GLOBAL CHANGE ECOLOGY

Peter P. Marra · Charles M. Francis
Robert S. Mulvihill · Frank R. Moore

The influence of climate on the timing and rate of spring bird migration

Abstract Ecological processes are changing in response to climatic warming. Birds, in particular, have been documented to arrive and breed earlier in spring and this has been attributed to elevated spring temperatures. It is not clear, however, how long-distance migratory birds that overwinter thousands of kilometers to the south in the tropics cue into changes in temperature or plant phenology on northern breeding areas. We explored the relationships between the timing and rate of spring migration of long-distance migratory birds, and variables such as temperature, the North Atlantic Oscillation (NAO) and plant phenology, using mist net capture data from three ringing stations in North America over a 40-year period. Mean April/May temperatures in eastern North America varied over a 5°C range, but with no significant trend during this period. Similarly, we found few significant trends toward earlier median capture dates of birds. Median capture dates were not related to the NAO, but were inversely correlated to spring temperatures for almost all species. For every 1°C increase in spring temperature, median capture dates of migratory birds averaged, across species, one day earlier.

Lilac (*Syringa vulgaris*) budburst, however, averaged 3 days earlier for every 1°C increase in spring temperature, suggesting that the impact of temperature on plant phenology is three times greater than on bird phenology. To address whether migratory birds adjust their rate of northward migration to changes in temperature, we compared median capture dates for 15 species between a ringing station on the Gulf Coast of Louisiana in the southern USA with two stations approximately 2,500 km to the north. The interval between median capture dates in Louisiana and at the other two ringing stations was inversely correlated with temperature, with an average interval of 22 days, that decreased by 0.8 days per 1°C increase in temperature. Our results suggest that, although the onset of migration may be determined endogenously, the timing of migration is flexible and can be adjusted in response to variation in weather and/or phenology along migration routes.

Keywords Climate change · Migratory birds · Phenology · Temperature · Timing of migration

P. P. Marra (✉)
Smithsonian Environmental Research Center,
P.O. Box 28, Edgewater, MD 21037, USA
E-mail: marrap@si.edu

C. M. Francis
Bird Studies Canada, P.O. Box 160,
Port Rowan, Ontario, N0E 1M0, Canada

R. S. Mulvihill
Powdermill Nature Reserve,
Carnegie Museum of Natural History,
1847 Route 381, Rector, PA 15677-9605, USA

F. R. Moore
Department of Biological Sciences,
University of Southern Mississippi,
Hattiesburg, MS 39406-5018, USA

Present address: C. M. Francis
National Wildlife Research Centre,
Canadian Wildlife Service,
Ottawa, Ontario, K1A 0H3, Canada

Introduction

Over the last century, the earth has experienced a general increase in mean surface air temperatures by about 0.5°C (Houghton et al. 1995) and many ecological processes have changed in response to this warming (Walther et al. 2002). Birds in particular have exhibited a variety of responses consistent with warming trends including earlier breeding dates (Crick et al. 1997; Ivanauskas et al. 1997; McCleery and Perrins 1998; Crick and Sparks 1999; Dunn and Winkler 1999; Brown et al. 1999; Bradley et al. 1999; Inouye et al. 1999; Hüppop and Hüppop 2003), range extensions (Thomas and Lennon 1999) and mistimed life history events (Visser et al. 1998; Thomas et al. 2001). Warming patterns, however, vary spatially and temporally (Easterling et al. 1997). This latter fact is of particular importance with reference to long-distance

migratory birds whose annual ranges extend from the tropics to temperate areas, where elevated spring temperatures may have advanced spring phenology. If long-distance migratory birds cannot adjust the timing and rate at which they migrate they may arrive back at temperate breeding areas at times that are suboptimal (Both and Visser 2001; Penuelas and Filella 2001).

Nearctic-Neotropical migratory birds over-wintering in tropical areas move north across latitudes in spring and arrive on temperate breeding grounds in approximately early May. Upon completion of breeding in late summer, individuals migrate south to overwintering sites. It is here in the tropics where they will spend the majority of the annual cycle from autumn until early spring. Current theory suggests that because of annual climatic stability on their tropical wintering grounds, relative to their temperate breeding areas, long-distance migratory birds depend on endogenous circannual rhythms to cue spring migration (Hagan et al. 1991). Strong empirical support for this comes from only a handful of Palearctic migratory bird species, but the data do uphold the hypothesis that migratory onset is primarily endogenous (Berthold and Querner 1981; Berthold 1984; Berthold and Terrill 1991; Gwinner 1990). Photoperiod and other environmental factors on wintering grounds are also thought to play a role in modifying departure schedules (Berthold 1993, 1996; Gwinner et al. 1985; Kok et al. 1990; Marra et al. 1998). Relative to the onset of migration, however, even less is understood about the factors that regulate the timing and rate of migration.

If the timing and rates of migration are inflexible they may result in individuals arriving at breeding areas at times when habitats are suboptimal because of earlier springs (Both and Visser 2001; Penuelas and Filella 2001). Evidence for such a constraint comes from work with one species of long-distance migrant, the Pied Fly-catcher (*Ficedula hypoleuca*) (Both and Visser 2001). Alternatively, rates of migration may be flexible and change as determined by factors such as food abundance and weather or both. For example, stopover length is known to vary with local habitat suitability and food abundance (Lindstrom 1991; Moore and Simons 1992) as well as with the energetic condition of individuals (Yong and Moore 1993), although these relationships are complex (Schaub and Jenni 2001). It follows then that the length of stopover can influence the rate of migration. Late winter storms, cold fronts, and unfavorable winds are also thought to modify rates of migration (Richardson 1978; Elkins 1993; Huin and Sparks 1998, 2000).

Examining how the timing and rate of migration have changed over time requires consistent sampling over long time periods. Migration counts, such as capture totals from standardized mist-netting, have been widely used to examine differences among and within species (such as different age-sex classes) in migration timing, and can also provide good information on annual variation in timing. Quantifying rates of migration for individual small songbirds is difficult because of the problems inherent in tracking small animals over large spatial scales (Webster et al. 2002, but see Wikelski et al. 2003). However, the rate of migration, here taken to include both stopover periods and actual flight times, can be estimated indirectly if multiple ringing sites are available along a flyway or north to south gradient by comparing the timing of passage at each of the sites. We examined whether the timing and rates of migration are fixed and constant across years or flexible and modified to correspond with environmental conditions such as temperature and plant phenology.

In this paper, we use data from relatively standardized mist netting to assess (1) the degree that the timing and rate of Nearctic-Neotropical bird migration have changed over time, and (2) the extent to which the timing and rate of migration is related to spring ambient temperature. We also compared migration dates with the North Atlantic Oscillation (NAO) which has been found to be correlated with migration dates for a number of European birds (Hüppop and Hüppop 2003).

We estimated the timing of migration based on median capture dates, which largely represent passage dates through the sites, from long-term netting data from 43 species of Nearctic-Neotropical migratory birds from one ringing station in the northern USA and another in southern Canada. To investigate how spring ambient temperatures influence the rate of northward bird migration, we compare migration dates from these two ringing stations with migration dates at a ringing station on the Gulf coast of Louisiana for a sample of species and years. We also examined how these responses compare to those of plants in the same area, using a long-term data set on lilacs as an index of plant phenology in spring.

Materials and methods

We used mist net capture data from two of the longest continuously operating ringing stations in North America that span a 40-year period (1961–2000). The first station is the Powdermill bird ringing station, located at the Powdermill Nature Reserve (PNR), a 900-ha field biological station of the Carnegie Museum of Natural History, which is situated along the western flank of Laurel Hill in eastern Westmoreland County, Penn., USA (40°10′N, 79°16′W; Fig. 1). PNR has a 10-ha ringing site (elevation 400 m) characterized by fields, small ponds and marshes, and low order riparian shrub–scrub habitats. Utech (1999) has extensively described the vegetation and climate at PNR. From 1961 to 2000, approximately 35 nylon mist nets (12×2.6 m, mixed 30 and 36-mm mesh size) were employed singly or in lines of up to 10 connected nets in gaps within and along the edges of habitats dominated by low (<4 m high) vegetation. Over the course of this study, the positions of these net lanes changed little and the same two or three people did all ringing. Ringing was conducted 5–6 days a week throughout the year, and the number of nets and hours of operation were recorded each day. Nets were

opened about half an hour before sunrise and were closed usually by mid-afternoon. Daily banding effort in spring averaged about 150 net hours over the course of the study (Leberman et al. 1990, unpublished data). Additional details of the banding procedures at Powdermill have appeared in successive 10-year summary reports (Leberman and Clench 1972; Leberman and Wood 1983; Leberman et al. 1994).

The second data set came from Long Point Bird Observatory (LPBO) near Port Rowan, Ontario, Canada (42°33′N, 80°10′W, Fig. 1). LPBO runs three stations along a vegetated sand spit that extends 30 km out into Lake Erie. At each station, migration monitoring has been carried out throughout the spring and autumn migration seasons, involving both mist-netting and observational counts. We restricted our analyses to the two stations (called Breakwater and the Tip) that have been operating since 1961. Mist-netting involved 10–15 nets at each station, which were usually run from half an hour before dawn for about 6 h. Positions and numbers of nets have changed occasionally, due to changes in the landscape from erosion and succession, but generally remained consistent within a season, such that capture dates should provide a fairly consistent measure of migration timing within each season. Further details of the sampling methods and vegetation at the sites are given by Francis and Hussell (1998) and Dunn (2000).
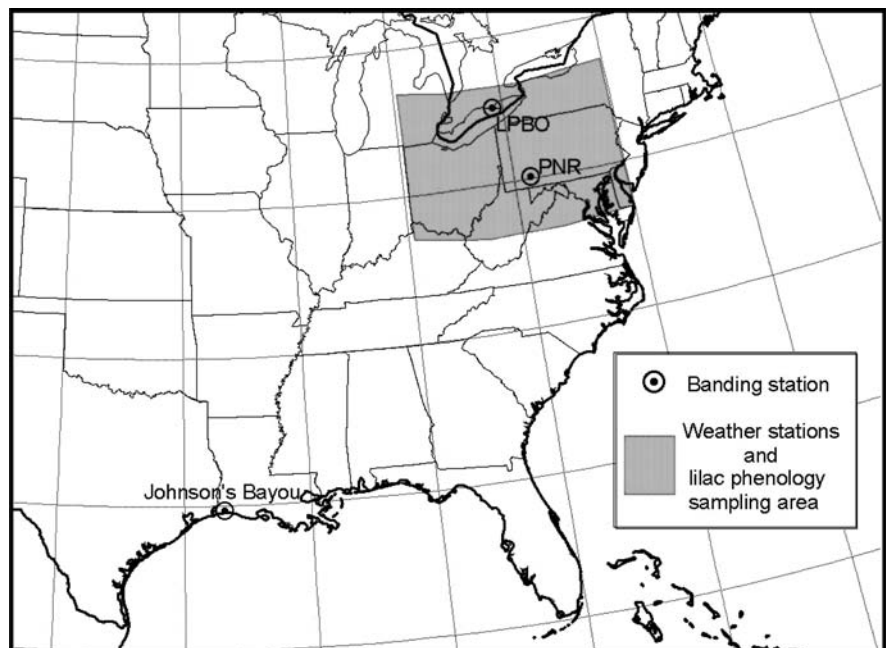
To examine rates of migration we compared migration dates at LPBO and PNR with those from a ringing site on the northern Gulf coast of the USA. The Louisiana study site is within the Johnson's Bayou chenier, a coastal woodland in western Louisiana (29°45′N, 93°37′W) and was monitored for migrating birds over 11 years (1988–1991, 1993–1996, 1998–2000). Between

28–32 mist-nets (12×2.6 m with 30-mm mesh) were opened for a total of about 225 net hours per day. Coastal woodlands (cheniers) are important spring stopover sites for Nearctic-Neotropical migrants because they provide a place to rest and replenish fat and protein stores following trans-Gulf flight (Moore and Kerlinger 1987; Yong and Moore 1997; Karasov and Pinshow 1998). The narrow strips of woodland are dominated by hackberry (*Celtis laevigata*). Understory species include yaupon (*Ilex vomitoria*), blackberry (*Rubus* L. sp.), greenbrier (*Smilax tamnoides*), poison ivy (*Toxicodendron radicans*), and cherokee rose (*Rosa laevigata*).

Temperature data

We used temperature data from the USA Historical Climatology Network (Easterling et al. 1997) on the NOAA web site http://lwf.ncdc.noaa.gov/oa/climate/research/ushcn/ushcn.html. To represent mean spring temperatures in the north-eastern USA and southern Canada, we selected all weather stations ($n = 122$) with continuous coverage throughout the 40-year period of the study in the area bounded by 38°N and 43°N, and between 75°W and 85°W (Fig. 1). For each station, we took the mean of the April and May adjusted mean monthly temperatures. The data had been adjusted for any changes in protocol at individual stations (such as changes in equipment, time of day of observations, location of sensors, etc.), as well as for urbanization bias (Easterling et al. 1997). For comparison, we also calculated similar indices of spring temperature for the two weather stations nearest each banding station (Erie, Pennsylvania, station 362682, 42°05′N, 80°11′W;

Fig. 1 Map of banding and weather stations and lilac sampling phenology region. Banding stations include Long Point Bird Observatory (LPBO), PNR and Johnson's Bayou

Unionville, Pennsylvania, station 369050, 39°54′N, 79°44′W). To estimate annual variation in spring temperatures in the southeastern USA, along the migration routes to these stations, we also calculated mean spring temperatures for all stations in the area bounded by 30°N and 38°N, and between the east coast and 93° to the west ($n = 202$ weather stations).

The NAO index data were derived from the Climatic Research Unit at the University of East Anglia, Norwich, UK (http://www.cru.uea.ac.uk/cru/data/nao.htm) following Hüppop and Hüppop 2003).

Plant phenology

To determine the relationship between annual variation in mean temperature and plant phenology, we used observations of first budburst dates of the ornamental purple common lilac (*Syringa vulgaris*) from a network of observation sites throughout eastern North America (Schwartz 1994). We use lilacs because these have the best long-term plant phenological data available in North America. We have no reason to believe that migratory birds regulate their rates of migration by lilac phenology, but their budburst dates are within the migration period of many of the bird species we examined, and they can be considered a surrogate for other native species of plants. Data were also available on leaf-out dates, but since leaf-out usually occurs in March and early April, prior to the arrival of most spring migrants, we focused our analysis on budburst data. We obtained budburst data from all stations between 38°N and 43°N, and between 75°W and 85°W from Mark D. Schwartz (University of Wisconsin-Milwaukee; Fig. 1). Because observations were not continuous across the whole 40-year time period for most stations, we calculated annual deviations from the long-term mean for each station, and then averaged these deviations across all available stations each year, to obtain an index of annual variation in plant phenology.

Analysis

The vast majority of birds captured at both stations were passage migrants that were captured only once and never seen again, suggesting most did not remain in the area more than a day after arrival (authors' unpublished data). For some species, especially at Powdermill, these passage migrants were mixed with local breeding populations. To minimize bias from birds that may have been captured several days after initial arrival, we only included first captures of each individual in a year, and excluded any birds first caught after 7 June in a year (when most passage migration is complete). As such, capture dates should closely approximate migration dates, defined as the date of passage through an area, or initial arrival at that site (in the case of local breeding birds).

At each station, median capture date was calculated for each species in each year to provide an annual estimate of migration timing. Because the starting dates of coverage varied among years, particularly at Long Point, for each species we included only years in which coverage began earlier than the earliest normal migration dates for that species (as determined from the time period across all years during which 99% of individuals migrated). We further excluded any years in which < 10 individuals were captured, as these may not give a good representation of the migration period for the species that year. Unlike first arrival dates, or mean capture dates, median dates are relatively unaffected by outliers (exceptionally early or late individuals). Furthermore, first arrival dates are likely to be biased by changes in effort or population size, which would affect the likelihood of detecting exceptionally early individuals arriving in an area.

We regressed median annual capture dates against year to test for long-term trends in migration dates, and against mean April–May temperatures (as described above) to estimate the relationship between mean temperature and migration date. We also compared median migration dates with the mean NAO index for December–March, following Hüppop and Hüppop (2003). To determine the overall relationship, across species, between migration timing and temperature, we calculated a relative migration date across species for each year. To do this we calculated the overall mean (across years) of the median passage dates for each species and then converted each annual median value into a deviation from that mean. We then averaged these deviations across species, to determine the degree to which a particular spring season was "early" or "late". We carried out a similar analysis for the lilac data, comparing the deviation in mean budburst dates across stations with mean spring temperature. All analyses were done using SAS version 8.0 (SAS Institute 1999)

Results

Mean spring temperatures (April/May) in the north-eastern USA varied over a 5°C range from 1961 to 2000 (Fig. 2). Annual variation in temperature throughout the northeast was highly correlated with temperature at the weather stations nearest each of the banding stations (Erie, Penn., $r = 0.92$, $P < 0.0001$; Unionville, Penn., $r = 0.86$, $P < 0.0001$), indicating that patterns near the banding stations are typical of those in the region. Annual fluctuations in the north-eastern USA were also strongly correlated with those in the south-eastern USA ($r = 0.76$, $P < 0.0001$) indicating that annual variation in temperature was similar throughout the eastern USA from the Gulf of Mexico north to southern Canada. There was a slight warming trend over this period in the northeast, but it was small relative to the annual variation and not statistically significant ($X = 0.019 \pm 0.015$°C/year, $t = 1.3$, $P = 0.2$).

Although most species showed a trend towards earlier median capture dates over time (PNR 27/32 species,
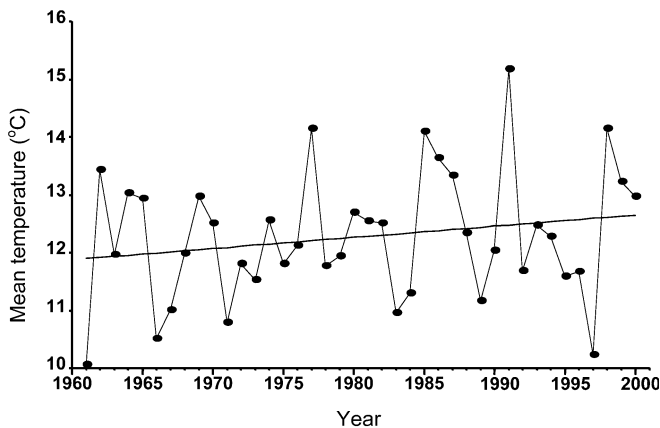
Fig. 2 Mean annual temperature in spring (April/May) in the north-eastern USA in the lilac phenology sampling area (see Fig. 1) from 1961–2000. *Line* gives the linear trend from 1961–2000, with an average change in temperature of 0.019 ± 0.015°C/year

$S = -184$; $P < 0.0002$, Sign-rank Test; LPBO 21/31 species, $S = -67$; $P < 0.19$, Sign-rank Test), few of the individual species were statistically significant (PNR 4/32 species; LPBO 0/31 species). The mean deviation in median capture dates across all species advanced earlier at Powdermill ($X = -0.05 \pm 0.03$ days/year; $t = -1.87$; $P = 0.07$), but not at Long Point ($X = -0.004 \pm 0.03$ days/year; $t = -0.2$, $P = 0.9$).

Median capture dates were much more strongly related to mean spring temperature for almost all species (PNR (29/32 species) $S = -258$; $P < 0.0001$, Sign-rank Test; LPBO (28/31 species) $S = -231$; $P < 0.0001$, Sign-rank Test) with many of the individual relationships being statistically significant (PNR 13/32 species; LPBO 17/31 species; 24/43 total species were significant at one or both stations; Table 1). At both stations, for every 1°C increase in spring temperature, the deviation in median capture dates from the long term mean, averaged across species, was one day earlier (PNR $r^2 = 0.30$, $P = 0.0003$; LPBO $r^2 = 0.37$, $P = 0.0001$; Fig. 3).

In contrast, there was little relationship with mean December–March values of the North Atlantic Oscillation. At Long Point, 23 species were positively correlated, 17 negatively correlated with NAO, none significantly so, while at Powdermill, 28 were positive and 17 negative, of which only three positive correlations were significant. The number of positive and negative correlations was not significantly different based on a sign test ($P > 0.1$ in both cases).

The interval between median capture dates in Louisiana and those at LPBO and PNR, about 2,500 km to the north, was inversely correlated to temperature (PNR 8/10 species, $X_{slope} = -1.42 \pm 0.52$; $S = -21.5$, $P < 0.03$, Sign-rank Test; LPBO, 9/11 species, $X_{slope} = -1.04 \pm 0.65$; $S = -18.0$, $P < 0.12$, Sign-rank Test) with an average interval of 22 days, that decreased by 0.8 days per 1 degree increase in temperature (Table 2).

To determine the relationship between annual variation in mean temperature and plant phenology, we used observations of first budburst dates of the purple common lilac as an index of annual variation in plant phenology. Budburst was highly related to temperature ($X_{slope} = -3.2 \pm 0.5$ days/degree, $t = -6.2$, $P = 0.0001$). This indicates that budburst advances about three times as much as migration dates in response to a given warming in temperature in spring.

Discussion

In contrast to many previous studies examining relationships between climate and bird phenological events our study found little long-term (over 40 years) trend toward earlier migration dates. This result makes sense since we also found no significant trend for increasing spring temperatures in eastern North America during this time period. Two recent meta-analyses clearly demonstrate that global warming patterns have resulted in phenological change in many species in many areas (Root et al. 2003; Parmesan et al. 2003). However, our results highlight the fact that advancing phenology is not observed in all areas, nor is it to be expected in all areas, owing to global variation in the rate of temperature change.

Our results do, however, suggest that long-distance Nearctic-Neotropical migratory birds adjust their timing by adjusting their rate of migration to match annual variations in ambient temperatures or associated factors such as leaf emergence and resource availability. In general, birds migrated earlier in warm years and later in colder years. This suggests that long-distance migratory birds would be able to respond fairly quickly if a long-term warming trend were apparent. This contrasts with the study of Both and Visser (2001) who found that the timing of breeding for one long-distance migrant, the Pied Flycatcher, in the Netherlands, was mismatched with the optimal times based on breeding success, and suggested this may be a constraint based on inflexible arrival times. In contrast to their study area in the Netherlands (Both and Visser 2001), Pied Flycatchers migrated early in warmer years in both Russia (Sokolov et al.1998) and in Germany (Hüppop and Hüppop 2003) suggesting that the constraints on timing of breeding may have been due to factors other than migration constraints.

The mechanisms underlying changes in migratory behavior are poorly understood. Most long-distance migrants are believed to use primarily endogenous cues and possibly subtle changes in day length to trigger migration. Therefore, it is unlikely that winter departure times would change to adjust to short-term changes in climate on northern breeding areas. While evolutionary changes could be expected over a multi-year time frame through selective processes, if early arrival conferred a strong selective advantage to earlier departure, year-to-year variation must be determined by other factors. One possibility is that correlated environmental changes between breeding and tropical overwintering sites could be used as cues by migratory birds to delay or accelerate departure. The strong correlation with winter NAO in

Table 1 Regressions of median capture dates of long-distance migratory birds at the Powdermill Nature Reserve (PNR) and Long Point Bird Observatory (LPBO) (1961–2001) against temperature. Only species with a minimum of 10 years and a minimum ten individuals captured in each year were used in the analysis. *NY* number of years in the analysis

Long-distance migratory species	PNR					LPBO				
	Slope	SE	r^2	NY	P	Slope	SE	r^2	NY	P
Archilochus colubris (Ruby-throated hummingbird)	−1.97	0.27	0.6	38	0.00	–	–	–	–	–
Contopus virens (Eastern wood pewee)	–	–	–	–	–	−1.45	0.45	0.28	29	0.00
Empidonax virescens (Acadian flycatcher)	−1.73	1.33	0.13	13	0.22	–	–	–	–	–
E. flaviventris (Yellow-bellied flycatcher)	−1.75	1.11	0.15	16	0.14	−1.55	0.51	0.26	28	0.00
E. traillii (Traill's Flycatcher)	0.19	0.64	0.00	34	0.76	–	–	–	–	–
E. minimus (Least flycatcher)	−1.54	0.48	0.22	39	0.00	−0.38	0.46	0.02	36	0.41
Hirundo rustica (Barn swallow)	−3.11	3.63	0.06	14	0.41	–	–	–	–	–
Polioptila caerulea (Blue-gray gnatcatcher)	−1.94	0.89	0.17	25	0.04	–	–	–	–	–
Dumetella carolinensis (Gray catbird)	−0.26	0.39	0.01	39	0.50	−0.85	0.42	0.11	36	0.05
Catharus ustulatus (Swainson's thrush)	−2.26	0.63	0.30	33	0.00	−0.41	0.59	0.02	33	0.50
C. fuscescens (Veery)	–	–	–	–	–	−1.06	0.47	0.15	31	0.03
Hylocichla mustelina (Wood thrush)	−0.56	0.90	0.01	33	0.54	−0.67	0.53	0.06	27	0.22
Vireo olivaceus (Red-eyed vireo)	0.14	0.45	0.00	39	0.75	−1.99	0.66	0.24	31	0.00
V. griseus (White-eyed vireo)	−0.52	0.87	0.02	24	0.56	–	–	–	–	–
V. gilvus (Warbling vireo)	–	–	–	–	–	−1.99	0.69	0.46	12	0.02
Dendroica virens (Black-throated green warbler)	–	–	–	–	–	−0.75	0.78	0.05	19	0.35
D. caerulescens (Black-throated blue warbler)	–	–	–	–	–	−1.11	0.70	0.15	16	0.14
D. magnolia (Magnolia warbler)	−1.63	0.49	0.24	38	0.00	−1.19	0.41	0.20	35	0.01
D. pensylvanica (Chestnut-sided warbler)	−0.56	0.95	0.02	16	0.56	−0.61	0.46	0.07	25	0.20
D. castanea (Bay-breasted warbler)	–	–	–	–	–	−1.06	0.75	0.20	10	0.19
D. petechia (Yellow warbler)	−0.39	0.43	0.02	39	0.38	−0.60	0.45	0.05	34	0.20
D. fusca (Blackburnian warbler)	–	–	–	–	–	0.03	0.67	0.00	12	0.96
D. palmarum (Palm warbler)	–	–	–	–	–	−1.57	0.62	0.27	19	0.02
Vermivora pinus (Blue-winged warbler)	−0.94	1.19	0.07	11	0.45	–	–	–	–	–
V. chrysoptera (Golden-winged warbler)	−2.24	0.84	0.25	23	0.01	–	–	–	–	–
V. peregrina (Tennessee warbler)	−2.43	0.38	0.55	35	0.00	−1.48	0.37	0.67	10	0.00
V. ruficapilla (Nashville warbler)	−1.78	0.52	0.26	35	0.00	−1.89	0.46	0.38	29	0.00
Mniotilta varia (Black and White warbler)	–	–	–	–	–	−0.40	0.78	0.02	19	0.62
Wilsonia canadensis (Canada warbler)	−0.92	0.48	0.09	39	0.06	−0.89	0.68	0.08	22	0.20
W. citrina (Hooded warbler)	0.23	0.77	0.01	19	0.77	–	–	–	–	–
W. pusilla (Wilson's warbler)	−1.28	0.41	0.24	33	0.00	−0.79	0.51	0.07	32	0.13
Setophaga ruticilla (American redstart)	−0.69	0.50	0.05	36	0.18	0.78	0.69	0.05	26	0.27
Oporornis philadelphia (Mourning warbler)	−1.86	0.69	0.22	28	0.01	−1.71	0.67	0.32	16	0.02
O. formosus (Kentucky warbler)	−0.97	1.65	0.04	11	0.57	–	–	–	–	–
Geothlypis trichas (Common yellowthroat)	−0.69	0.39	0.08	39	0.08	−1.32	0.58	0.14	34	0.03
Icteria virens (Yellow-breasted chat)	−0.80	0.90	0.04	20	0.38	–	–	–	–	–
Seiurus noveboracensis (Northern waterthrush)	−1.33	0.53	0.15	37	0.02	0.51	1.05	0.01	19	0.3
S. aurocapilla (Ovenbird)	−0.89	1.16	0.05	12	0.46	−1.55	1.51	0.24	32	0.00
Icterus galbula (Northern oriole)	−0.82	0.95	0.07	12	0.40	−1.44	0.53	0.19	34	0.01
Piranga olivacea (Scarlet tanager)	–	–	–	–	–	−2.49	0.82	0.40	16	0.01
Passerina cyanea (Indigo bunting)	−0.90	0.43	0.11	39	0.04	−1.30	0.52	0.22	24	0.02
Pheucticus ludovicianus (Rose-breasted grosbeak)	−0.41	1.36	0.01	12	0.77	−1.85	0.54	0.26	36	0.00

Europe suggests this could be a factor there (Hüppop and Hüppop 2003), but for eastern North American migrants, we found no such correlation.

The comparison with the Louisiana data suggests that long-distance Nearctic-Neotropical migratory birds adjust their rate of migration to match annual variations in ambient temperatures. Linkages between bird migration and weather have been observed for many years. It has long been known that large movements of migratory birds follow weather fronts (Richardson 1978). Saunders (1959) analyzed 40 years of first arrival dates for migrants and found that arrival was later in cold years and earlier in warm years. Recently, Sokolov et al. (1998) found that the timing of migration for 20 migratory species (including Pied Flycatcher) passing through the Courish Spit of the Baltic in Eastern Europe

was correlated with temperature. In a similar study, Huin and Sparks (2000) found for three species of long-distance Palearctic migrants that arrival date on breeding areas correlated well with temperature in southern Europe in the month preceding arrival in Britain, again suggesting a link between temperature and rates of migration. Our results support these findings.

Few studies have been able to quantify actual rates of migration, primarily due to the difficulty in tracking individual small birds over large spatial scales (Webster et al. 2001; but see Wikelski et al. 2003). Huin and Sparks (1998) tackled this problem by comparing first and mean arrival dates for the Swallow (*Hirndo rustica*) at multiple geographic locations throughout Britain and found that movement rates were faster in "early" or warm years and slower in "later" or cold years.
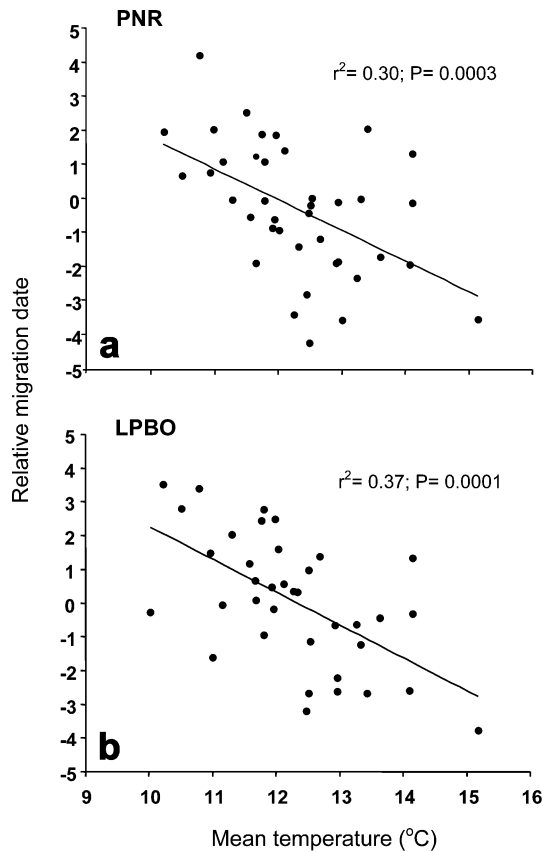
Fig. 3 Deviation in median migration dates from long-term mean (relative migration date) in relation to mean annual temperature for **a***PNR* Powdermill Nature Reserve (mean of 31 species) and **b***LPBO* Long Point Bird Observatory (mean of 32 species)

Similarly, our analysis of 15 species of Nearctic-Neotropical migratory birds revealed a trend for intervals between annual median capture dates to be shorter in warm years and longer in cold years between the Louisiana station and the two ringing stations to the north. These data combined with our data on the timing of migration support the hypothesis that rates of movement during spring migration can be modified to compensate for environmental variability.

Measuring rates of migration indirectly is difficult and subject to multiple sources of error. For example, all the species included in this analysis have breeding ranges extending at least partially between Louisiana and the northern ringing stations. If enough of these individuals reach their breeding ground destination prior to arriving at the northern ringing stations this could significantly change the magnitude of the wave of birds captured at the northern ringing stations. Furthermore, although we recognize that birds migrating through the southern Louisiana station may not be migrating along the same flyways as the birds sampled by the northern ringing stations, we are assuming that their migration timing at that latitude is similar. More widespread data are required to test this assumption.

Ambient temperature and plant phenology may be involved directly or indirectly in regulating the northward migration of birds. The timing and rate of migration, for example, may not be regulated by temperature per se but by factors allied with temperature and the northward advancing vernal front, such as leaf emergence and associated resource availability, as well as other climate factors correlated with temperature such as wind. Separating these various factors to isolate the underlying mechanisms driving rates of migration can be difficult. Temperature is correlated with a suite of associated climatic factors important to the timing and rate of migration, such as winds, cold fronts, and late winter storms (Richardson 1978), all of which may speed up or slow down waves of migratory birds (Åkesson et al. 2002). Winds can be either favorable to migration, such as tailwinds from the south or an impediment as would be the case if headwinds were originating from the north. Tailwinds and headwinds may be more or less severe during extreme temperatures making these factors difficult to separate in our analysis. Furthermore, tailwinds are thought to be more common in El Nino years, which also tend to be warmer years, and the opposite may also be true in La Nina years. Colder springs may also be the result of the occasional late winter storm and can also cause high levels of mortality (Holmes et al. 1986) or possibly slow down migration by reducing foraging opportunities and the ability of migratory birds to rebuild fat stores critical for migration.

The northward progression of leaf out in spring, otherwise known as the green wave (Schwartz 1998), is closely linked to temperature and may provide important habitat for migratory birds during spring migration. Leaf-out can be important both in the food it provides for herbivorous insects that are prey to birds as well as the protection foliage may offer to camouflage birds from predators. Such factors can all contribute to the rate at which migratory birds can move northward. In our study, we examined the relationship between temperature and lilac bud burst to determine how phenology might be related to rates of migration. We found that the impact of temperature on lilac bud burst phenology is about three times greater than it is on bird phenology (1 day/degree change). The fact that plants are more sensitive to changes in temperature than are birds is of no great surprise. Several other studies have reported highly correlated changes between plant phenology and temperature (e.g., Visser et al. 1998; Penuelas and Filella 2001). Birds may not be able to respond to temperatures as quickly as the plants that are synchronized to local variability in ambient temperatures. Moreover, for a migratory organism, it is probably not adaptive to respond too quickly to temperature since temperature itself can change drastically in short time periods. Despite this, a correlation between mean deviation of bird migration dates and bud burst dates is significant ($B = 0.12306 \pm 0.05890$ days migration/day bloom, $t = 2.09$, $P = 0.04$). Although this result is interesting, biologically there is no obvious reason to expect bird migration to be influenced directly by lilac bloom dates since the long-distance migratory birds in this

Table 2 Regressions of median capture dates of long-distance migratory birds between Johnson's Bayou, Louisiana to the Powdermill Nature Reserve (PNR) and Long Point Bird Observatory (LPBO) (1988–1991, 1993–1996, 1998–2000). For inclusion in the analysis, a minimum of ten individuals needed to be captured in a given year. *NY* number of years in the analysis

Species	PNR					LPBO				
	Slope	SE	r^2	NY	P	Slope	SE	r^2	NY	P
Contopus virens (EasternWood Pewee)	–	–	–	–	–	1.25	1.09	0.21	7	0.30
Dumetella carolinensis (Grey Catbird)	0.75	1.57	0.04	8	0.65	−0.74	2.33	0.02	8	0.76
Catharus ustulatus (Swainson's Thrush)	−3.95	3.51	0.20	7	0.31	−0.14	1.34	0.0	9	0.92
C. fuscescens (Veery)	–	–	–	–	–	1.47	0.71	0.46	7	0.09
Hylocichla mustelina (Wood Thrush)	–	–	–	–	–	−1.40	1.34	0.18	7	0.34
Vireo olivaceus (Red-Eyed Vireo)	−3.66	2.92	0.18	9	0.25	−6.70	3.14	0.39	9	0.07
V. griseus (White-eyed Vireo)	−2.98	2.23	0.23	8	0.23	–	–	–	–	–
Dendroica magnolia (Magnolia Warbler)	0.31	1.01	0.01	8	0.77	−0.80	0.64	0.21	8	0.26
Vermivora peregrina (Tennessee Warbler)	−2.01	1.73	0.18	8	0.29	–	–	–	–	–
Wilsonia citrina (Hooded Warbler)	−0.46	1.63	0.01	8	0.79	–	–	–	–	–
Geothlypis trichas (Common Yellowthroat)	−1.19	1.62	0.10	7	0.49	−1.81	2.27	0.11	7	0.46
Seiurus noveboracensis (Northern Waterthrush)	−0.63	1.22	0.04	9	0.62	–	–	–	–	–
S. aurocapilla (Ovenbird)	–	–	–	–	–	−0.39	0.64	0.06	8	0.57
Passerina cyanea (Indigo Bunting)	−0.34	1.14	01	9	0.78	−1.30	1.39	0.15	7	0.39
Pheucticus ludovicianus (Rose-breasted Grosbeak)	–	–	–	–	–	−0.90	1.95	0.04	7	0.66

study do not specialize on lilac trees. Lilacs may however, provide a suitable surrogate species for the phenology of more relevant tree species critical to the northward progression of migratory birds.

Temperature can also have direct and indirect effects on insect development rates (e.g., Buse and Good 1996; Dewer and Watt 1992) which may influence food availability to migratory birds. For example, because temperature can influence plant phenology, it can also delay or stimulate insect emergence and thereby somewhat control the abundance of herbivorous insects that are prey to migrating birds. This in turn can have important impacts on the length of bird stopover and the rate of migration by limiting the ability of birds to rebuild depleted fat stores.

Understanding the genetic and environmental underpinnings of migratory behavior and other life history strategies will provide important insights into the effects that climate change will have on animal populations. Migratory birds will undoubtedly be affected by changes in our climate, but they may also be capable of rapid phenotypic (Przyblo et al. 2000) and genetic (Pulida et al. 2001) responses over short time periods. Furthermore, to understand the mechanistic basis underlying earlier arrival dates of many migrants species (see references cited above) and to better predict how climate may impact migratory animals in the future we need to more thoroughly explore the relationship between climate and rates of bird migration.

References

Åkesson SG, Walinder L, Karlsson L, Ehnbom S (2002) Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. J Avian Biol 33:349–357

Berthold P (1984) The endogenous control of bird migration: a survey of experimental evidence. Bird Study 31:19–27

Berthold P (1993) Bird migration. A general survey. Oxford University Press, Oxford

Berthold P (1996) Control of bird migration. Chapman and Hall, London

Berthold P, Querner U (1981) Genetic basis of migratory behavior in European warblers. Science 212:77–79

Berthold P, Terrill SB (1991) Recent advances in studies of bird migration. Annu Rev Syst 22:357-378

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298

Bradley NL, Leopold AC, Ross J, Huffaker W (1999) Phenological changes reflect climate change in Wisconsin. Proc Natl Acad Sci USA 96:9701–9704

Brown JL, Li S-H, Bhagabati N (1999) Long-term trend toward earlier breeding in an American bird: a response to global warming? Proc Natl Acad Sci USA 96:5565–5569

Buse A, Good JEG (1996) Synchronization of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur*) under simulated climate change. Ecol Entomol 21:335–343

Crick HQP, Sparks TH (1999) Climate change related to egg-laying trends. Nature 399:423–424

Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. Nature 388:526

Dewer RC, Watt AD (1992) Predicted changes in the synchrony of larval emergence and budburst under climatic warming. Oecologia 89:557–559

Dunn EH (2000) Temporal and spatial patterns in daily mass gain of magnolia warblers during migration. Auk 117:12–21

Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows throughout North America. Proc R Soc Lond B 266:2487–2490

Easterling DR, Karl TR, Mason EH, Hughes PY, Bowman DP, Daniels RC, Boden TA (eds) (1997) United States Historical Climatology Network (USA HCN) Monthly Temperature and Precipitation Data. ORNL/CDIAC-87, NDP-019/R3. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge

Elkins N (1993) Weather and bird behaviour, 2nd edn. Poyser, Calton

Francis CM, Hussell DJT (1998) Changes in numbers of land birds counted in migration at Long Point Bird Observatory, 1961–1997. Bird Popul 4:37–66

Gwinner E (1990) Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod. In: Gwinner E (ed) Bird migration. Springer, Berlin Heidelberg New York, pp 257–268

Gwinner E, Biebach H, vonKries I (1985) Food availability affects migratory restlessness in caged Garden Warblers (Sylvia borin). Naturwissenschaften 72:51–52

Hagan JM, Lloyd-Evans TL, Atwood JL (1991) The relationship between latitude and the timing of spring migration of North American landbirds. Ornis Scand 22:129–136

Holmes RT, Sherry TW, Sturges FW (1986) Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecol Monogr 56:201–220

Houghton JT, Meria Filho LG, Callender B, Harris N (eds) (1995) Intergovernmental Panel on Climate Change (IPCC). Climate change 1995: the science of climate change. Cambridge University Press, Cambridge

Huin N, Sparks TH (1998) Arrival and progression of the swallow Hirundo rustica through Britain. Bird Study 45:361–370

Huin N, Sparks TH (2000) Spring arrival patterns of the Cuckoo Cuculus canorus, Nightingale Luscina megarhynchos, and Spotted Flycatcher Musciapa striata in Britain. Bird Study 47:22–31

Hüppop O, Hüppop K (2003) North Atlantic Oscillation and the timing of spring migration in birds. Proc R Soc Lond B 270:233–240

Inouye DW, Barr B, Armitage KB, Inouye BD (2000) Climate change is affecting altitudinal migrants and hibernating species. Proc Natl Acad Sci USA 97:1630–1633

Ivanauskas F, Nedzinskas V, Zalakevicius M (1997) The impact of global warming upon spring arrival of birds. Acta Zool Ornithol 6:31–36

Karasov WH, Pinshow B (1998) Changes in lean mass and in organs of nutrient assimilation in a long-distance migrant at a springtime stopover site. Physiol Biochem Zool 50:115–118

Kok OB, Van Ee CA, Nel DG (1990) Daylength determines departure date of the spotted flycatcher (Muscicapa striata) from its winter quarters. Ardea 79:63–66

Leberman RC, Clench MH (1972) Bird-ban ding at Powdermill, 1971, and ten years reviewed. Powdermill Nature Reserve Research Report No. 30. Carnegie Museum, Pittsburgh

Leberman RC, Wood D S (1983) Bird-banding at Powdermill: twenty years reviewed. Powdermill Nature Reserve Research Report No. 42. Carnegie Museum, Pittsburgh

Leberman RC, Mulvihill RS, Wood DS (1990) Bird-banding at Powdermill, 1988, including an analysis of banding effort for the period 1962–1988. Powdermill Nature Reserve Research Report No. 49. Carnegie Museum, Pittsburgh

Leberman RC, Mulvihill RS, Niedermeier M (1994) Bird-banding at Powdermill: 1991 and thirty years reviewed. Powdermill Nature Reserve Research Report No. 52. Carnegie Museum, Pittsburgh

Lindstrom A (1991) Maximum fat deposition rates in migrating birds. Ornis Scand 22:12–19

Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886

McCleery RH, Perrins CM (1998) Temperature and egg-laying trends. Nature 391:30–31

Moore FR, Kerlinger P (1987) Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47–54

Moore FR, Simons TR (1992) Habitat suitability and stopover ecology of Neotropical landbird migrants. In: Hagan JM III, Johnston DW (eds) Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, pp 345–355

Parmesan C, Ryrholm N, Stefanescus C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (2003) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 421:37–42

Penuelas J, Filella I (2001) Responses to a changing world. Science 294:793–795

Przyblo R, Sheldon BC, Merila J (2000) Climatic effects on breeding and morphology: evidence for phenotypic plasticity. J Anim Ecol 69:395–403

Pulida F, Berthold P, Moh G, Querner U (2001) Heritability of the timing of autumn migration in a natural bird population. Proc Soc R Lond B 268:885–993

Richardson WJ (1978) Timing and the amount of bird migration in relation to we ather: a review. Oikos 30:224–272

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Saunders AA (1959) Forty years of spring migration in southern Connecticut. Wilson Bull 7:208–219

SAS Institute (1999) The SAS system for Windows, release 8.00. Cary, N.C.

Schaub M, Jenni L (2001) Variation of fuelling rates among sites, days and individuals in migrating passerine birds. Funct Ecol 15:584–594

Schwartz MD (1994) Monitoring global change with phenology: the case of the spring green wave. Int J Biometeorol 38:18-22

Schwartz MD (1998) Green-wave phenology. Nature 394:839–840

Sokolov LV, Markovets MY, Shapoval AP, Morozov YG (1998) Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. Avian Ecol Behav 1:1–21

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. Nature 399:213

Thomas CD, Blondel J, Perret P, Lambrechts MM, speakman JR (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598–2600

Utech FH (1999) Checklist of the vascular plants of Powdermill Nature Reserve, Westmoreland County, Pennsylvania. Carnegie Museum of Natural History Special Publication No. 20. Carnegie Museum, Pittsburgh

Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (Parus major). Proc R Soc Lond B 265:1867–1870

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-C, Hoegh-Guldberg O, Bairlein B (2002) Ecological responses to recent climate change. Nature 416:389–395

Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. Trends Ecol Evol 17:76–82

Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH (2003) Costs of migration in free-flying songbirds. Nature 423:704

Yong W, Moore FR (1993) Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. Condor 95:934–943

Yong W, Moore FR (1997) Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263–278