Avian migration phenology and global climate change

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There is mounting evidence that global climate change has extended growing seasons, changed distribution patterns, and altered the phenology of flowering, breeding, and migration. For migratory birds, the timing of arrival on breeding territories and over-wintering grounds is a key determinant of reproductive success, survivorship, and fitness. But we know little of the factors controlling earlier passage in long-distance migrants. Over the past 30 years in Oxfordshire, U.K., the average arrival and departure dates of 20 migrant bird species have both advanced by 8 days; consequently, the overall residence time in Oxfordshire has remained unchanged. The timing of arrival has advanced in relation to increasing winter temperatures in sub-Saharan Africa, whereas the timing of departure has advanced after elevated summer temperatures in Oxfordshire. This finding demonstrates that migratory phenology is quite likely to be affected by global climate change and links events in tropical winter quarters with those in temperate breeding areas.

Global warming (1) has altered the phenology and distribution of many plant and animal species, resulting in marked changes from the level of individuals to whole communities (2–7). Elevated temperatures have affected population dynamics (8) and have advanced events such as leaf unfolding (9), flowering (10), emergence (11), and breeding (12–15), whereas leaf fall has become delayed, leading to an extended growing season (9). In some cases there is evidence that the timing of avian migration is affected by climatic variation (2, 16–20). Climate change may pose particular problems for migratory birds that spend different parts of the annual cycle in different parts of the world (19), and it is unclear how conditions in their winter quarters provide information on the optimal timing of migration (21, 22). Shifts in the phenology of insects in Europe have been more rapid than changes in the migratory phenology of pied flycatchers, *Ficedula hypoleuca*, leading to mistimed reproduction (23).

For migrant birds, the timing of their arrival and their physical condition on the breeding grounds are important determinants of reproductive success and fitness (23, 24). Although the effects of global climate change on temperate organisms are becoming well documented (4–7), the factors that determine changes in migratory phenology are poorly understood (19, 22, 24). Long-distance migrants may be constrained in their plastic responses to climate change by endogenous rhythms that control migration (23, 25, 26) although laboratory experiments demonstrate that evolutionary changes in the timing of migration may occur over a short period (27), and empirical studies suggest that there is considerable phenotypic plasticity in migration timing (17, 28). Recent analysis of migrant birds in Helgoland, Germany, demonstrates that the arrival time of short-distance migrants correlates well with local temperature, whereas the arrival time of long-distance migrants is best explained by the North Atlantic Oscillation Index (NAOI, an index of air pressure over the North Atlantic Ocean). Based on these results, van Noordwijk (22) proposed three hypotheses that might explain the earlier passage of long-distance migrants. First, they may be leaving Africa at the same date but are able to complete their migration more rapidly because foraging conditions in early spring in Europe are better in years when the NAOI is high, giving rise to warmer, wetter, and windier conditions. Second, if the weather in Africa is correlated with the NAOI, then seasons in Africa may also be, which in turn means that birds might leave earlier. Large-scale climatic indices such as the NAOI and the Southern Oscillation Index (SOI) are known to affect the climate and vegetation productivity of Africa (29, 30) and may be proxies for a combination of climatic conditions that trigger migration (31). Third, the weather in Africa may not have changed, but natural selection may have altered the trigger for initiating migration.

Here, I show that the U.K. arrival date of 17 of 20 species of birds has advanced over the past 30 years, responding to increased temperature trends in their African over-wintering grounds. The departure date of migrant birds has also advanced in parallel with the change in arrival date. The timing of departure of migrant birds from the U.K. is correlated with increased summer minimum temperatures. Overall, the duration of stay of migrant birds in the U.K. has remained unchanged over time, but the whole period has shifted earlier by an average of 8 days over the last 30 years.

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Methods

Data for SOI and NAOI were obtained from the Climate Analysis Section of the National Center for Atmospheric Research (www.cgd.ucar.edu/cas/catalog/climind/soi.html). The winter (December, January, and February) SOI is computed by using the difference between monthly mean sea level pressure anomalies (mb) at Tahiti and Darwin (32). The winter and summer (June, July, and August) NAOI used are based on the difference of normalized sea level pressures (mb) between Ponta Delgada, Azores, and Stykkisholmur, Iceland (33). Mean winter surface air temperature anomalies (°C) for Africa south of 20° N were obtained from the National Climatic Data Center (lwf.ncdc.noaa.gov/oa/climate/research/ghcn/ghcngrid.html). Summer minimum and maximum temperature (°C) data for Oxford were obtained from the U.K. Meteorological Office (www.met-office.gov.uk/climate/uk/stationdata/oxforddata.txt).

I used dates of first arrival and last departure for 20 species of migrant birds (Table 1) in Oxfordshire, U.K., collected by the Oxford Ornithological Society from 1971 to 2000 (34). The species were selected following the criteria that they were all trans-Saharan migrants and that each species had a minimum of 25 records for both arrival date and departure date over the 30-yr period. Rather than analyzing the trend for each species independently, I used a simple metaanalysis in which the slopes of regressions were considered as measures of effect size (4, 6). For each of the 20 species, I calculated the slopes of linear regressions of arrival date against year, winter SOI, winter NAOI, and winter sub-Saharan African temperature anomaly. Slopes of departure date were calculated by regression against year, summer NAOI, and Oxford summer maximum and summer minimum temperature. For each set of regressions, Kolmogorov–Smirnov tests confirmed that the slopes were distributed normally, allowing the use of a one-sample Student t test to test the mean slope against the null hypothesis of no change over time

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Abbreviations: SOI, southern oscillation index; NAOI, North Atlantic oscillation index.

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Table 1. Slopes of linear regressions for 20 species of migrant bird in Oxfordshire (1971 to 2000)

Species	Arrival date vs. year	Departure date vs. year	Duration vs. year	Arrival date vs. African winter temperature anomaly	Departure date vs. minimum Oxford temperature
Common Cuckoo, *Cuculus canorus*	−0.51	−0.93	−0.58	8.37	1.57
Common Swift, *Apus apus*	−0.30	−0.06	0.20	1.53	−0.06
European Turtle-Dove, *Streptopelia turtur*	−0.31	−0.29	−0.35	−0.48	−1.07
Little Ringed Plover, *Charadrius dubius*	−0.76	−0.81	−0.15	−4.98	4.65
Eurasian Hobby, *Falco subbuteo*	−0.04	0.56	0.58	1.33	0.33
Spotted Flycatcher, *Muscicapa striata*	−0.25	−0.08	0.18	−3.24	−0.40
Common Redstart, *Phoenicurus phoenicurus*	−0.09	0.12	0.07	−1.96	−0.78
Whinchat, *Saxicola rubetra*	0.07	0.53	0.39	−1.92	−1.97
Northern Wheatear, *Oenanthe oenanthe*	−0.37	0.11	0.58	−1.47	0.02
Sand Martin, *Riparia riparia*	−0.58	−0.38	0.18	0.05	−2.51
Barn Swallow, *Hirundo rustica*	−0.44	−0.50	0.05	0.45	−2.62
Northern House Martin, *Delichon urbica*	−0.67	−0.65	0.02	−8.02	−5.56
Common Grasshopper-Warbler, *Locustella naevia*	−0.27	−0.75	−0.58	−0.94	−0.22
Sedge Warbler, *Acrocephalus schoenobaenus*	−0.23	−0.39	−0.27	−6.26	−4.23
Eurasian Reed-Warbler, *Acrocephalus scirpaceus*	−0.31	−0.46	−0.19	−10.52	−5.88
Willow Warbler, *Phylloscopus trochilus*	−0.07	−0.34	−0.29	−0.26	−9.55
Garden Warbler, *Sylvia borin*	−0.03	−0.39	−0.18	−7.10	−4.76
Common Whitethroat, *Sylvia communis*	−0.23	0.18	0.63	−3.14	−5.27
Lesser Whitethroat, *Sylvia curruca*	0.02	−0.54	−0.46	−6.29	−4.26
Yellow Wagtail, *Motacilla flava*	0.04	−0.23	−0.28	2.21	−7.58
Mean	−0.268	−0.266	−0.022	−2.131	−2.506
SE	0.053	0.092	0.084	0.958	0.758
One-sample *t* test	−5.033	−2.887	−0.267	−2.225	−3.309
Significance (2-tailed)	<0.001	<0.009	>0.05	<0.05	<0.004

Arrival date, departure date, and duration of stay in Oxfordshire against year; arrival date in Oxfordshire against African winter temperature anomaly (°C); departure date from Oxfordshire against minimum and maximum Oxford temperature anomaly (°C). A one-sample *t* test was used to test each mean vs. against the null hypothesis of no effect (a slope of zero).

(that is, H_0, mean slope across all species, is zero) (4, 35). All tests were two-tailed and were performed on SPSS.

Phenological trends may be related to underlying population trends (19), rather than directly to changes in parameters such as temperature. Of the 20 species included in this study, there are reliable measures of U.K. population trends for 13 species (36). I used Spearman's rank correlation to examine the relationships between percentage change in population from 1970 to 1999 and slopes of arrival date and departure date.

Results

Seventeen species of migrant birds showed negative slopes of arrival date in Oxfordshire plotted against year (arriving earlier in the year) whereas only three species showed a trend toward later arrival (binomial test, $P < 0.003$). The mean slope of arrival date against year was −0.268 and demonstrated a significant departure from the null model of no change over time (one-sample Student's *t* test of mean slope against 0; $t = -5.033$, d.f. = 19, $P < 0.001$; Fig. 1*a*). This result equates to an average change in arrival date of −8.03 days over the 30-yr period. Very few studies have looked at patterns of departure date in relation to climate change (4, 6), and I assumed that departure date would be delayed because the extended growing season in Europe (9) would improve foraging conditions in the late summer and early fall. Contrary to this prediction, a significant proportion of species (15 of 20) showed a negative slope of departure date plotted against year (binomial test, $P < 0.05$). The mean slope of departure date (−0.266) differed significantly from zero (*t* test of slope against 0; $t = -2.887$, d.f. = 19, $P < 0.009$; Fig. 1*a*) and equates to an average change in departure date of −7.98 days over the 30-yr period. The arrival and departure dates of many of the 20 species have varied in parallel (Fig. 2), and across species there is a significant correlation between the slopes of arrival and departure ($r = 0.562$, $n = 20$, $P < 0.01$). As a result, there has been no significant change in the duration of the period that the migrant bird species are resident in Oxfordshire (*t* test of slope against 0; $t = -0.267$, d.f. = 19, $P > 0.05$; Fig. 1*a*).

The slopes of arrival date in Oxfordshire against the winter SOI and the winter NAOI did not differ significantly from zero (winter SOI, $t = -1.337$, d.f. = 19, $P > 0.05$; winter NAOI, $t = -1.148$, d.f. = 19, $P > 0.05$; Fig. 1*b*). Mean winter temperature anomalies (°C) for Africa south of 20° N were strongly related to arrival date in Oxfordshire (*t* test of slope against 0; $t = -2.225$, d.f. = 19, $P < 0.04$; Fig. 1*b*). Records show that the continent of Africa is warmer than it was 100 yr ago and that the rate of warming is not dissimilar to that experienced globally (1). For the period 1971 to 2000, the winter temperature anomaly for Africa shows a significant positive correlation with time ($r = 0.474$, $n = 30$, $P < 0.008$), equating to a rise in temperature of 0.6°C. Contrary to the second hypothesis proposed by van Noordwijk (22), the African winter temperature anomaly is not significantly correlated with winter NAOI ($r = -0.234$, $n = 30$, $P > 0.05$). Nor is it correlated with temperatures in Oxford (minimum and maximum temperature in Oxford for January, February, March, and April all have $r < -0.290$, $n = 30$, $P > 0.05$), indicating that birds are unlikely to be able to use temperature in sub-Saharan Africa to predict the temperatures on their breeding grounds.

Slopes of departure date from Oxfordshire were unrelated to the summer NAOI (*t* test of slope against 0; $t = -1.188$, d.f. = 19, $P > 0.05$; Fig. 1*c*), or summer maximum temperature in Oxford (*t* test of slope against 0; $t = -0.022$, d.f. = 19, $P > 0.05$; Fig. 1*c*). There was, however, a significant relationship between migrant bird departure date and minimum summer temperature in Oxford (*t* test of slope against 0; $t = -3.309$, d.f. = 19, $P <$

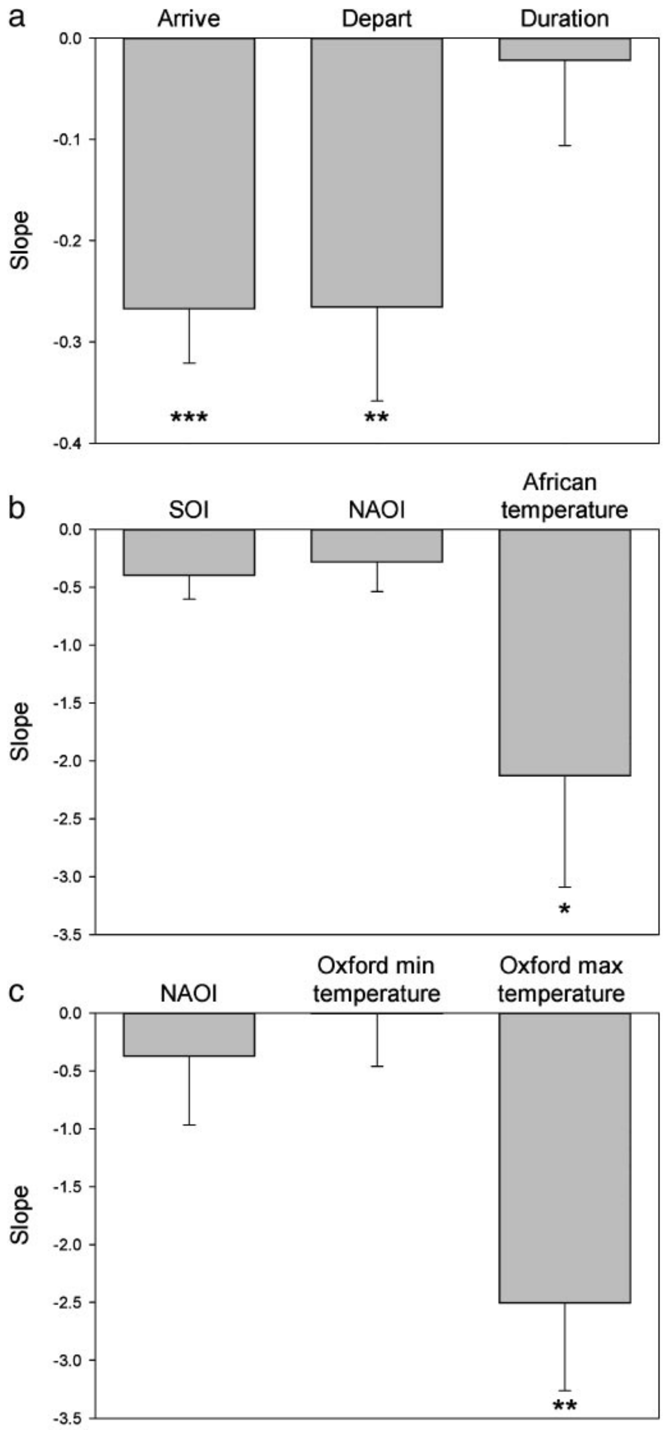

Fig. 1. Mean (−SE) slopes of linear regressions for 20 species of migrant bird in Oxfordshire from 1971 to 2000. (*a*) Arrival date, departure date, and duration of stay in Oxfordshire against time. (*b*) Winter SOI, winter NAOI, and winter surface air temperature anomaly for Africa south of 20°N against arrival date in Oxfordshire. (*c*) Summer NAOI, Oxford summer maximum temperature, and Oxford summer minimum temperature against departure date from Oxfordshire. Significance of one-sample *t* test of mean slope vs. null hypothesis of no effect (slope = 0); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

0.004; Fig. 1*c*). Minimum summer temperature in Oxford has increased significantly over the past 30 yr ($r = 0.449$, $n = 30$, $P <$ 0.02).

The U.K. populations of many bird species are in decline, and in many cases the decline commenced in the mid-1970s (36), so it is possible that phenological changes in migration date are related to underlying population trends rather than to changes in temperature. I found no support for the hypothesis that changes in arrival date ($r_s = 0.091$, $n = 13$, $P > 0.05$) or departure date ($r_s = -0.201$, $n = 13$, $P > 0.05$) are related to population trends although reliable population data are available for only 13 of the 20 species in this study (36).

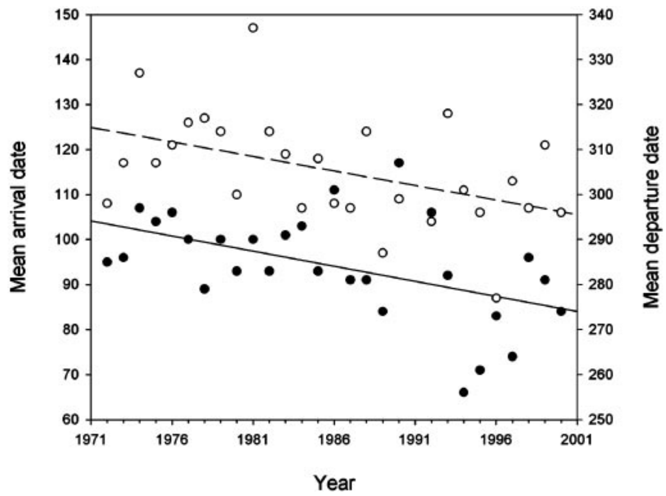

Fig. 2. Linear regressions on the arrival date (filled circles, solid line) and departure date (open circles, dashed line) of Northern House Martins, *Delichon urbica*, in Oxfordshire, from 1971 to 2000. Arrival date: slope = −0.671, $r^2 = 0.243$, $P < 0.08$. Departure date: slope = −0.647, $r^2 = 0.207$, $P < 0.02$. There is no significant difference between the two slopes ($t = 0.101$, d.f. = 54, $P >$ 0.05).

Discussion

The earlier arrival of birds in Oxfordshire and the significant relationship between the sub-Saharan winter temperature anomaly and arrival date are consistent with the hypothesis that climate change is advancing the phenology of avian migration. Seventeen of 20 species showed a trend toward earlier arrival, and the magnitude of the overall trend (arrival date: −2.68 days per decade) agrees well with previous studies on migration (17, 18, 20). van Noordwijk's first hypothesis (22), that arrival times are advanced by improved foraging conditions in Europe in years of high NAOI rather than earlier departure from Africa, is not supported by my results. I found no effects of NAOI on arrival date, and the significant effect of temperature in sub-Saharan Africa suggests that dates of departure from the over-wintering grounds have advanced. It remains possible that the duration of migration has reduced over the past 30 yr, but the current data do not permit this to be tested. The second hypothesis postulated a relationship between NAOI and African weather, and that birds were leaving Africa earlier because of advancing seasons. I found no relationship between sub-Saharan winter temperature and winter NAOI, but the pattern of temperature in Africa supports the hypothesis that the seasons have advanced. My results are at odds with those of Hüppop and Hüppop (17), who report a strong relationship between NAOI and the trends in arrival date of long-distance migrants, but other studies have concluded that the NAOI is of little direct importance to the phenology of long-distance migration (16). van Noordwijk's third hypothesis (22) is that the climate of Africa has not changed, but that migratory timing has changed following evolved changes in the trigger for migration. I found strong evidence for temperature changes in sub-Saharan Africa, in agreement with recent research on the African climate (29). It therefore seems likely that this change has affected migratory phenology through plasticity (17, 28), although it remains possible that evolutionary changes have occurred (27).

Thus, the arrival date of trans-Saharan migrants in Europe seems to depend on conditions in sub-Saharan Africa at the time of departure from their winter feeding grounds, and not on the weather conditions found in the Europe at that time (23, 24), which the birds could not predict. The importance of climate in assumedly influencing the availability of resources on wintering grounds and hence the date of springtime arrival is emphasized in phenological models of migration (37). This finding is further supported by a recent empirical study that demonstrated that winter habitat quality determines the physical condition of migrant American redstarts, *Setophaga ruticilla*, which in turn directly affects the timing of their migration and the date of their arrival on temperate breeding grounds (24).

In this study, three species of birds showed a weak trend toward later arrival on the breeding grounds (whinchat, *Saxicola rubetra*; lesser whitethroat, *Sylvia curruca*; and yellow wagtail *Motacilla flava*). It is unclear why these species do not show advancement in arrival date. Previous studies have recorded similar trends for whinchat (38, 39), lesser whitethroat (39), and common whitethroat, *Sylvia communis* (38), and it is possible that their migration strategy differs from the other species studied.

The trend toward earlier departure from the breeding grounds is contrary to my prediction based on the extended growing season in Europe. Rather than migrants lengthening their stay in northern latitudes, the breeding season seems to have remained relatively constant and so birds are departing earlier for their winter grounds. Many bird species show trends toward earlier reproduction over the past 30 yr (13, 15). It is possible that the trends in earlier departure date reported here are causally related to earlier arrival and earlier reproduction. There is some evidence that the timing of reproduction may affect departure date (40). In Mountain white-crowned sparrows, *Zonotrichia leucophrys oriantha*, interannual variation in migration date was related to reproductive schedule, departure being delayed by ≈ 1 day for every 2 days of delay in nesting (40). Many long-distance migrants seem to be under selective pressure to minimize the time spent migrating (41, 42). Studies on sedge warblers, *Acrocephalus schoenobaenus*, have shown that the best strategy seems to be to start migration as early as possible, maximizing the probability of encountering rich stopover sites and arriving to sites south of the Sahara as quickly as possible (43).

This study clearly demonstrates a highly probable link between global climate change and the migratory phenology of many bird species. Earlier arrival on the breeding grounds is related to temperature in the sub-Saharan winter quarters and may permit earlier establishment of a territory, advancing egg laying. The trend toward earlier departure of migrant birds parallels the trend in arrival dates and may reflect pressures to commence migration once breeding is complete. There is strong selection on the timing of migration and breeding (24, 26), and changes in the timing of arrival and departure may reflect adaptive responses to global climate change (27); however, the complex relationships between phenological events across trophic levels make it likely that many long-distance migrants will be adversely affected by climate change. Furthermore, warming in Africa is accelerating (29), making it progressively more likely that phenology in breeding grounds will become out of phase with changes in the winter quarters.

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