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Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change

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Abstract

Monitoring studies find that the timing of spring bird migration has advanced in recent decades, especially in Europe. Results for autumn migration have been mixed. Using data from Powdermill Nature Reserve, a banding station in western Pennsylvania, USA, we report an analysis of migratory timing in 78 songbird species from 1961 to 2006. Spring migration became significantly earlier over the 46-year period, and autumn migration showed no overall change. There was much variation among species in phenological change, especially in autumn. Change in timing was unrelated to summer range (local vs. northern breeders) or the number of broods per year, but autumn migration became earlier in neotropical migrants and later in short-distance migrants. The migratory period for many species lengthened because late phases of migration remained unchanged or grew later as early phases became earlier. There was a negative correlation between spring and autumn in long-term change, and this caused dramatic adjustments in the amount of time between migrations: the intermigratory periods of 10 species increased or decreased by >15 days. Year-to-year changes in timing were correlated with local temperature (detrended) and, in autumn, with a regional climate index (detrended North Atlantic Oscillation). These results illustrate a complex and dynamic annual cycle in songbirds, with responses to climate change differing among species and migration seasons.

Keywords: bird migration, climate change, NAO, passerine, phenology, temperature, temporal trend

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Introduction

Variation in climate is known to affect the distributions, abundances, and phenologies of many organisms. These include impacts over many millennia during directional shifts in the Earth's climate (Williams *et al.*, 2004), responses to medium-term environmental change over several decades (Parmesan, 2006), and short-term responses to annual fluctuations in weather (Post & Stenseth, 1999). Recently, long-term monitoring programs have reported dramatic biotic changes correlated with anthropogenic climate change (Bradley *et al.*, 1999; Parmesan & Yohe, 2003). As evidence accumulates from diverse taxa around the world, a causative connection between climate change and many biotic responses becomes increasingly plausible (Parmesan, 2006).

Long-term migration monitoring data are available from a few permanent bird observatories and organized networks of amateur observers (Hüppop & Hüppop, 2003; Gordo *et al.*, 2005; Sauer *et al.*, 2006; Gordo, 2007; Sparks *et al.*, 2007). Most monitoring programs began in the 1960–1980s, but a few extend back to the early 20th century or before (Wilson *et al.*, 2000; Butler, 2003; Strode, 2003; Hubálek, 2004). These data have been used primarily to test for changes in the timing of migration. Results from European observatories are widely acknowledged to record a sharply advanced spring migration in recent decades, and strong associations between migration timing and regional weather conditions (reviewed by Lehikoinen *et al.*, 2004; Gienapp *et al.*, 2007; Gordo, 2007).

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The rate of climate warming has been more gradual in eastern North America than in Europe (Hansen *et al*., 2006), and the temporal shifts in avian migration are accordingly less obvious. In fact, most studies of spring migration in North America have found little consistent or convincing evidence of phenological change (Wilson *et al*., 2000; Strode, 2003; Marra *et al*., 2005; Mills, 2005; MacMynowski & Root, 2007; MacMynowski *et al*., 2007; Miller-Rushing *et al*., 2008). Several studies that purport to find advances in spring migration in North America (Butler, 2003; Ledneva *et al*., 2004; Murphy-Klassen *et al*., 2005) recorded only the first individual of each species observed informally by bird watchers. Few data are available for autumn migration, and these suggest no consistent change in timing (Mills, 2005; MacMynowski & Root, 2007). Clearly, there is a need for additional analyses of long-term monitoring data from North America, and for information on both spring and autumn seasons.

This paper reports changes in the timing of migration in many species of land birds captured over 46 years at a banding station in western Pennsylvania, USA. We expected to find some shifts in migration phenology because of the moderate increase in average temperatures across much of North and Middle America in recent decades (Easterling *et al*., 1997; Hansen *et al*., 2006). The prediction is clearest for spring migration, because of well-known advantages of early nesting (Perrins, 1970; Dunn, 2004). In autumn, departure may occur earlier under a warming climate if nesting is completed earlier, or later if the extended season encourages additional nesting attempts (Jenni & Kéry, 2003). We evaluated the association between trends in migration timing and trends in North American weather conditions by testing whether year-to-year variation in phenology was correlated with climate. The strengths of our study emerge from the duration and size of the dataset, our standardized application of a reliable methodology over many decades, information on the full distribution of migration for a large number of species, and attention to both spring and autumn migration.

Methods

The dataset

We compiled data on the timing of migration from bird banding records collected from autumn 1961 through spring 2006 at Powdermill Nature Reserve (PNR), a field station operated by Carnegie Museum of Natural History in Westmoreland Co., PA, USA (elevation 400 m; 40°10′N, 79°16′W). The 10 ha banding site is characterized by small fields, marshland, and low scrub habitats (Utech, 1999). The PNR station operates 5–6 days per week year-round; during spring and autumn migration there are about 35 12 m mist nests (30 and 36 mm mesh) in use each day. The banding methods, locations of the net lanes, and even the personnel remained largely unchanged during this study. Two people, R. C. L. and R. S. M., banded and measured >90% of birds. Although our data originate from only this single locality, the results should be broadly representative of bird migration across eastern North America: PNR is not located in proximity to physical barriers, such as large water bodies or mountains, that might concentrate migrants under certain weather conditions.

Our analysis focused on birds captured during spring and autumn migrations. Migration periods were defined separately for each species after inspecting the temporal distribution of captures. We first eliminated most birds of local breeding or wintering origin by discarding juveniles judged to have fledged recently and individuals that had been previously banded in the same year. The end of spring migration was defined by the disappearance of unbanded individuals; the onset of autumn migration was characterized by the appearance of increasing numbers of unbanded birds. If our sample inadvertently contained a few individuals of local breeding or wintering origin, they were vastly outnumbered by passage migrants. A species was included only if we captured at least 10 different individuals in at least 10 different years. This left us with 120 455 captures of 58 species during spring migration, and 273 562 captures of 70 species during autumn migration.

Changes in phenology under climate change, and the relationship between migration and weather conditions, are likely to vary among species according to their life history and ecology. For example, while short-distance migrants can facultatively adjust spring migration to match regional weather conditions, species that overwinter in the tropics are probably unaware of conditions to the north (Lehikoinen *et al*., 2004) and instead use day length or endogenous mechanisms to synchronize the start of spring migration (Gwinner, 1977, 1996). We collected information on wintering and breeding distributions from the North American Christmas Bird Count (which is conducted each year during early winter; Sauer *et al*., 1996), the North American Breeding Bird Survey (Sauer *et al*., 2006), and our own observations of local breeding birds. Every species was considered a *long-distance migrant* if it overwintered all or mostly to the south of North America, or a *short-distance migrant* if it wintered primarily in the southern United States. The breeding range of a species was classified as *local* if it breeds at PNR, or *northern* if it breeds primarily to the north of, or at much higher elevation than, the banding station. We hypothesized that species that routinely or facultatively rear multiple broods (usually one to three, depending on circumstances during the breeding season) may show different changes in migratory timing than species that always rear a single brood. This is because multiple-brooded species can prolong the breeding season in favorable years by rearing extra broods, and may therefore initiate autumn migration later in years when spring migration was early (Møller, 2002; Jenni & Kéry, 2003). Information on the broodedness of species in our study was obtained from Poole (2008).

Climate data

We tested for associations between weather and annual variation in migratory timing. Regional temperature data came from the 25 weather stations within 200 km of PNR that participate in the United States Cooperative Observing Network. Mean monthly temperatures were available from 1961 to 2005 at each station, with adjustment for changes in equipment, methodology, and urbanization of the surroundings (Williams *et al.*, 2007). We calculated annual mean temperatures during spring migration (March–May) and autumn migration (August–October), with the contribution of each weather station weighted by the inverse of the distance between the station and PNR.

We downloaded the daily North Atlantic Oscillation (NAO) index for 1961 to 2006 from the web site of the U. S. National Center for Atmospheric Research (www.cgd.ucar.edu/cas/jhurrell/indices.html). These data reflect a natural large-scale difference in air pressure between the subarctic and subtropical regions of the northern Atlantic Ocean. High values correspond to a deep low pressure system near Iceland, which draws strong westerly winds from the western north Atlantic and maintains relatively warm and wet conditions in eastern North America (Hurrell, 1995). We included the average NAO index for winter (December–February) in analyses of spring migration, and the average index for summer (June–August) in analyses of autumn migration, because previous studies have identified lagged effects of NAO on bird migration (Hüppop & Hüppop, 2003; Vähätalo *et al.*, 2004; Jonzén *et al.*, 2006).

Statistical analysis

We used mixed-effects repeated measures analyses of variance to test for long-term changes in the timing of migration and for associations between timing and breeding distribution, migration distance, broodedness, and weather. Spring and autumn migration were analyzed separately. The repeated responses were the five dates by which 10%, 25%, 50%, 75%, and 90% of individuals had been captured. High correlations among the five responses within seasons precluded separate analyses of each. We focused on passage of quantiles because they are less sensitive to sample size and uncorrected outliers than measures of distributional extremes, such as first arrival dates (Tryjanowski & Sparks, 2001; Mills, 2005). The random component of both models included species, the species-by-year interaction, and the species-by-repeated response. Fixed effects were year, migration distance and its interaction with year, breeding range and its interaction with year, number of broods and its interaction with year, regional temperature during migration, the NAO index for the preceding season, and the repeated response and its interactions with other fixed effects. Interactions with year tested whether species, categories of species, or the five quantiles showed different trends in arrival dates. Temperature and NAO were both residuals after regression against year, in order to eliminate potentially spurious correlations that would arise if both migration timing and climate show long-term trends. Thus, the analysis asked whether unexplained year-to-year variation in migration timing is associated with annual fluctuations in weather, rather than asking whether long-term phenological change is associated with climate change. The models were implemented in SAS PROC GLIMMIX (SAS Institute (2006), *The GLIMMIX Procedure*, Cary, NC, USA, p. 149; available at http://support.sas.com/).

We used canonical correlation analysis to test the correlation between spring and autumn seasons in the timing of migration and in long-term changes in migration timing. This method, a multivariate extension of standard bivariate correlation analysis, begins with two sets of variables and finds the linear combination of each set, called a canonical variate, that maximizes the correlation between the canonical variates (Hotelling, 1936). The two sets of variables in the first analysis were the mean dates of capture of the 10%, 25%, 50%, 75%, and 90% quantiles in the two seasons, and for the second analysis they were changes in dates (slopes from regressions of quantiles against year). Observations were the 51 species common to both spring and autumn samples.

Results

Mean annual regional temperature increased significantly over the duration of the study [b ($^{\circ}\mathrm{C\,yr}^{-1}$) = 0.021 ± 0.006 SE; $r = 0.46$, $P = 0.002$]. Most warming occurred in summer and winter; temperatures during spring and autumn migration showed upward but nonsignificant trends ($P > 0.19$ in both cases; Appendix S1). The annual mean NAO index increased marginally

($b = 0.0032 \pm 0.0012$; $r = 0.25$, $P = 0.098$). Although the average summer NAO showed no change (Appendix S1; $r = -0.08$, $P = 0.62$), a significant increase in winter NAO ($b = 0.0114 \pm 0.0036$; $r = 0.43$, $P = 0.003$) was associated with increasingly mild winters in eastern North America.

Spring migration

Spring migration at PNR became earlier between 1961 and 2006, but the pattern varied among species and phases of migration. The mixed-effects linear model, treating as repeated measures the 10%, 25%, 50%, 75%, and 90% passage times of each species, confirmed the overall effect of year on timing (Table 1). There was also a weak interaction between year and quantile (the repeated measure), indicating that the five quantiles showed slightly different trends through time. In particular, the early and middle phases of migration (10–50% quantiles) became earlier while the latest phase (90% quantile) showed no change (Fig. 1a). As a result, the overall duration of migration lengthened over the years. Averaged over all species, the elapsed time between the 10% quantile and the 90% quantile increased by 0.08 days yr^{-1} (SE = 0.035, $P = 0.016$), an increase of 4 days between 1961 and 2006. Separate regressions of timing against year for each species confirmed that advancement of early quantiles was widespread (Appendix S2). For example, slopes for the date of 10% passage were negative in 47 of the 58 species ($P < 0.0001$, two-tailed binomial test), 19 of the 47 negative slopes were significant ($P < 0.0001$), and only one species had a significantly positive slope (barn swallow, *Hirundo rustica*).

The significant effect of spring temperature residuals in the repeated measures analysis showed that migrants arrived earlier in years with relatively warm regional temperatures, independent of any long-term trend in temperature itself (Table 1). Annual fluctuations in temperature were associated with changes of about

Table 1 Summary of two repeated measures mixed-effects models testing for changes in the timing of migration at PNR

	Spring migration		Autumn migration	
Effect	Estimate	*P*	Estimate	*P*
Random effects variance components (and SE)				
Species	**125.3 (24.6)**	**0.001**	**167.3 (29.5)**	**0.001**
Species × Year	**0.0087 (0.002)**	**0.001**	**0.0629 (0.012)**	**0.001**
Species × Quantile	**122.9 (1.86)**	**0.001**	**307.2 (3.80)**	**0.001**
Fixed effects parameter estimates (and *F*-ratio)				
Quantile	**(981.4)***	**0.0001**	**(1846.1)***	**0.0001**
Year	**−0.041 (19.65)**	**0.0001**	−0.073 (0.16)	0.6889
Migration distance	**−14.24 (43.20)**	**0.0001**	**29.72 (69.59)**	**0.0001**
Breeding range	12.94 (3.50)	0.0666	**−11.99 (40.67)**	**0.0001**
Number of broods	2.68 (0.04)	0.8484	−0.001 (0.01)	0.9322
Temperature residuals	**−0.374 (133.5)**	**0.0001**	**0.077 (4.54)**	**0.0331**
NAO residuals	−0.132 (0.44)	0.5050	**1.751 (29.25)**	**0.0001**
Year × Migration distance	−0.035 (1.40)	0.2373	**0.212 (9.93)**	**0.0025**
Year × Breeding range	−0.055 (3.77)	0.0523	0.039 (0.34)	0.5596
Year × Number of broods	−0.020 (0.08)	0.7758	0.030 (0.19)	0.6680
Quantile × Year	(2.35)*	0.0518	**(7.71)***	**0.0001**
Quantile × Migration distance	**(214.0)***	**0.0001**	**(6.62)***	**0.0001**
Quantile × Breeding range	**(203.9)***	**0.0001**	**(798.9)***	**0.0001**
Quantile × Number of broods	(1.04)*	0.3886	(0.81)*	0.5172
Quantile × Temperature	**(3.35)***	**0.0095**	(0.25)*	0.9097
Quantile × NAO	(0.31)*	0.8715	(0.65)*	0.6238

The five repeated measures were the dates of capture of 10%, 25%, 50%, 75%, and 90% of individuals (quantiles). Species were included as random subjects. Regional temperature and the NAO index were both trend-corrected residuals for the period 1961–2005. For the analysis of spring migration, temperature was averaged from March to May and the NAO index was averaged from December to February. For the autumn analysis, temperature was from August to October and NAO was from June to August. Migration distance differentiates neotropical migrants from species that winter in southern North America, breeding range differentiates species that breed locally from those that breed entirely north of PNR, and the number of broods is either 1 or variable (usually 1–3). Estimates are variance components for random effects and parameter estimates for fixed effects; those marked with an asterisk (*) are too numerous to list. Figures in bold indicate significant effects.

PNR, Powdermill Nature Reserve; NAO, North Atlantic Oscillation.

2–3 days in the timing of migration (Fig. 2a). An interaction between temperature and quantile arose because the advancing effect of temperature was strongest during early phases of migration. High winter NAO residuals were not correlated with arrival date.

Long-distance neotropical migrants arrived at PNR much later than short-distance migrants (Fig. 3a, Table 1), and species with more northern breeding distributions migrated slightly earlier than locally breeding species (Fig. 3c). The lack of strong interactions between year and breeding range or migration distance indicated that trends in migration timing were similar for all types of species, except that species breeding locally showed somewhat more advanced arrival dates than northern breeders (Fig. 4a). Differences among categories of species in the tempo of passage were revealed by strong interactions between quantile and both migration distance and breeding range (Table 1). Long-distance migrants passed through more quickly than short-distance migrants (Fig. 3a), and northern breeders passed more quickly than local breeders (Fig. 3c). Differences in the duration of passage were large: the middle 80% of all individuals was captured over a period of 19.7 days for long-distance migrants and 29.3 days for short-distance migrants. For northern and local breeding species, the corresponding values were 18.1 and 27.4 days, respectively. Broodedness was unrelated to the timing of spring migration, the trend in timing through the years, or the duration of passage (Table 1).

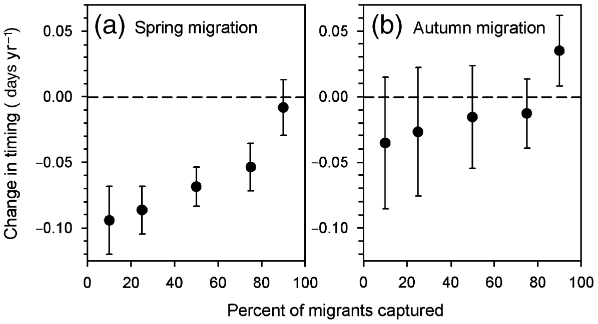

Fig. 1 Average .changes (± 1 SE) in the timing of songbird migration at PNR, calculated separately for the dates by which the 10%, 25%, 50%, 75%, and 90% quantiles were captured. Sample sizes are 58 species in spring and 70 species in autumn. Negative values reflect a shift toward earlier migration between 1961 and 2006.

Estimates of random effects in the analysis of spring migration illustrated considerable variation among species in mean migration timing, even after accounting for fixed effects. The species-by-year component reflected heterogeneity among species in their long-term changes in timing. The species-by-quantile variance component demonstrated that differences among the five measures of timing varied among species, because species exhibited highly variable rates of migration through PNR.

Autumn migration

There was no overall change in autumn migration timing over the years. As in spring, the five measures of timing differed in their temporal trends, with early migrants appearing slightly earlier and late individuals becoming later (Fig. 1b; Table 1). As a consequence, the time between the 10% and 90% quantiles increased on

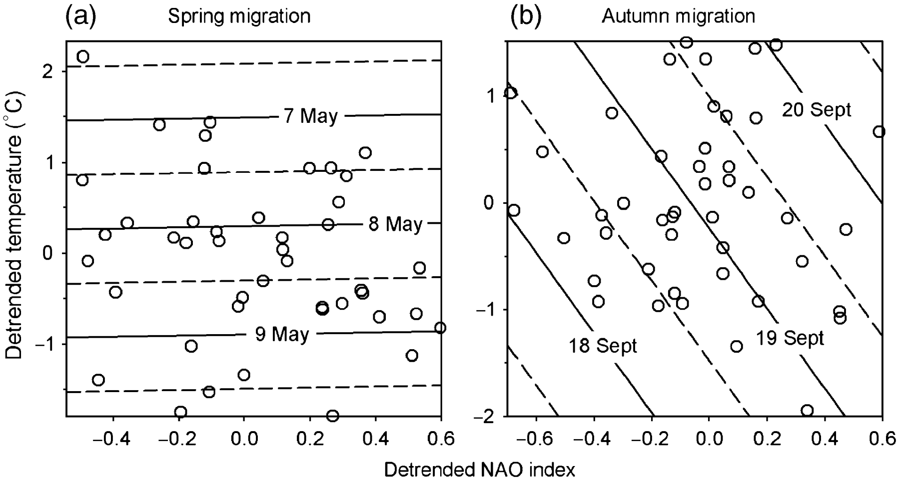

Fig. 2 Spring migration (a) was advanced in years with high spring temperature, and autumn migration (b) was advanced in years with high autumn temperature and summer NAO. Temperatures, NAO values, and migration timing were all corrected for yearly trends. The contour lines represent a surface estimated from models predicting the date of passage of the 50% quantile based on spring temperature and winter NAO (a) or autumn temperature and summer NAO (b). Open symbols represent observed values for the 45 years.

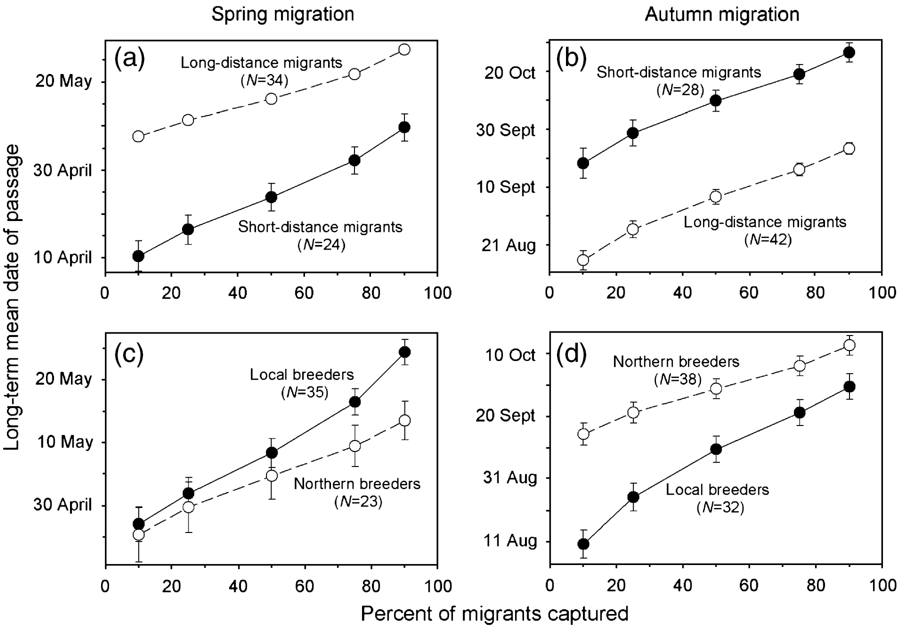

Fig. 3 Distribution of migration timing at PNR in spring and autumn. Timing was measured by the dates (± 1 SE) at which 10%, 25%, 50%, 75%, and 90% of individuals were captured. Results are shown separately for species with different migration distances and breeding distributions. In both seasons, long-distance migrants and northern breeders passed more quickly.

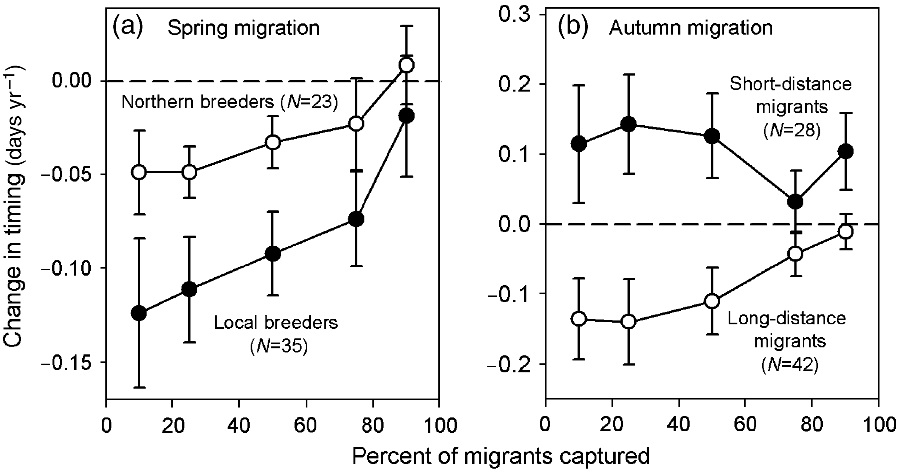

Fig. 4 Long-term changes in the timing of spring migration (a) for species that breed locally or to the north of PNR, and autumn migration (b) for species that winter primarily in North America (short-distance migrants) or in the neotropics (long-distance migrants). Shown are averages (± 1 SE) of slopes from separate regressions against year for the dates on which 10%, 25%, 50%, 75%, and 90% of individuals were captured.

average by 0.071 days yr^{-1} (SE = 0.018, $P = 0.0001$), or about 3.2 days over 45 years. Migration occurred significantly later in years when the detrended summer NAO index was high and local temperatures were relatively warm (Fig. 2b). Species that breed to the north of PNR departed late and neotropical migrants departed early (Figs 3b and d). The interaction between year and migration distance arose because long-distance and short-distance migrants showed opposite trends through time (Fig. 4b). The temporal distribution of passing migrants differed among categories of species, with northern breeders passing through PNR relatively quickly (Fig. 3d). This was reflected in a highly significant interaction between quantile and breeding range (Table 1). As in the spring, these differences were quite large: the middle 80% of individuals passed through over 28.4 days for northern breeders and 50.4 days for local breeders. There was again no influence of number of broods on migration timing, the trend in timing through the years, or the duration of passage.

Large random effects of species, species-by-year, and species-by-quantile indicated that species varied substantially in their migration timing, their changes in timing through the years, and in their duration of passage. Indeed, separate regressions on the 90% passage date for each of the 70 species produced 18 slopes significant at the $\alpha = 0.05$ level, which is far more than expected by chance ($P < 0.0001$, two-tailed binomial test). But 13 of these significant slopes were positive and five negative, reflecting sharp differences among species in phenological change.

Comparison between seasons

A strong negative relationship between seasons in average date of passage indicated that the earliest species in spring migrated latest in autumn (Fig. 5a). The dates of all five quantiles in spring were highly negatively correlated with all five quantiles in autumn ($P = 0.0001$, canonical correlation analysis; Table 2A). There were no species migrating early in both spring and autumn, or late in both seasons (Fig. 5a). If the intermigratory period is measured as the time between 50% quantiles in spring and autumn, then its average duration varied from 67 days in the barn swallow to 225 days in the fox sparrow (*Passerella iliaca*). Species migrating early in spring and late in autumn tended to be short-distance migrants with northern breeding distributions ($P < 0.0022$ for both migration distance and breeding distribution, MANOVA on the two canonical axes in Fig. 5a). The number of broods was unrelated to the timing of migration ($P > 0.2$, MANOVA).

There was also a negative correlation between the changes in migration timing in spring and autumn: species that arrived increasingly early in spring became later in autumn, and those becoming later in spring departed increasingly early in autumn (Fig. 5b). Canonical correlation analysis showed that long-term changes in the first three quantiles in both seasons were negatively associated with each other (Table 2B; $P = 0.0355$). Changes in timing of later migration phases were not clearly correlated between spring and autumn. Most species experienced total changes in duration of the summer season of no more than a few days between 1961 and 2006 (Fig. 5b). However, the change was much greater in a few cases. Species for which the intermigratory period shortened by >15 days included barn swallow, American redstart (*Setophaga ruticilla*), ovenbird (*Seiurus aurocapilla*), and white-eyed vireo (*Vireo griseus*). Several other species experienced increases of >20 days in the intermigratory period (red-winged blackbird *Agelaius phoeniceus*, indigo bunting *Passerina cyanea*, and blue-winged warbler *Vermivora pinus*). Change in duration of the intermigratory period was not associated with migration distance, breeding distribution, or broodedness (in all cases $P > 0.6$, MANOVA on the two canonical axes in Fig. 5b).

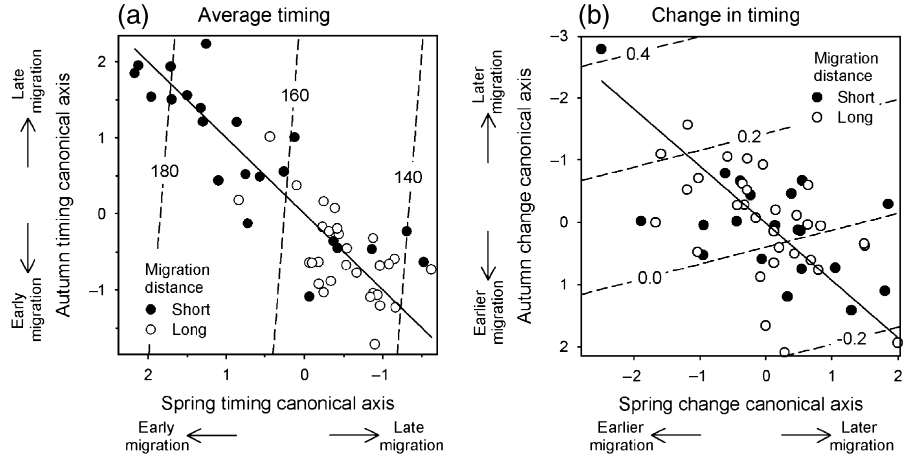

Fig. 5 Negative correlations between the average timing of migration in spring and autumn (a) and between changes in migration timing in spring and autumn (b) for the 51 species that occurred in both seasons. The axes are canonical variates derived from the five quantiles used to measure migration time (date of capture of 10%, 25%, 50%, 75%, and 90% of individuals). Solid lines are major axis regressions fit to the data. The contours in A represent a surface showing the number of days between the 50% quantiles in spring and autumn, estimated by multiple regression on the canonical axes. The contours in B illustrate change in the time spent on the summer range (days/year between 50% quantiles); species in the lower right decreased the time spent on the summer range. Long-distance migrants, represented by the open symbols, were captured late in the spring and early in autumn.

Table 2 Results of two canonical correlation analyses comparing the timing of migration between spring and autumn (A) and comparing the changes in timing between the two seasons (B)

	Quantile (%)				
	10	25	50	75	90
(A) Mean timing over all years (canonical correlation = 0.87, $P = 0.0001$)					
Spring migration	0.779	0.786	0.810	0.844	0.864
Autumn migration	−0.969	−0.967	−0.932	−0.899	−0.898
(B) Change in timing through the years (canonical correlation = 0.62, $P = 0.0355$)					
Spring migration	0.689	0.348	0.147	0.117	0.283
Autumn migration	−0.827	−0.599	−0.543	0.038	0.188

Timing was measured by the dates of passage for each species of the five quantiles describing the distribution of migrants. Changes in timing are slopes from regressions of quantile dates against year. Entries in the table are correlations between the canonical variates and the original variables (quantile dates). Observations are the 51 species common to both seasons.

Discussion

This analysis of an uninterrupted 46-year record from an eastern North American bird banding station revealed that the timing of migration has advanced significantly in the spring, while there was no consistent change in the timing of autumn migration. However, it is inaccurate to designate migration as occurring simply earlier or later, because trends varied among species and phases of migration. In fact, there was widespread lengthening of the duration of passage, because the earliest individuals arrived earlier through the years, especially during spring migration, while the latest individuals did not change or appeared somewhat later. Individual species showed very different patterns of phenological change in both seasons: those that advanced spring migration tended to delay autumn migration, and vice versa. This led to a few dramatic increases and decreases in the duration of the intermigratory period. These data agree with the trend toward earlier spring arrival reported previously, and with studies showing inconsistent shifts in timing of autumn migration. However, a close look at our results suggests a few cautionary messages for interpreting studies of avian phenology and climate.

One message is that previous studies may have exaggerated the extent to which spring migration is occurring earlier in recent years. Especially in Europe, sharp advances in spring migration are widely reported (Lehikoinen *et al*., 2004; Gienapp *et al*., 2007; Sparks *et al*., 2007). Corresponding changes in North America have been more subtle or absent (Wilson *et al*., 2000; Strode, 2003; Marra *et al*., 2005; Mills, 2005; Murphy-Klassen *et al*., 2005; MacMynowski & Root, 2007; MacMynowski *et al*., 2007). While part of the difference between continents may reflect real contrasts in the extent or impact of climate change, some of the difference may also arise from how migration timing is measured. Many European studies take the first individual observed in spring as a measure of timing (e.g. Tryjanowski *et al*., 2002; Cotton, 2003; Sparks *et al*., 2007; Sokolov & Gordienko, 2008). Our results show that these early individuals have advanced their arrival by the greatest extent. The first 10% of the distribution of migrants arrived at PNR nearly 1.0 day earlier per decade, whereas the entire distribution changed by about 0.4 days per decade (slope from Table 1). Previous analyses of later phases of migration make clear that the entire distribution of migrants is not traveling much earlier, at least in North American species (Mills, 2005; MacMynowski *et al*., 2007; but see Miller-Rushing *et al*., 2008). In Europe, as well, changes in timing of later parts of the distribution are less obvious (Ahola *et al*., 2004; Jonzén *et al*., 2006; Tottrup *et al*., 2006a; Rubolini *et al*., 2007). All these data taken together suggest that the emphasis on first arrival dates may have resulted in some overestimation of the extent to which spring migration has advanced in recent decades. Studies of autumn passage may be less prone to exaggerating phenological change because they rarely record the appearance of the first- or last-observed individual, and this may partly explain the less dramatic changes reported for the timing of migration in autumn (e.g. Mills, 2005). However, our results and others show that important differences remain between spring and autumn in patterns of change in migration timing (Fig. 1; Tottrup *et al*., 2006a, b).

A second message emerging from our study relates to the causal link between phenology and changing climate. Many previous studies report strong associations between bird migration and long-term regional weather records (Hubálek, 2003; Hüppop & Hüppop, 2003; Marra *et al*., 2005; Sparks *et al*., 2007; Miller-Rushing *et al*., 2008). However, the causal connection has remained unclear because such associations are inevitable whenever phenology and climate are both changing. In other words, once a shift in the timing of migration is discovered, then *any* feature of the environment that changes over the same time period can appear to be correlated with migration. Our analysis of detrended data eliminates the potential for spurious correlations between phenology and weather. We found that unexplained variation in the timing of both spring and autumn migration was significantly associated with detrended temperature, and autumn timing was associated with detrended summer NAO data (Fig. 2). This represents additional evidence that annual fluctuations in weather can influence bird migration (e.g. Lehikoinen *et al*., 2004).

After the short-term impact of weather is demonstrated, implicating a gradually changing climate in long-term phenological change is a reasonable further step in the argument. This is one of three lines of evidence suggesting that directional climate change has caused shifts in biotic phenology in many parts of the world. (1) Short-term fluctuations in weather variables can sometimes be linked to phenological variation, and reasonable mechanisms underlying these links can be proposed (Post & Stenseth, 1999; Saino *et al*., 2007; this study). The assertion is that the same mechanisms relating weather to phenology might account for long-term changes in timing if changes in climate are also directional. (2) Concordant shifts in the phenology of many biological process have been noted across numerous species of plants and animals, mostly in the directions predicted by the mechanisms derived from evidence (1) (Bradley *et al*., 1999; Parmesan & Yohe, 2003; Cleland *et al*., 2007). (3) The phenological shifts noted in evidence (2) appear to be largest in geographic regions in which climate change has been greatest (Dunn & Winkler, 1999; Both *et al*., 2004). These observations taken together implicate recent large-scale changes in climate as probable causative agents of change in biotic phenology in general. For our study, this implies that the continuous effect of year in spring may be due to long-term change in temperature, and the interaction between year and quantile in autumn may be due to changes in both NAO and temperature. Obviously, changes in numerous other variables could also be involved.

Our results agree with previous studies reporting no consistent trend in autumn timing over recent decades (North America: Mills, 2005; MacMynowski & Root, 2007; this study; Europe: Cotton, 2003; Jenni & Kéry, 2003; Anthes, 2004; Tottrup *et al*., 2006b; Sparks *et al*., 2007). However, the changes that did occur in autumn were correlated with those in spring, and a combination of the two created dramatic changes in annual phenology. The negative correlation in Fig. 5b indicates that, rather than shifting both migrations earlier or later, many species moved their spring and autumn migrations in opposite directions. As a result, several species increased or decreased the time between spring and autumn migrations by several weeks over the 46 years of this study. The responses of particular species were not easily interpretable in terms of their natural history. There was no association with breeding distribution, migration distance, or broodedness, and close examination of **Appendix S2** reveals no obvious ecological correlates of changing intermigratory duration.

Cryptic geographic substructure of populations may help explain variation among species. Birds that breed in temperate areas frequently have multiple subpopulations that mix during migration but can have different seasonal schedules and different reactions to climate change (Nolan & Ketterson, 1990; Bearhop *et al*., 2005; MacMynowski & Root, 2007). At the same time, changes in climate and habitat quality in both wintering and summering areas are spatially heterogeneous (Bell, 2007; Both & te Marvelde, 2007; Saino *et al*., 2007). Geographic heterogeneity in conditions could generate the lengthening duration of migrations that we observed. Spring migration would become more drawn out, for example, if subpopulations that arrive earliest also experienced the most warming in their wintering areas. The same could occur if late-arriving subpopulations suffered a decline in winter habitat quality, which delayed their departure for the north. Geographic heterogeneity in the fates of early- and late-migrating subpopulations is also consistent with the negative correlation among species in timing trends between spring and autumn passage (Fig. 5b). When a subpopulation that migrates late in spring increases in frequency, the entire spring migration of that species becomes later. If subpopulations follow the same pattern that species do, illustrated by the negative correlation in average timing between seasons (Fig. 5a), then a shift toward late-migrating birds in spring would be accompanied by earlier autumn migration. In summary, geographic structuring of populations, and changes in the relative abundance of subpopulations, may help explain intriguing variation among species, without invoking unknown species-specific ecological or life-history traits.

Recent research on biotic responses to climate change has had unexpected benefits for understanding how animal phenology is regulated. In the case of bird migration, it has been noted that long-distance migrants overwintering in the tropics are less sensitive to spring weather conditions on the migration path than short-distance migrants (Hagan *et al*., 1991; Forchhammer *et al*., 2002; Hüppop & Hüppop, 2003; Stervander *et al*., 2005). This supports an older hypothesis that phenology is governed by day length in long-distance migrants and by variation in climate in short-distance migrants (Kok *et al*., 1991; Berthold, 1996; Gwinner, 1996). An alternative model is that the onset of migration is sensitive to climate in both groups of birds, but that weather conditions in the tropics are only weakly correlated with conditions farther north along the migratory route (Saino & Ambrosini, 2008). Recent advances in climate and migration suggest that both explanations might be true. Although some variation in the arrival of long-distance spring migrants is accomplished by adjustment of migratory speed rather than date of departure from wintering areas (Marra *et al*., 2005; Jonzén *et al*., 2006; Gordo, 2007), there is also evidence that departure from the tropics can be modified by weather (Saino *et al*., 2004; Gordo *et al*., 2005).

Recent large-scale changes in temperature and precipitation are occurring faster than those recorded over the geologic record of the Holocene (Thompson *et al*., 2006; Ammann *et al*., 2007), and the lack of analogous climatic events within the past few thousand years makes it difficult to predict what the future holds for migrant songbirds (e.g. Williams & Jackson, 2007). There are indications already that changes in migration timing can cause mistimed associations between arrival on the breeding grounds and egg-laying or food supply (Both & Visser, 2001; Visser & Both, 2005). Our results suggest additional mechanisms by which shifts in phenology may be of biological significance. For example, heterogeneity among species in phenological change (Fig. 5a) implies that the species composition of assemblages that co-occur during migration and early breeding periods may be altered (Rotenberry & Chandler, 1999). In addition, correlated changes in phenological trends between spring and autumn migrations (Fig. 5b) may represent a constraint on the onset and duration of breeding that could affect future rearrangement of phenology. Altogether, these results show that net effects of climate change on bird populations will be variable and difficult to predict (Travis & Futuyma, 1993; Davis *et al*., 2005).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Changes in meteorological conditions between 1961 and 2005. Temperatures (A, C) are averaged over the 25 weather stations within 200 km of the PNR banding site, with each station's contribution weighted by the inverse of its distance from PNR. For temperature, *spring* is March–May and *autumn* is August–October. For the NAO index (B, D), *winter* is December–February and *summer* is June–August. Dashed lines were estimated by least squares regression.

Appendix S2. Summary of migration timing for individual species. Timing is reported for the 10% and 50% quantiles of captured individuals in spring, and for the 50% and 90% quantiles in autumn. Years is the number of years with at least 10 individuals captured; the mean time of passage is the Julian date; the slope and SE refer to the rate of change in timing of passage (days yr^{-1}) estimated from linear regression. Species with <10 years' data are not included. Migration distance differentiates species that winter primarily in southern North America (short) from those that winter in the tropics (long). Breeding range distinguishes between species that breed near the banding station from those that breed entirely to the north or at higher elevation.