*

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The onset of migration in birds is assumed to be primarily under endogenous control in long-distance migrants. Recently, climate changes appear to have been driving a rapid change in breeding area arrival. However, little is known about the climatic factors affecting migratory birds during the migration cycle, or whether recently reported phenological changes are caused by plastic behavioural responses or evolutionary change. Here, we investigate how environmental conditions in the wintering areas as well as *en route* towards breeding areas affect timing of migration. Using data from 1984 to 2004 covering the entire migration period every year from observatories located in the Middle East and northern Europe, we show that passage of the Sahara Desert is delayed and correlated with improved conditions in the wintering areas. By contrast, migrants travel more rapidly through Europe, and adjust their breeding area arrival time in response to improved environmental conditions *en route*. Previous studies have reported opposing results from a different migration route through the Mediterranean region (Italy). We argue that the simplest explanation for different phenological patterns at different latitudes and between migratory routes appears to be phenotypic responses to spatial variability in conditions *en route*.

Keywords: birds; migration; phenology; climate change; normalized difference vegetation index

1. INTRODUCTION

Migration phenology in long-distance avian migrants is assumed to be controlled by endogenous rhythms (Berthold 1996) with some degree of plasticity in the migratory programme (Biebach *et al.* 1986). In the Northern Hemisphere, spring temperatures have increased during the past decades affecting, among others, species' physiology, breeding ranges and phenology (Walther *et al.* 2002).

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Timing of breeding area arrival is crucial for migratory birds to profit from the summer peak in food availability, thereby optimizing their reproductive output (Both *et al.* 2006). As consistent patterns of earlier arrival to their northern Europe breeding areas have been found (Thorup *et al.* 2007), a number of questions arise: what factors drive these changes and which cues do the migrants use to determine optimal arrival? In fact, we know little about which climatic variables affect migrants during different seasons and phases of the migration cycle (Stenseth & Mysterud 2005).

Timing of spring migration can be affected by environmental conditions in two ways. The first occurs prior to departure from wintering areas where ecological conditions can affect individuals' physiology, e.g. body condition (Ottoosson *et al.* 2005). The second occurs during the migration period, where improved ecological conditions at stopover sites with an abundance of food can reduce the time required to replenish fuel stores (Ahola *et al.* 2004).

Recently, Jonzén *et al.* (2006) showed that long-distance migrants have advanced their passage through Italy, making the journey earlier in the season, and argued that this trend is the result of a climate-driven evolutionary change. However, Both (2007) argued that this trend might be caused by improved environmental conditions in the wintering areas, or *en route*, while Gienapp *et al.* (2007) found no evidence to support or disprove either an evolutionary or plastic response. Our objective is to assess the average relationship between timing of migration at different latitudes for several species of long-distance Palaearctic migrants in the eastern and the central Mediterranean flyways, and to analyse changes in the duration of migratory periods relative to environmental conditions, both in wintering areas and *en route* towards breeding areas.

2. MATERIAL AND METHODS

We used standardized ringing data on five long-distance migratory species trapped *en route* from African wintering areas through the Middle East (Israel) and just before arrival at their breeding areas in northern Europe (Finland) during the period 1984–2004. Timing of migration was analysed for three population measures (first 5, 50 and 95% of the spring total), subsequently referred to as 'migration phases'. Migration duration is defined as the difference in passage dates between the Middle East and northern Europe for each migration phase.

We used the monthly normalized difference vegetation index (NDVI) for the period 1984–2000 as a proxy measure for the actual ecological conditions (e.g. food availability; Pettorelli *et al.* 2005) in the species-specific wintering areas (Wisiz *et al.* 2007) prior to departure (February/March) and the area in Europe traversed prior to arrival at the breeding areas (April/May; figure 1). The African spring NDVI and the European spring NDVI were then related to our phenological results in the Middle East and northern Europe, respectively (electronic supplementary material, methods).

We conducted two complementary analyses that have similar findings, thus reported together in §3. First, we fitted models for each species and migration phase, estimating changes in the *timing of migration*, the effect of NDVI on the timing of migration as well as the effect of NDVI on *migration duration* through Europe. Second, we fitted linear mixed models including all independent variables as fixed variables and their interactions as well as the three phases of migration as a repeated factor. Our data include observations of three phases of migration over 21 years from five species at two locations, in total 630 observations (electronic supplementary material, methods).

Finally, we relate our results and results published by Jonzén *et al.* (2006) to NDVI in the eastern and western flyways between Africa and Europe, to investigate whether migrants following the two flyways experienced differently changing NDVI over time. This included comparing changes in: (i) African winter NDVI

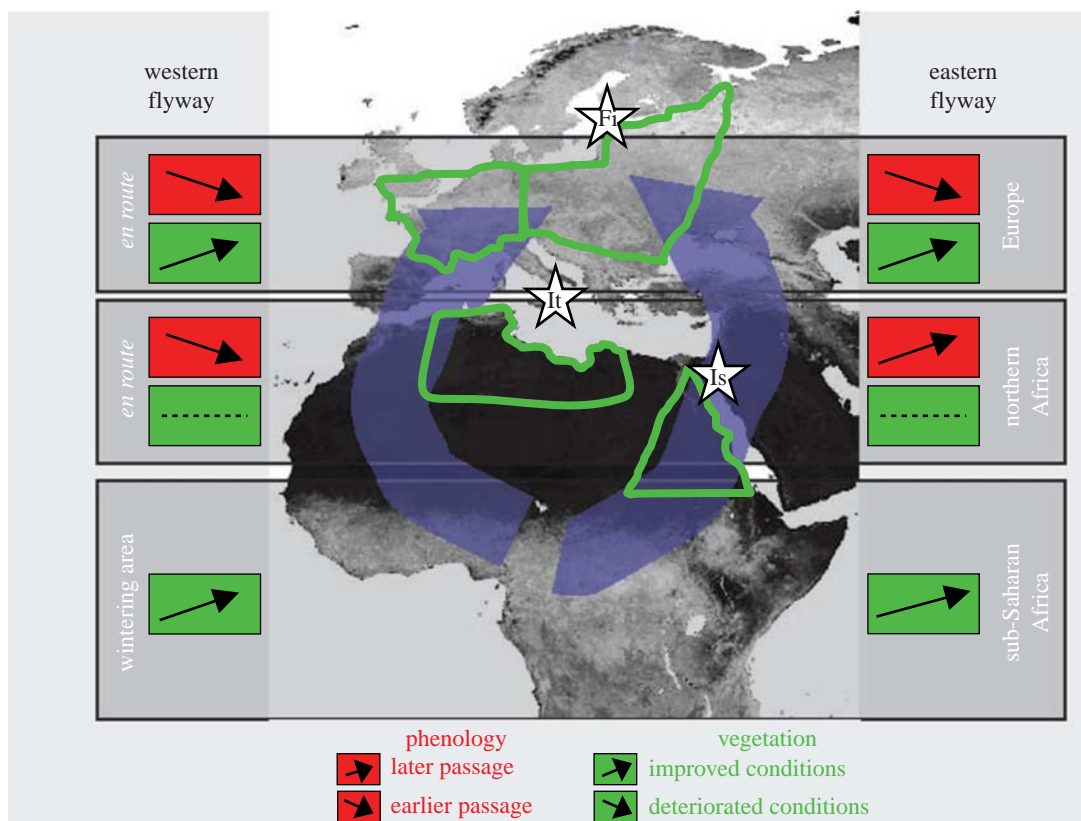


Figure 1. Schematic of changes in the timing of migration for five long-distance migratory birds during the period 1984–2004 (red boxes) and changes in environmental conditions (NDVI) for the period 1984–2000 (green boxes) in the wintering areas and *en route* for the two major flyways (blue arrows) between Africa and Europe. Green areas were analysed for environmental conditions (NDVI) and the three ringing stations are indicated (Fi, Finland; It, Italy; Is, Israel). Phenological data on the western flyway are from Jonzén *et al.* (2006).

(December–February) over time in the species-specific wintering areas in western and eastern Africa (electronic supplementary material, figure 1), (ii) NDVI along the central North African and northeastern African flyways (March), and (iii) European spring NDVI between western and eastern European flyways (April; figure 1).

3. RESULTS

For the five long-distance migratory birds, we found different trends in the timing of migration at different latitudes (interaction term; latitude \times year: $p < 0.0001$, $F = 16.3$, d.f. = 1). Figure 2*a* shows delayed passage through the Middle East when compared with little phenological change in northern Europe. The difference was most clear for the portion of the populations that arrive early, apparently decreasing towards no overall difference between latitudes for the portion of the populations that arrive late (latitude \times year \times migration phase: $p = 0.004$, $F = 5.52$, d.f. = 2). The species showed different trends in the timing of migration (year \times species: $p = 0.004$, $F = 3.93$, d.f. = 4), most likely caused by different migration strategies. Overall, NDVI affects the timing of migration differently at different latitudes (latitude \times NDVI: $p = 0.006$, $F = 7.76$, d.f. = 1). Figure 2*b* shows that, in all phases of migration, high African spring NDVI delays passage, and for the first phases of migration, the European spring NDVI correlated with earlier passage in northern Europe. When included in the same model, both year and NDVI correlated well with the phenological patterns, suggesting a causal

relationship with spring advancement. Furthermore, advanced European spring NDVI seems to cause a shorter migration duration in the first phases of migration (5 and 50%; figure 2*c*) and the overall analysis indicates more rapid migration in years with high European spring NDVI (NDVI: $p = 0.024$, $F = 5.21$, d.f. = 1; electronic supplementary material, table 1). Excluding whitethroat from the analyses, the species showing the most westerly ring recoveries (electronic supplementary material, figure 2) did not change the results.

The African winter NDVI increased significantly in both western and eastern Africa (west: 0.013 ± 0.001 unit NDVI per year; east: 0.007 ± 0.002 unit NDVI per year). In central and northeastern North Africa, NDVI showed no change over time (central: $p = 0.37$, $t = 0.93$, $R^2 = 0.05$; northeastern: $p = 0.60$, $t = -0.52$, $R^2 = 0.02$). Finally, the European spring NDVI increased equally throughout the period in western Europe (slope: 0.005 unit NDVI per year, $R^2 = 0.28$, $p = 0.02$) and eastern Europe (slope: 0.006 unit NDVI per year, $R^2 = 0.32$, $p = 0.01$; slopes not significantly different: $p > 0.1$, $t = 1.58$, d.f. = 34; figure 1).

4. DISCUSSION

During a period of improving conditions in the wintering areas, five species of long-distance migratory birds showed overall delayed spring passage of the Sahara Desert. This indicates a delayed onset

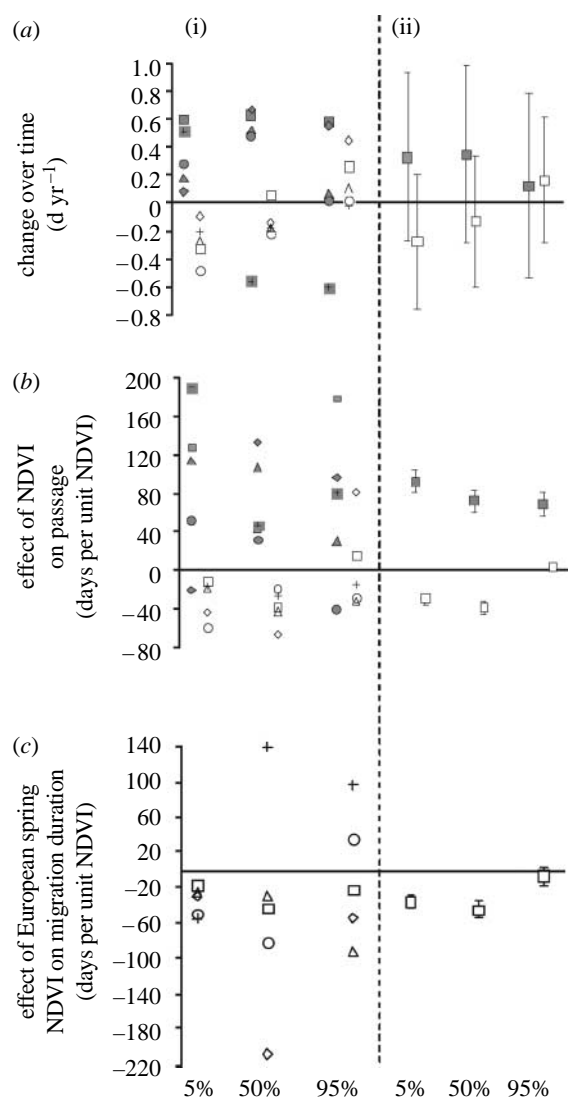


Figure 2. Species-specific changes in the timing of three phases of spring migration (first 5, 50 and 95% of the spring total) in five species of long-distance migratory birds (lessor whitethroat (triangles), whitethroat (squares), black-cap (circles), chiffchaff (diamonds) and willow warbler (plus symbols)) when passing the Middle East (filled symbols) and northern Europe (empty symbols) analysed for: (a) change in passage (d yr^{-1} ; 1984–2004); (b) relationship between passage in the Middle East and African spring NDVI as well as passage in northern Europe and European spring NDVI (days per unit NDVI; 1984–2000: positive values indicate later passage); and (c) relationship between change in migration duration and European spring NDVI (days per unit NDVI; 1984–2000: negative values indicate reduced migration duration). The five slope estimates for each phase of migration are based on separate model fits and are hence independent. (i) Individual estimates. (ii) Mean values, where error bars are 95% confidence intervals based on the summed sampling variances of each species estimate, $(\sum \text{var}(x_i)) \times (1/5)^2$.

of migration. Overall, trends in the timing of migration in the Middle East were different from the trends in northern Europe, commensurate with a reduced migration period, where advantageous conditions reduce travel times during the second part of their migration. These phenological patterns indicate a high degree of phenotypic plasticity in the timing of migration through Europe, with migrants adjusting

their timing of migration to the actual conditions *en route* and thereby optimizing their time of arrival at the breeding areas.

In contrast to our results, Jonzén *et al.* (2006) described an advanced passage of long-distance migrants through Italy during approximately the same time period covered by this study. These contradictory results may have been caused by: (i) improved conditions along the western flyway making the birds migrate faster when compared with the eastern flyway, (ii) a difference in the latitude between the ringing stations: the Italy data may reflect a response to conditions in Europe, and (iii) monitoring of different populations. At least during autumn migration, North European migrants seem to circumvent the ecological barriers of the Sahara Desert and the Mediterranean Sea as opposed to crossing them (Fransson *et al.* 2005). Furthermore, Pilastro *et al.* (1998) observed that some species of migratory songbirds trapped in Italy had circumvented the Mediterranean Sea. This implies that a large proportion of birds trapped in Italy may belong to southern European populations. Hence, prior to being trapped, the birds had traversed southwestern Europe where environmental conditions improved in contrast to the central North Africa where conditions were more constant (this study).

We found small advances in arrival to northeast Europe, which supports the conclusions by Both *et al.* (2004). Contrary to Gordo *et al.* (2005), who argued that improved winter conditions cause earlier breeding area arrival, we found delayed initiation of migration with improving winter area conditions. Hence, migrants may benefit from improved conditions in the wintering areas by optimizing the chance of safely passing the Sahara Desert. With delayed onset of migration and advanced conditions *en route*, the migratory birds have to speed up migration through Europe to take advantage of a climate-induced earlier spring. This supports the study by Marra *et al.* (2005) showing advanced migration with higher spring temperatures *en route* through North America. As most birds included in our data are second-year birds (electronic supplementary material, table 2) and hence on their first northward migration, it seems unlikely that the observed patterns result from birds reacting to previously experienced favourable conditions.

Data on passing migratory birds are most likely to be from a mixture of populations of different origin, and differences between locations may increase with distance. Hence, different responses by different populations may cause the patterns observed in this and former studies. Also, local weather conditions may cause between-species correlations in data on passing migratory birds (Knape *et al.* in press), potentially restricting conclusions drawn from phenological studies. Furthermore, different species and even individuals may follow different decision rules (Bowlin *et al.* 2005) and may not base their decisions during flight and stopover on the progression of vegetation, but rather follow simpler decision rules. Also, using average values of NDVI from large areas can be problematic as NDVI may vary considerably and may even indicate different conditions, e.g.

food availability in Africa and spring advancement in Europe. However, adjustment of migration in response to environmental conditions *en route* combined with the observed large variation in phenological patterns indicate that at least some degree of phenotypic plasticity control the timing of breeding area arrival. It seems unlikely that the relatively fine-scale adjustment along the migratory route could be caused by microevolutionary changes. Yet, resolving this question requires analyses of phenology at the onset of spring migration and studies of evolutionary changes within populations.

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