

Changes in spring arrival of Nearctic-Neotropical migrants attributed to multiscalar climate

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Abstract

Climate-related changes associated with the California marine ecosystem have been documented; however, there are no studies assessing changes in terrestrial vertebrate phenology on the Pacific coast of western North America. We analyze the spring phenology of 21 Nearctic-Neotropical migratory songbird species in central and northern CA. Using observational and banding data at multiple sites, we evaluate evidence for a change in arrival timing being linked to either nonclimatic or multiscalar climatic explanations. Using correlation analysis, of the 13 species with a significant ($P < 0.10$) change in arrival, the arrival timing of 10 species (77%) is associated with both temperature and a large-scale climate oscillation index (El Niño Southern Oscillation, ENSO; North Atlantic Oscillation, NAO; and/or Pacific Decadal Oscillation, PDO) at least at one location. Eight of the 13 species (62%) are advancing their migratory timing. All species for which spring arrival is associated with climate at multiple locations are exhibiting changes ($n = 5$) and all species lacking evidence for association between migration phenology and climate ($n = 3$) exhibit no change. Migrants tend to arrive earlier in association with warmer temperatures, positive NAO indices, and stronger ENSO indices. Twelve species negatively correlate ($P \leq 0.05$) with local or regional temperature at least at one location; five species negatively correlate with ENSO. Eleven species' arrival is correlated ($P \leq 0.05$) with NAO; 10 are negatively associated. After an exhaustive literature search, this is apparently the first documentation of an association between NAO and migratory phenology in western North America.

Keywords: California, climate change, ENSO, MEI, migration, NAO, Pacific flyway, passerine, PDO, phenology

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Introduction

Over the past decade, hundreds of studies have detected a signal of climatic change in plants and animals around the planet (see references in IPCC, 2001; Parmesan & Yohe, 2003; Root *et al.*, 2003). Phenology has been analyzed as an indicator of ecosystem response to global warming (Parmesan, 2006) and anthropogenic influence on climate (Root *et al.*, 2005). There is widespread concern about asynchronous changes in spring phenology between trophic levels (see review Visser *et al.*, 2004), as well as interest in the spatial coherence of changes within species (e.g. Sanz, 2003; Huppoc &

Winkel, 2006). Geographical differences in the effects of global warming can have serious consequences for species which rely on resources spread across a hemisphere (Cotton, 2003). Thus, migratory bird phenology has received considerable attention in evaluating the current and future impacts of climatic change (see review Lehikoinen *et al.*, 2004). Specifically, spring migratory phenology has implications for the timing of breeding (Both & Visser, 2001; Ahola *et al.*, 2004), as well as reproductive success (Smith & Moore, 2005; Coppack *et al.*, 2006).

The majority of phenological studies have focused on multiple species at single sites (e.g. Bradley *et al.*, 1999; Cotton, 2003; Ledneva *et al.*, 2004; Stervander *et al.*, 2005) or single species at multiple locations (e.g. Dunn & Winkler, 1999). None of these studies, however, has

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evaluated the evidence for changes in species at several locations in conjunction with independent evidence of a species' phenological association with multiscalar climate. Yet, there is wide recognition of the value and need for large scale, comparative studies of migration (Ballard *et al.*, 2003; Kelly & Hutto, 2005).

Furthermore, while climate-related changes associated with the California marine ecosystem (Hare & Mantua, 2000; Sydeman *et al.*, 2001) and western North American spring plant phenology (Cayan *et al.*, 2001) have been documented, there are no assessments of phenological changes to terrestrial vertebrates along the Pacific coast of North America. In this analysis, we evaluate 20–30 years of continuous data (1969–2003) on the spring arrival of 21 long-distance, Nearctic–Neotropical migrant songbirds in central- and northern-coastal California at multiple locations for each species. We assess whether changes in spring migratory phenology are strongly linked to recent climatic change.

Our objective is to determine whether those species that do exhibit changes in arrival are more or less likely to have the timing of their arrival associated with multiscalar climatic variables than those species that are not exhibiting significant changes in arrival. We evaluate two alternate, nonclimatic explanations for species' trends (i.e. changes in reporting and changes in species' population sizes).

Our approach engages the spatial and temporal complexity of migratory passage by incorporating multiple scales of species and climate data into the analyses. To increase the robustness of our results, we do not rely on a single indicator or single data set in our study.

We assessed two types of species' arrival data (banding and observation), two scales of species' arrival data (site-specific and regional), and two locations (inland and coastal). Similarly, we examined climate variables at the local, regional, and continental scales. Particularly, El Niño–Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) are important climatic and ecological influences on coastal California (e.g. Hare & Mantua, 2000; Sydeman *et al.*, 2001; Castello & Shelton, 2004). We also investigated the North Atlantic Oscillation (NAO) due its influence on Atlantic ecosystems (e.g. Forchhammer *et al.*, 2002) where many of the Nearctic–Neotropical migrants have wintering ranges. Furthermore, spring NAO indices correlate with the annual reproductive success of songbirds in the US Pacific Northwest (Nott *et al.*, 2002). This is apparently the first study to evaluate whether NAO is also associated with the timing of migration in western North America; recent research has detected a significant correlation between NAO and migratory phenology in eastern North America (MacMynowski & Root, 2007). Finally, we considered three different temporal phases

of migration: first arrival date, onset of continuous migration, and the median date of migratory passage. By evaluating these temporal variables of the arrival distribution along with different spatial aspects, we can gain insight into the within-season dynamics of migration and the biological implications of the observed changes.

Materials and methods

Data sources

We obtained spring songbird arrival data for coastal central and northern California from two sources: the US Bird Banding Laboratory (USBBL) and the original records used to compile seasonal summaries published in *North American Birds* (NAB) and its associated preceding publications (i.e. *Field Notes*, *National Audubon Society Field Notes*, *American Birds*).

From the USBBL data, we chose two banding locations in California. These were the only banding locations in central and northern California that met the following criteria. The banding season had to extend from at least Julian day 45–160 (mid-February–early June). At a minimum, one bird had to be banded a day with no more than a 3-day gap between birds banded. Additionally, we required a minimum of 10 years with no gaps greater than 3 years between seasons that met the criteria above. Data at Station 1 (37.33°N, 121.83°W, near San Jose) were available from 1983 to 1997 and at Station 2 (37.83°N, 122.66°W, near Point Reyes) from 1969 to 2002. Each station's overall migratory pattern is distinct, and thus, we consider the species' observations to be independent (Fig. 1).

Because recaptured birds are mostly local breeding residents (originally captured in previous years; PRBO Conservation Science, unpublished data), they may arrive earlier than newly banded birds. Thus, at Banding Station 2, we conducted analysis of two sets of data (i.e. with and without recaptures). When recaptures are included, the median of first arrivals is from 1 to 5 days earlier than when recaptures are not included. Differences in the median of arrival were negligible. There were no differences in the statistical significance of arrival trends for the first arrival or the median of migration. Thus, given no significant differences, and for consistency with Banding Station 1, we report the results using the USBBL data set (no recaptures).

Our second source of central- and northern-California data came from NAB regional coordinators S. Glover and L. Cole. They provided hand-written archives of the species-sighting reports submitted to them, and previous editors, by local observers, most of whom are regular contributors. The NAB data have been

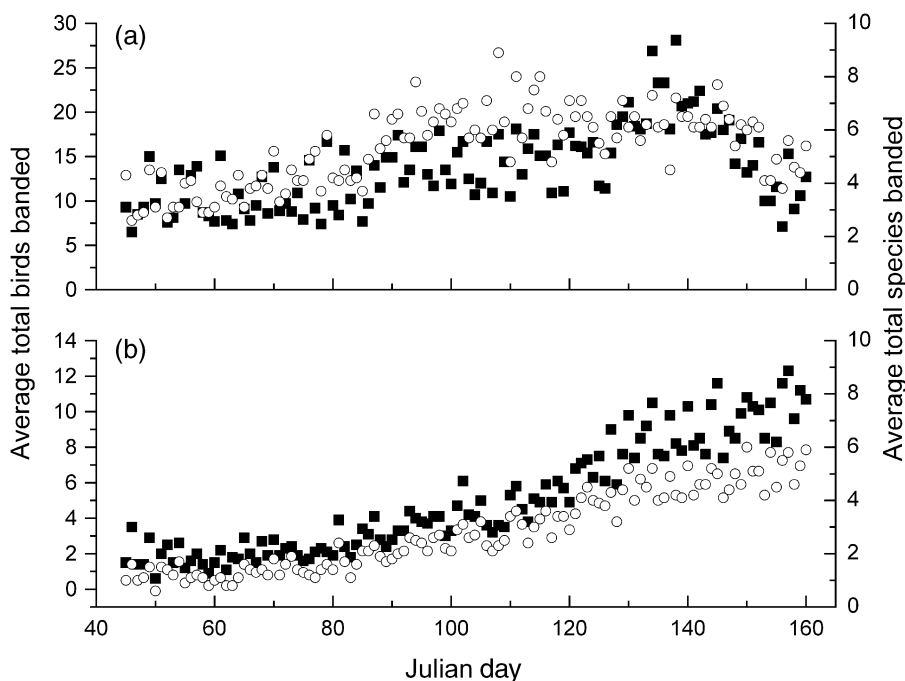


Fig. 1 Seasonal arrival distribution of all spring migrants at Banding Stations 1 (a) and 2 (b). Open circles indicate averaged total species banded, while closed squares are average total birds banded.

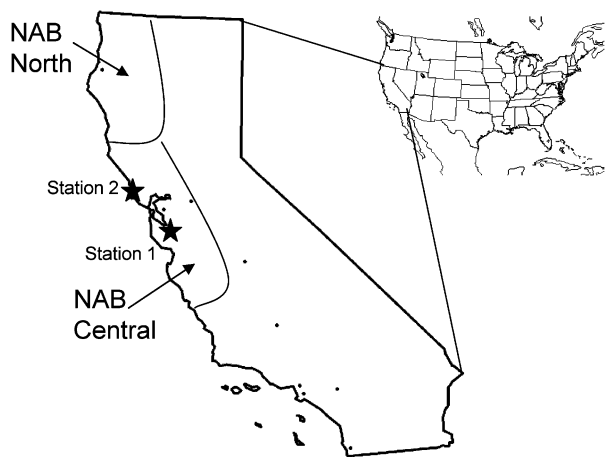


Fig. 2 Study region.

recorded from 1980 to 2003, with some species records only until 1994. To accommodate early sighting of swallows, we defined the NAB season as beginning on Julian day 32 (February 1) to Julian day 160. When conducting analyses, we only considered reports from the first part of a species' arrival to minimize the effect of declining observation effort over the season. The NAB data were divided into two groups: coastal central and northern California (Fig. 2). The dividing line, the Sonoma-Mendocino county line, was chosen due to

geography and the fact that reporting effort (number of local observers providing reports) was lower in northern California. Thus, we create two areas of relative internal similarity.

Species selection

Our analyses focus upon long-distance Nearctic-Neotropical migrants. None of the species selected is non-migratory in central or northern California. All species breed in this region, but not necessarily near the coast. Additionally, being migratory enhances the chances of being reported in NAB data because observers focus on species not seen for several months.

In addition to being a Nearctic-Neotropical long-distance migrant, the species must have met these data-criteria to be included: (1) a minimum of 10 individuals banded in a year or one sighting per year for NAB data, (2) no more than a 3 year gap between years with the minimum number of birds banded or sighted, (3) a span of at least 10 years with no gaps longer than 3 years, and (4) the total number of missing years must be less than a third of the years within the continuous span. Seven species met these criteria at the banding stations, five of which occur at both banding sites. Twenty species met these criteria from the NAB data, with 13 in common between central and northern CA. The 21 species recorded in either data set are listed in Table 1.

Table 1 Species list

Common name	Scientific name
Barn Swallow	<i>Hirundo rustica</i>
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>
Cliff Swallow	<i>Hirundo pyrrhonta</i>
House Wren	<i>Troglodytes aedon</i>
Lazuli Bunting	<i>Passerina amoena</i>
MacGillivray's Warbler	<i>Oporornis tolmiei</i>
Nashville Warbler	<i>Vermivora ruficapilla</i>
Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>
Olive-sided Flycatcher	<i>Contopus borelais</i>
Orange-crowned Warbler	<i>Vermivora celataa</i>
Swainson's Thrush	<i>Catharus ustulatus</i>
Vaux's Swift	<i>Chaetura vauxi</i>
Pacific Slope Flycatcher	<i>Empidonax difficilis</i>
Warbling Vireo	<i>Vireo gilvus</i>
Western Kingbird	<i>Tyrannus verticalis</i>
Western Tanager	<i>Piranga ludoviciana</i>
Western Wood-Pewee	<i>Contopus sordidulus</i>
Wilson's Warbler	<i>Wilsoniia pusilla</i>
Yellow Warbler	<i>Dendroica petechia</i>

Dates of arrival

Three temporal phases of migration are used in trend and climate-association analyses: (1) first arrival date of the season, (2) onset of continuous migration, and (3) median date of the migratory period. Each metric has its particular strengths and weaknesses, with each capturing a different ecological aspect of migration (see discussion in MacMynowski & Root, 2007). For the banding data, we use all three metrics, while for the NAB data we use only the first two, because changing observer effort over the season makes the median date unreliable. To minimize the influence of outliers on trends, we exclude years where a species' arrival date is greater than two standard deviations from the mean of all years of data for that species.

The first date of arrival is simply the first record of the season. We defined the onset of continuous migration for banding data as the date during the species' passage through the site when the daily gaps between capturing individuals of a given species were no greater than three continuous days. For the NAB data, we identified the two calendar months with the largest number of records for a given species and defined the onset of continuous migration as the median date of arrival within those two consecutive months. We only consider the first 2 months of the NAB season because observer effort is expected to decline as the season progresses and first sightings have been

made; thus, for this data set, we can only evaluate the two metrics of initial migratory passage. For the banding data, the median date of the annual migratory period for each species is the date on which 50% of the total individuals have been banded during the spring season. We include this common metric of arrival to enable comparison with analyses of migration elsewhere.

Climate association

We calculated the Pearson correlation coefficient (over years) between each migration date (i.e. first arrival date, onset of continuous migration, and median date) and climate variables at the local, regional, and continental scales (Table 2). For the local scale, we used monthly minimum temperatures recorded at the National Weather Service COOP weather station closest to the banding location: San Jose International Airport (37°21'N, 121°54'W) for Station 1 and Petaluma, CA (38°15'W, 122°36'W) for Station 2. We used these data to calculate mean monthly temperatures. We selected a centrally located COOP station for the NAB data: San Francisco International Airport (37°37'N, 122°23'W) for central CA and Eureka (40°49'N, 124°10'W) for Northern CA. For the regional scale, we created monthly regional averages of coastal western US (30–50°N, 115–125°W) mean temperature anomalies from gridded Historical Climatology Network data [i.e. temperature deviations from the 1961 to 1990 mean calculated on a 5° × 5° scale (Peterson & Vose, 1997)].

At the continental climatic scale, we evaluated a species' association with the North Atlantic Oscillation (NAO), the PDO, and the ENSO. For NAO, we used a station-based index (<http://www.cgd.ucar.edu/~jhurrell/nao.stat.other.html>). We used the Multivariate ENSO Index (MEI) for ENSO associations: <http://www.cdc.noaa.gov/people/klaus.wolter/MEI/mei.html>. PDO indices were obtained from http://www.jisao.washington.edu/data_sets/pdo/ (Mantua *et al.*, 1997).

We calculated the correlation coefficient between the arrival date and the climate variable for the month of arrival and the preceding month. Climate conditions in these proximal months most likely have the strongest link to conditions experienced immediately before or during migration, and thus, are more informative than a single seasonal mean.

Based upon the correlations between arrival dates and the climate variables described above, we categorized each species based upon the likelihood (very likely, likely, possible, none) that the species' phenology is influenced, directly or indirectly, by climate. To enhance the robustness of our analysis, we incorporated multiple scales of climate association *and* multiple data sites

Table 2 Arrival dates, trends, and climate associations

Species	Location	Climate	Begin	End	First arrival date				Continuous arrival date			
					Median	<i>b</i>	<i>P</i>	<i>r</i> ²	Median	<i>b</i>	<i>P</i>	<i>r</i> ²
Barn Swallow	NAB-C	VL	1980	2003	54	-0.71	0.01	0.32	65	-0.56	0.01	0.36
	NAB-N		1980	2003	76	-2.35	0.00	0.67	82.5	-0.15	0.55	0.03
	BBL-2		1977	2000	107	0.27	0.46	0.04	127	1.52	0.04	0.32
Black-headed Grosbeak	NAB-C	VL	1979	1994	88	-0.98	0.15	0.20	98	-1.09	0.01	0.49
	NAB-N		1980	1992	107	-0.29	0.46	0.08	110.5	-0.96	0.03	0.48
	BBL-1		1985	1997	116	-0.04	0.93	0.00	121	0.66	0.50	0.05
Black-throated Gray Warbler	NAB-C	L	1979	1994	89	-1.07	0.37	0.06	101.5	-0.57	0.41	0.05
	NAB-N		1979	1994	101	-0.93	0.05	0.34	103	-1.46	0.00	0.68
Blue-gray Gnatcatcher	NAB-C	N	1979	2002	65	0.45	0.48	0.03	78	0.24	0.45	0.04
Cliff Swallow	NAB-C	L	1981	2003	53	0.11	0.62	0.02	54	0.15	0.08	0.20
House Wren	NAB-C	P	1982	2003	49	0.92	0.20	0.12	71	1.42	0.04	0.30
	NAB-N		1982	1994	94.5	-0.95	0.30	0.15	94.5	-1.05	0.29	0.16
Lazuli Bunting	NAB-C	P	1979	1994	103	-0.97	0.01	0.43	111	-0.71	0.05	0.28
MacGillivray's Warbler	NAB-C	P	1979	1994	105	-0.46	0.46	0.05	110	-0.34	0.13	0.20
	NAB-N		1981	1992	110	0.19	0.68	0.03	111	0.56	0.17	0.22
Northern Rough-wing Swallow	NAB-C	P	1979	2003	53	-0.49	0.10	0.15	61	-0.51	0.04	0.21
Nashville Warbler	NAB-C	L	1979	1994	55	0.55	0.63	0.02	109	0.35	0.10	0.21
	NAB-N		1980	1994	92.5	0.89	0.70	0.02	108.5	-0.65	0.64	0.03
Olive-sided Flycatcher	NAB-C	L	1979	2003	102.5	0.15	0.39	0.04	107	0.14	0.26	0.07
	NAB-N		1979	1992	118	0.57	0.41	0.08	127	0.47	0.54	0.04
Orange-crowned Warbler	NAB-C	L	1979	1994	57	0.39	0.64	0.02	60	-0.31	0.59	0.03
	BBL-1		1985	1997	67	-1.40	0.06	0.30	86	-1.41	0.14	0.19
	BBL-2		1969	2002	72.5	0.22	0.16	0.06	79	0.06	0.64	0.01
Pacific slope Flycatcher	BBL-1	P	1986	1997	85	-0.61	0.24	0.15	92	-0.17	0.83	0.01
	BBL-2		1969	1997	103	-0.28	0.18	0.08	113	-0.04	0.89	0.00
Swainson's Thrush	NAB-C	L	1979	1992	107	-0.83	0.21	0.13	114	0.03	0.96	0.00
	BBL-1		1983	1997	114.5	0.10	0.82	0.00	118	-0.67	0.11	0.22
	BBL-2		1969	2002	122	-0.04	0.64	0.01	125	0.15	0.07	0.11
Vaux's Swift	NAB-C	L	1979	1994	77	-1.47	0.40	0.06	113	-0.49	0.04	0.29
	NAB-N		1980	1994	102	0.15	0.83	0.00	106.5	0.12	0.76	0.01
Warbling Vireo	NAB-C	VL	1979	2003	76	-0.32	0.03	0.23	80	-0.32	0.01	0.34
	NAB-N		1981	2003	90	-1.00	0.01	0.42	92	-1.19	0.00	0.50
	BBL-1		1987	1997	113.5	0.38	0.55	0.08	119.5	-0.09	0.95	0.00
	BBL-2		1969	2000	103	0.45	0.18	0.07	120	0.32	0.11	0.11
Western Kingbird	NAB-C	VL	1979	2003	81	-0.56	0.02	0.28	94	-0.62	0.02	0.27
	NAB-N		1979	2003	105	-0.01	0.98	0.00	109	0.02	0.91	0.00
Western Tanager	NAB-C	N	1979	1994	78	1.73	0.32	0.08	107	0.16	0.91	0.00
	NAB-N		1979	1994	106	0.17	0.89	0.00	116	0.51	0.70	0.02
Western Wood-Pewee	NAB-C	L	1979	2003	106	0.03	0.83	0.00	109	-0.03	0.85	0.00
	NAB-N		1980	2003	121.5	-0.38	0.35	0.07	127	-0.46	0.29	0.09
Wilson's Warbler	NAB-C	VL	1979	1994	77	-0.01	0.99	0.00	82	-0.23	0.22	0.10
	NAB-N		1981	1994	97	-0.10	0.84	0.00	103	-0.64	0.08	0.25
	BBL-1		1983	1997	88	-1.78	0.01	0.45	98	-1.40	0.15	0.18
	BBL-2		1969	2002	93	0.03	0.81	0.00	95.5	-0.13	0.28	0.04
Yellow Warbler	NAB-C	N	1979	1994	90	0.31	0.84	0.01	102	0.23	0.59	0.18

Four categories of association between a species' phenology and climate are defined: (1) very likely (VL, significant correlations ($P < 0.10$) of the same sign for both temperature and a climate index at two or more locations); (2) likely (L, significant correlations of the same sign for both temperature and a climate index at one location); (3) possible (P, significant correlation with only one climate variable or inconsistent signs for climate variables between locations); and (4) none (N, no significant correlations between arrival and climate variables). Trends in arrival over the study period were calculated with linear regression. Data-location: BBL-1, banding station 1; BBL-2, banding station 2; NAB-C, central region; NAB-N, northern region.

for each species into the assessment. The subjective probabilities that we derive from these associations are based upon the consistency of evidence for climate correlation at all data sites available for each species. Correlations with temperatures at the local and regional scale are evaluated together.

We define four categories of association between a species' phenology and climate: (1) very likely (significant correlations ($P < 0.10$) of the same sign for both temperature and a climate index at *two or more* locations), (2) likely (significant correlations of the same sign for both temperature and a climate index at *one* location), (3) possible (significant correlation with only one climate variable or inconsistent signs for climate variables between locations), and (4) none (no significant correlations between arrival and climate variables). In other words, a species categorized as very likely to be tracking climate has a correlation ($P < 0.10$) of the same sign with temperature (regional or local) at two locations *and* a correlation ($P < 0.10$) of the same sign for the same climate index (i.e. NAO, PDO, or ENSO) at two or more data sites. The signs of the temperature correlation and the climate-index correlation are considered independently (e.g. a species can be negatively correlated with temperature, but positively correlated with NAO, PDO, or ENSO).

Seasonal arrival distribution

To compare the arrival distribution of four species in common between the two banding sites, we plotted the total number of individuals of each species banded on a given Julian day for all years of data. From these distributions, possible peaks in migration were identified using a 'peak-picking' algorithm that searched 7-day time units for days on which the number of individuals recorded were at least 25% of the maximum daily total for the season (OriginLab Corporation, 2002). Peaks resulting from a year or two of unusually high records or not part of a several day trend were disregarded. Finally, a curve was fit to the arrival distribution using the daily totals and the one to two peaks identified for each species. Nonlinear curve fitting was conducted with an unweighted Lorentz function and the Levenberg–Marquardt least-squares-fitting algorithm (OriginLab Corporation, 2002).

In order to compare species with different relative abundances, arrival distributions were standardized by dividing the total number of birds banded on a given Julian day by the total number of birds of that species collected throughout the entire season (i.e. arrival distributions were based on percentages of total annual captures rather than absolute numbers).

Results

Climate variables

At all COOP stations, the spring mean minimum temperature (March, April, and May) increased during the study period ($b = 0.036\text{--}0.078\text{ }^{\circ}\text{C yr}^{-1}$, $r^2 = 0.11\text{--}0.41$, $P < 0.05$). The seasonal mean maximum temperature significantly increased only at Eureka ($b = 0.088\text{ }^{\circ}\text{C yr}^{-1}$, $r^2 = 0.39$, $P < 0.01$). Monthly mean minimum temperatures for all stations, except Petaluma, correlated with ENSO and PDO from February to May (MEI: $r = 0.38\text{--}0.53$, $P < 0.05$; PDO: $r = 0.38\text{--}0.52$, $P < 0.02$) and NAO only in May ($r = -0.30$ to -0.37 , $P < 0.08$).

Correlation between arrival date and climate

Using the criteria specified in the Methods, five species categorized as highly likely climate associates, eight species are likely associates, five species are possible associates, and three species show no evidence of a climatic association with their migratory phenology (Table 2).

Five species negatively correlate ($P \leq 0.05$) with ENSO at least at one location (Swainson's Thrush, Nashville Warbler, Pacific Slope Flycatcher, Wilson's Warbler, Orange-crowned Warbler). Eleven species' arrival is correlated ($P \leq 0.05$) with NAO at least at one location; 10 are negatively correlated. Nine species' phenology is correlated ($P < 0.10$) with PDO at least at one location and four are correlated at multiple locations. Four species were positively associated; four were negatively associated; and one species had mixed signs at different locations.

The most consistent climate-index associates are: Orange-crowned Warbler [ENSO (negative) and NAO (positive) at both banding sites], Wilson's Warbler [ENSO (negative) at both Station 1 and northern CA region, PDO (negative) at Station 2 and northern CA], and Warbling Vireo [ENSO (negative) and NAO (positive) at both banding sites]. There is some variability between and within central and northern California. For central and northern NAB species, only two species were consistently associated (i.e. same index, $P < 0.10$) between the regions. Most of the other 11 species' arrival dates are correlated in one region and not the other. For the banding data, correlations for three of five species are consistent between locations.

Temperature-arrival associations are more frequent than climate index associations. Twelve species negatively correlate ($P \leq 0.05$) with local or regional temperature at least at one location. Between the banding stations, three of five species' arrival dates consistently correlate (i.e. same sign, $P \leq 0.05$) with local or regional

temperature. For the central and northern California NAB regions, six of 13 species are consistently correlated with regional temperature.

Trends in phenology

Thirteen of the 21 species (62%) exhibit a change ($P < 0.10$) in either the first arrival date or onset of continuous migration (Table 2). Of those, eight are arriving earlier (62%), two are later (15%), and three are uncertain due to different signs at different data sites. Of the 13 species, 10 (77%) are classified as likely or highly like climate associates. The remaining three species are possible climate associates. Only one trend is detectable in the median date of migration (Barn Swallow, $b = 1.10$, $P = 0.02$, $r^2 = 0.31$).

The NAB data are more consistent in the detection of trends between sites (Table 2). Eight of 13 species with NAB data are consistent between regions, with three species arriving earlier in both regions (Warbling Vireo, Black-headed Grosbeak, Barn Swallow). For the banding data, three species exhibit a trend at one location and not the other; one species exhibits no change; and one species has trends in opposite directions at each location (Swainson's Thrush).

Effort analysis

We detect no observational bias from the NAB data. Even though general bird observations might be increasing (i.e. increasing human population), there is no evidence for an increase in reporting of the species in this analysis. For the northern region, there is no change in the number of reports ($P = 0.40$) over the study period even though the total number of records is lower than the central region. For the central region, reporting is constant ($P = 0.99$) through 1995. From 1995 to 2003, there is a sharp decrease in reports, possibly due to a change in archival patterns or a change in editor. One editor noted more recent emphasis placed upon unusual sightings compared with regular arrivals.

We have no reason to suspect reinforcing bias – bias in the same direction as our findings – in the banding data (see 'Discussion'). We can be assured of minimum effort at both stations from Julian day 45 and consistently through the season until Julian day 160. Data on banding effort (i.e. net hours) from 1976 to 2002 were obtained for Station 2. Spring banding effort declined over the study period at this location ($b = -116$ birds yr^{-1} , $r^2 = 0.39$, $P < 0.01$), with a sharp drop in 1989 when banding switched from 7 to 3 days per week. We would expect declining effort to result in later detection, and hence, trends toward later arrival if banding

effort was a significant factor affecting species' apparent phenology.

We found the seasonal total of net hours at Station 2 to be significantly correlated with the total number of birds banded in a season [$r = 0.43$, $P = 0.03$, outlier year (1997) removed]. Effort data were not available for Station 1, and therefore as a proxy of total effort at this station, we calculated the seasonal sum of the total birds banded. The annual seasonal total of birds at this site declined from 1988 onwards ($b = -103$ birds yr^{-1} , $r^2 = 0.79$, $P = 0.01$). While declining annual totals are also consistent with declines of some songbird populations (e.g. Ballard *et al.*, 2003), there is no linear trend in the spring seasonal rate of birds captured at Station 2 (average birds per net hour, 1976–2002, $P = 0.32$), which suggests that overall encounters are not consistently declining over the study period. Neither the seasonal total of birds nor the seasonal rate of capture is correlated with spring MEI or PDO indices. However, there is a notable range of birds banded per net-hour (4.3–11 birds/100 h at Station 2). Thus, seasonal totals may be indicative, but certainly not robustly predictive, of total banding effort. This is a caveat when evaluating these data, but it indicates that our finding of earlier phenological change is conservative, [i.e. changes toward earlier arrival may counter-influenced by declining effort and/or declining species' populations (see 'Discussion')]. This may help explain the trends toward later arrival at Station 2; however, at Station 1, three species are arriving earlier.

Additionally, we correlated the first arrival date for each species with the total effort (total birds banded for Station 1 and net hours for Station 2) during the month of the species' arrival for the entire study period. No species at Station 1 had significant ($P < 0.10$) correlations and four of the six species at Station 2 were also uncorrelated. The two species' at Station 2 with significant correlations were positively associated [i.e. earlier detection of arrival with decreasing banding effort (Pacific Slope Flycatcher, $r = 0.67$, $P < 0.01$; Orange-crowned Warbler, $r = 0.63$, $P < 0.01$)]. This counterintuitive correlation suggests that the association between effort and arrival for these species is spurious or unknown.

Comparison of migration between locations

The banding-station results suggest regional differences, both between locations and amongst species, over a much smaller area (Figs 1 and 3). While the median date of arrival is similar for all four species in common between the sites, three species' first arrival dates are approximately a week apart and one species (Pacific Slope Flycatcher) is detected 18 days later at

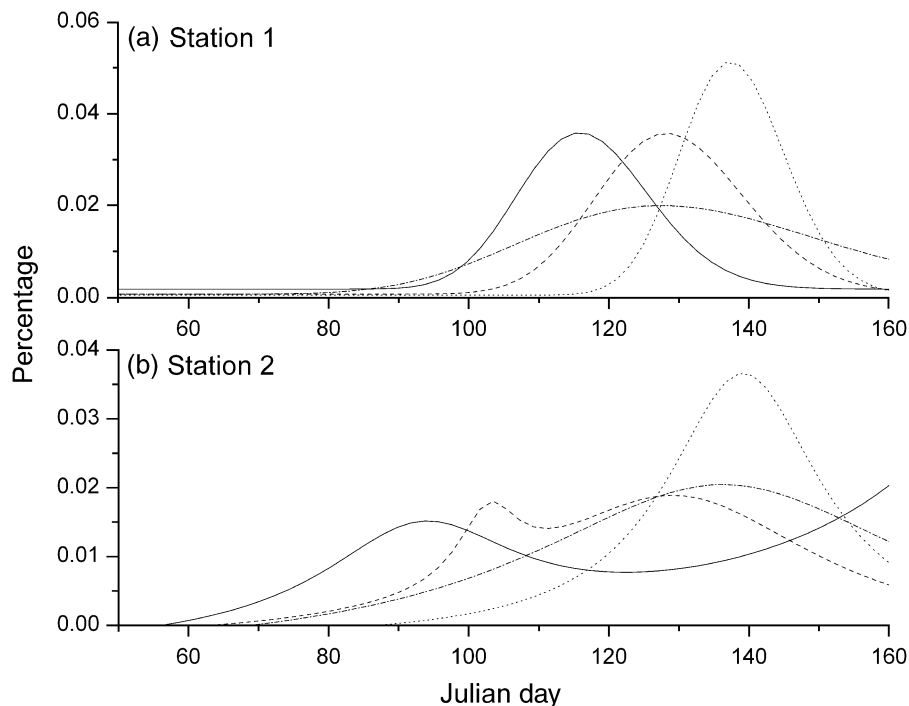


Fig. 3 Seasonal arrival distribution of four species. Solid, Orange-crowned Warbler [$r^2 = 0.84$ (a), 0.76 (b)]; dash, Wilson's Warbler [$r^2 = 0.85$ (a), 0.78 (b)]; dot, Swainson's Thrush [$r^2 = 0.95$ (a), 0.86 (b)]; dash dot, Pacific Slope Flycatcher [$r^2 = 0.66$ (a), 0.67 (b)]. (a) Banding Station 1. (b) Banding Station 2.

Station 2 compared with Station 1. Quite strikingly, the pattern and timing of arrival of the Swainson's Thrush are nearly identical between the sites (Fig. 3). In comparison, considerable numbers of Orange-crowned Warblers arrive nearly 3 weeks earlier at Station 2 compared with Station 1; this is possibly attributed to resident birds in the vicinity of Station 2. Furthermore, Station 2 captures an increase in abundance of this species during the late spring season, which is probably due to the movements of offspring of local breeding populations of this earliest arriving Neotropical warbler. In contrast, captures at Station 1 are near zero by late spring, suggesting only adults are passing through this region. The Wilson's Warbler exhibits a two peaked distribution at Station 2, with the timing of only the second peak simultaneous with Station 1.

For two species, there is an unexpectedly long lag between the median first arrival date of the species in the central CA region and its median first banding. For the Warbling Vireo, according to the NAB data, the median of first arrival is Julian day 76; in comparison, the median of first banding at Station 1 is Julian day 114 and at Station 2 is Julian Day 103 – 3–4 weeks later. The Wilson's Warbler is similar, with a difference of nearly 2 weeks between first sighting and first banding. Another two species, however, have more similar dates of first

sighting and first banding (Orange-crowned Warbler, Swainson's Thrush).

Discussion and conclusions

Our multisite, multiscalar analyses of changes in the spring arrival of long-distance migrants in California indicate three major conclusions. First, species whose arrival is likely or highly likely associated with climate at multiple scales constitute the majority of species in this region that are exhibiting trends in arrival date. Second, there are notable differences within a relatively small area (i.e. <150 km between banding stations), suggesting the need for multiple data sources and larger-scale research to detect and assess the impacts of climatic change on migration of birds. Third, public-network observer-collected data are highly valuable, even when banding stations are located in proximity. Compared with the banding stations, the local observers provided information on more species (e.g. hard to capture in nets due to habitat or behavior) and a diversity of guilds (e.g. aerial insectivores) that are generally not recorded at banding stations. Obviously, however, the value of a type of data is linked to the purpose of analysis.

We find compelling evidence that (1) climate-associated species are changing, while (2) species' without

evidence for the influence of local, regional, or continental climate on their arrival in central or northern California are not shifting their phenology. Multiscalar and multisite data were used to assess each species: the analysis is not dependent upon one location, one data type, or one climatic variable. Furthermore, the species group was not preselected in any way to bias the species toward climatic association. The selection of species was solely based on data availability and criteria set *a priori* (see 'Materials and methods').

In addition to climatic influences on species' behavior, two alternate explanations for the phenological changes detected in migrant species can be considered: (1) an increase in the number of birds (i.e. increasing species' population, Tryjanowski & Sparks, 2001) and (2) an increase in reporting (increasing size of observer populations). Much concern has been directed toward overall declining populations of Nearctic-Neotropical migrants (e.g. Terborgh, 1989). A recent analysis in the study region detected widespread population declines and no increases (Ballard *et al.*, 2003). This study examined autumn migrants in coastal California, which include distant populations, as well as California breeding populations; furthermore, the results were consistent with regional changes identified by the North American Breeding Bird Survey. Thus, we expect that migrant populations in western North America are at best stable or declining, thereby decreasing the probability of banding or observing most species examined in this study. If declining populations of species is the predominant factor responsible for the observed trends, we would expect more trends toward later arrival (i.e. more difficult and fewer, and therefore later, sightings/bandings). This is not the case; the majority of changing species are consistently arriving earlier.

We examined the issue of reporting bias in the analysis of the data and found no specific reason for concern. For the banding data, all locations and years of data met minimum efforts criteria (see 'Materials and methods'). Effort for Stations 1 and 2 decreased in the second half of the study period compared with first half. For the observer-based data, records have been consistent through the entire reporting period in northern California (1979–2003) and most of the reporting period in central California (1979–1994). In northern California, there were notably fewer reports from 1997 to 2003. Again, as explained above with the decreased bird population, a decrease in reporting would increase the likelihood of missed observations and, consequently, bias trends toward later arrival.

Thus, we conclude that climatic change is the most likely explanation for the majority of spring phenological changes in arrival observed amongst these 21 species of long-distance, Nearctic-Neotropical migrants.

This supplements existing research suggesting differential responses between short- and long-distance migrants (Butler, 2003; Jenni & Kery, 2003; Lemoine & Bohning-Gaese, 2003). Butler (2003) finds that short-distance migrants are arriving nearly 2 weeks earlier in eastern New York while long-distance migrants arrive only 4 days earlier on average. Although such a comparison was not possible in this analysis due to confounding of short-distance migrants and wintering populations, we find eight of the long-distance migrant species in this study are arriving earlier (as well as species not changing their phenology; Table 2). Clearly, our results identify multiple species of long-distance migrants that have climatic influences on some aspect of their migratory schedule and are exhibiting significant changes in spring migratory phenology.

Notably, we find that 11 species' arrival timing is correlated with NAO; the majority (90%) of these species arrives earlier when NAO is stronger. While NAO is widely associated with migratory phenology in Europe (e.g. Zalakevicius, 2001; Forchhammer *et al.*, 2002; Kanuscak *et al.*, 2004; Stervander *et al.*, 2005), this analysis is the first documentation of a significant relationship between spring migratory phenology and NAO in western North America that we could find and apparently only the second such report in North America (see, for eastern North America, MacMynowski & Root, 2007). Furthermore, Nott *et al.* (2002) detected a relationship between songbird reproductive success and springtime NAO in the Pacific Northwest of the United States. It appears that NAO is an important factor in passerine life history across the continent and merits further investigation on both coasts.

Climate might be influencing spring migratory phenology in western North America through a number of mechanisms. First, spring temperatures in the region have increased (see 'Results'). Previous research has indicated that spring plant phenology (Cayan *et al.*, 2001) and butterfly emergence (Forister & Shapiro, 2003) are also correspondingly advanced in the region. Migrants might be able to take advantage of earlier availability of migratory fuel and speed their migration (e.g. Ahola *et al.*, 2004). As a result, earlier arrival may confer a competitive advantage in securing territory (e.g. Møller, 1994; Lozano *et al.*, 1996) or selecting a high-quality mate (Bensch & Hasselquist, 1992). Also, increasing temperatures might have enabled some migrants to winter further north; research in the Nearctic has documented that some short-distance migrants shift their distributions in response to winter temperature (Butler *et al.*, 2007), but such studies are not available for species wintering in the Neotropics.

Second, large-scale climate oscillations (i.e. NAO, ENSO) influence conditions over wide regions, includ-

ing both wintering grounds and the migratory route. NAO is known to affect temperature, winds, and precipitation throughout Europe, North America, and Africa (Hurrell *et al.*, 2003). Likewise, ENSO affects winter and spring climate worldwide. Specifically, moderate to strong El Niño conditions bring higher rainfall and cooler temperatures to the California coast (Castello & Shelton, 2004). Proposed mechanisms of NAO influence on spring migratory timing include: stronger winds to assist migration, improved foraging on wintering grounds, decreased migration distance by wintering farther north, and earlier development of spring (Vahatalo *et al.*, 2004). ENSO might be similarly influential: light southerly winds from March to May are more prevalent in western North America during El Niño years, which can assist migration (Nott *et al.*, 2002). Studies have also linked ENSO to predeparture conditions on the wintering grounds (Sillert *et al.*, 2000; Strong & Sherry, 2000).

In summary, we find that Nearctic-Neotropical migrants in western North America tend to arrive earlier in association with warmer temperatures, positive NAO indices, and stronger MEI indices. Climatic conditions might be influencing migratory timing through: (1) timing of spring and insect emergence, (2) conditions on the wintering grounds and predeparture body condition, and (3) favorable winds to assist migration.

While species with the most consistent correlations with climate variables are advancing their phenology, there are also species with climate correlations and no detected changes. No obvious species' characteristics (i.e. transient-only vs. local-breeder, diet, size, location of wintering grounds) explain these patterns. However, we suggest several geographic factors that might account for these inconsistencies. First, migrants depart from a wide range of Neotropical wintering grounds and thereby experience different climatic cues and conditions, particularly between the Pacific and Atlantic coasts during El Niño years. Second, there are many populations mixing during migration; first arrival dates might only reflect migrants from one region (e.g. the nearest subpopulation, which is more or less influenced by a particular climate variable than other populations).

Third, for some species, it is unknown whether the individual observed or banded is a transient migrant or returning resident breeder. The three species with the most frequent climate correlations (Warbling Vireo, Wilson's Warbler, and Orange-crowned Warbler) are abundant breeders in the study region. We can speculate that the first individuals of these species, as reflected in the first arrival dates, are breeding residents arriving earlier to take advantage of advancing spring in the region. Furthermore, a species' rate of migration might only advance over parts of the migratory route,

depending upon habitat and spring phenology. This might explain the phenological differences between central and northern California (i.e. only two of the 13 species in the NAB data set are consistent between the regions). After all, while there is widespread evidence of earlier migration for many passerines (Lehikoinen *et al.*, 2004), there is also evidence of constraints on advancing spring phenology for other species (Both & Visser, 2001; Sanz, 2003; Ahola *et al.*, 2004).

Thus, like many other previous analyses elsewhere, we identify widespread advances in phenology, but these are not universal among the species examined. A phenological study – even a multisite, regional analysis like this one – is a spatial and temporal snapshot of migrants' travel through a climatically and ecologically complex environment.

We note that while climate is clearly correlated with the arrival of many Neotropical migrant species, it is unclear how the early-season changes affect the bulk of the species' populations. While only one species' median date of migration is significantly changing ($P < 0.05$), the median of migration correlates with climate as frequently as the earlier phases of migration. This suggests two different interpretations. The first is methodological. Given the annual fluctuations in capture effort, the median of arrival has too much variance to detect a trend, and thus, it is actually shifting as much as the earlier migratory waves, but is not detectable in this analysis given the variability. Thus, phenology is changing throughout the migratory period and affecting the majority of the population.

On the other hand, if the unchanging median phenology is not methodological, the observed phenological changes disproportionately affect earlier migrants, particularly males of the many species of passerines for which males migrate earlier (Stewart *et al.*, 2002). This scenario could lead to different selective pressures for early season fitness (Moller, 2004), or, conversely, affect such a small proportion of the population that shifting migratory phenology has little potential for changes in breeding success, and thus, abundance of a species (e.g. Wilson & Arcese, 2003). Of course, either scenario is dependent upon the concurrent changes in other aspects of ecosystem phenology, such as vegetation and insects, upon which the birds depend for migratory and breeding resources (Both & Visser, 2001; Visser & Holleman, 2001). In either case, climate, and therefore climatic change, has an obvious role in some aspects of migratory phenology, but the species' population and ecosystem-wide consequences are yet uncertain.

The detailed analysis of multiple data sites and types lends insight into migratory phenology over larger scales. The preponderance of studies, thus far have examined single-site data to detect climatic influences

(e.g. Crick *et al.*, 1997; Winkel & Hudde, 1997; Penuelas *et al.*, 2002), though a few studies have considered larger scales, but only for single species (e.g. Dunn & Winkler, 1999). If studies are to extend beyond local detection to characterizing specific changes, and possible impacts, upon individual species or populations, it will be important to use larger scales of research and multiple data sites to examine how extensive the changes are and the different factors involved.

The results from central and northern California suggest how different an impression one could have of species' behavior if only one region or one banding location were analyzed. Most of the species examined are sighted 3 weeks later in northern California compared with central California; the range is 5–45 days between first arrival dates within a species. Only three of 13 species associate with NAO in northern California, compared with eight of 22 species in central California.

The differences in migration patterns, trends, and climate associations identified at the different sites and scales could be due to differences in data collection, multiscalar geographical features of the sites, and/or different routes taken by the migrants. Even though the two banding stations are within 150 km of each other, one is directly on the coast and the other is approximately 40 km inland. At smaller scales, the sites differ in local vegetation, as well as surrounding landscape features. These, as well as unidentified wind or cloud patterns, could influence migrants' arrival within an area; however, it is less clear how macroscale features would strongly influence one species and not another (e.g. the difference in initial arrival dates for the same species at the two stations). Ongoing analyses of migratory passage at other inland and coastal banding sites in North America will hopefully yield further understanding.

The larger scale assessment of species' arrival (NAB records) yielded more consistency in climate correlations and trends. For both regions, ENSO, PDO, and temperature associations are comparable. Furthermore, there were data on more than twice as many species. Species that are low in numbers (e.g. some Warblers) or less likely to be caught in mist nets (e.g. Swallows) were consistently reported by NAB observers because the observers were not constrained to a narrow habitat (such as a single banding site) and were eager to find unusual species. Thus, even though sampling is not as systematic as banding data, and clearly not as useful for some studies (such as assessing changes in abundance), public networks collecting bird phenological data can be very useful for global change analyses (e.g. Van Vliet *et al.*, 2003).

Finally, from a methodological perspective, we note the differences in the detection of trends depending

upon which arrival metrics are used. The first sighting of a species is most susceptible to outliers (Marra *et al.*, 2005), and particularly for sex-differential migratory species, generally captures the arrival of males (e.g. Stewart, 1986). In this sense, while sensitive to changes, information on first arrival incompletely captures the biology of entire species. The increased variance from outliers might explain why fewer trends were recorded for this metric. A measure of the onset of continuous migration has the advantage of minimizing outliers and indicating the start of the migratory period for the bulk of individuals within a species. The median of the migratory period clearly captures the midpoint of a species' passage through a region, but is less of an indicator of species' response to changes early in the spring migratory period (MacMynowski & Root, 2007). This might explain why only one trend was identified in the median of migratory passage.

In summary, our in-depth analyses provide evidence that spring Nearctic-Neotropical migrants in California whose arrival is likely or highly likely associated with climate constitute the majority of species that are exhibiting statistically significant trends toward earlier arrival. We find that temperature, ENSO, and NAO are correlated with spring migratory phenology in the region. Furthermore, the spatial and temporal complexity of migratory passage strongly indicates the importance of using larger scales of research and multiple data sites to examine the extent of phenological changes across species' ranges and populations.

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References

- Ahola M, Laaksonen T, Sippola K, Eeva T, Raino K, Lehikoinen E (2004) Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology*, **10**, 1610–1617.
- Ballard G, Geupel G, Nur N, Gardali T (2003) Long-term declines and decadal patterns in population trends of songbirds in western North America (1979–1999). *Condor*, **105**, 737–755.

- Bensch S, Hasselquist D (1992) Evidence for active female choice in a polygynous warbler. *Animal Behaviour*, **44**, 301–311.
- 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. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 9701–9704.
- Butler CJ (2003) The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis*, **145**, 484–495.
- Butler JR, MacMynowski DP, Laurent C, Root TL (2007) Temperature-associated dynamics of passerine winter distributions. *AMBIO*, in press.
- Castello A, Shelton M (2004) Winter precipitation on the US Pacific coast and El Niño-Southern Oscillation events. *International Journal of Climatology*, **24**, 481–497.
- Cayan DR, Kammerdiener SA, Dettinger MD, Caprio JM, Peterson DH (2001) Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society*, **82**, 399–415.
- Coppack T, Tottrup AP, Spottiswoode C (2006) Degree of protracted reflects level of extrapair paternity in migratory songbirds. *Journal für Ornithologie*, **147**, 260–265.
- Cotton PA (2003) Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 12219–12222.
- Crick H, Dudley C, Glue D, Thomson D (1997) UK birds are laying earlier. *Nature*, **388**, 526.
- Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **266**, 2487–2490.
- Forchhammer M, Post E, Stenseth N (2002) North Atlantic Oscillation timing of long- and short-distance migration. *Journal of Animal Ecology*, **71**, 1002–1014.
- Forister ML, Shapiro AM (2003) Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology*, **9**, 1130–1135.
- Hare S, Mantua N (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, **47**, 103–146.
- Huppert O, Winkel W (2006) Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migration routes. *Journal of Ornithology*, **2**, 344–353.
- Hurrell J, Kushnir Y, Otterson G, Visbeck M (2003) *The North Atlantic Oscillation: Climatic Significance and Environmental Impact*. American Geophysical Union, Washington, DC.
- IPCC (2001) *Climate Change 2001: The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, New York.
- Jenni L, Kery M (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **270**, 1467–1471.
- Kanuscak P, Hromada M, Tryjanowski P, Sparks TH (2004) Does climate at different scales influence the phenology and phenotype of the River Warbler *Locustella fluviatilis*? *Oecologia*, **141**, 158–163.
- Kelly J, Hutto RL (2005) An east–west comparison of migration in North American wood warblers. *Condor*, **107**, 197–211.
- Ledneva A, Miller-Rushing AJ, Primack RB, Imbres C (2004) Climate change as reflected in a naturalist's diary, Middleborough, Massachusetts. *Wilson Bulletin*, **116**, 224–231.
- Lehikoinen E, Sparks TH, Zalakevicius M (2004) Arrival and departure dates. *Advances in Ecological Research*, **35**, 1–32.
- Lemoine N, Bohning-Gaese K (2003) Potential impact of global climate change on species richness of long-distance migrants. *Conservation Biology*, **17**, 1–11.
- Lozano G, Perreault S, Lemon R (1996) Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. *Journal of Avian Biology*, **27**, 164–170.
- MacMynowski DP, Root TL (2007) Climate and the complexity of migratory phenology: sexes, migratory distance, and arrival distribution. *International Journal of Biometeorology*, **51**, 361–373.
- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, **78**, 1069–1079.
- Marra PP, Francis CM, Mulvihill RS, Moore F (2005) The influence of climate on the timing and rate of spring bird migration. *Oecologia*, **142**, 307–315.
- Moller AP (2004) Protandry, sexual selection, and climatic change. *Global Change Biology*, **10**, 2028–2035.
- Møller AP (1994) Phenotype dependent arrival time and its consequences in a migratory bird. *Behavioural Ecology and Sociobiology*, **35**, 115–122.
- Nott MP, Desante DF, Siegel RB, Pyle P (2002) Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. *Global Ecology and Biogeography Letters*, **11**, 333–342.
- OriginLab Corporation (2002) *Origin 7.0*. Northampton. OriginLab Corporation, MA, USA.
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Penuelas J, Filella I, Comas P (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology*, **8**, 531–544.
- Peterson TC, Vose RS (1997) An overview of the Global Historical Climatology network database. *Bulletin of the American Meteorological Society*, **78**, 2837–2849.
- Root TL, MacMynowski DP, Mastrandrea M, Schneider SH (2005) Human-modified temperatures induce species' changes: joint attribution. *Proceedings of the National Academy of Sciences of the United States of America*, **21**, 7465–7469.

- Root TL, Price J, Hall K, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Sanz J (2003) Large-scale effects of climate change on breeding parameters of pied flycatchers in Western Europe. *Ecography*, **26**, 45–50.
- Sillett TS, Holmes RT, Sherry TW (2000) Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science*, **288**, 2040–2042.
- Smith R, Moore F (2005) Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioural Ecology and Sociobiology*, **57**, 231–239.
- Stervander M, Lindstrom A, Jonzen N, Anderson A (2005) Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. *Journal of Avian Biology*, **36**, 210–221.
- Stewart PA (1986) Fall migration of twelve species of wood warblers through coastal Virginia. *North American Bird Bander*, **11**, 83–86.
- Stewart RLM, Francis CM, Massey C (2002) Age-related differential timing of spring migration within sexes in passerines. *Wilson Bulletin*, **144**, 264–271.
- Strong A, Sherry T (2000) Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology*, **69**, 883–895.
- Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P, Buffa J (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. *Progress in Oceanography*, **49**, 309–329.
- Terborgh J (1989) *Where have all the birds gone? Essays on the conservation and biology of birds that migrate to the American tropics*. Princeton University Press, Princeton, NJ.
- Tryjanowski P, Sparks TH (2001) Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*. *International Journal of Biometeorology*, **45**, 217–219.
- Vahatalo A, Raino K, Lehikoinen A, Lehikoinen E (2004) Spring arrival of birds depends on the North Atlantic Oscillation. *Journal of Avian Biology*, **35**, 210–216.
- Van Vliet AHJ, de Groot RS, Bellens Y *et al.* (2003) The European Phenology Network. *International Journal of Biometeorology*, **47**, 202–212.
- Visser M, Both C, Lambrechts M (2004) Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research*, **35**, 89–110.
- Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London – Series B*, **268**, 289–294.
- Wilson S, Arcese P (2003) El Niño drives timing of breeding but not population growth in the song sparrow (*Melospiza melodia*). *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 11139–11142.
- Winkel W, Hudde H (1997) Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and pied flycatchers (*Ficedula hypoleuca*). *Journal of Avian Biology*, **28**, 187–190.
- Zalakevicius M (2001) Bird migration and the climate: a review of the studies conducted in Lithuania in the context of climate change. *Acta Zoologica Lituanica*, **11**, 200–218.