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RESEARCH ARTICLE

Long-term changes in the seasonal timing of landbird migration on the Pacific Flyway

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ABSTRACT

The seasonal phenology of latitudinal movements is one of the key life-history traits of migratory birds. We used quantile regression to examine long-term changes in the timing of spring and autumn migration in 5 species of migratory passerine birds captured at a banding station in northern California, USA, over a 22 yr period from 1987 to 2008. Our 5 study species included 3 short-distance migrants, Pacific-slope Flycatcher (*Empidonax difficilis*), Orange-crowned Warbler (*Oreothlypis celata*), and Wilson's Warbler (*Cardellina pusilla*); and 2 long-distance migrants, Swainson's Thrush (*Catharus ustulatus*) and Yellow Warbler (*Setophaga petechia*). Median timing of migration advanced in spring for 2 of the 5 species (−2.5 days decade^{-1}) but was delayed during autumn migration for 3 of the species (+2.9 days decade^{-1}). The duration of the migration period also became compressed in some species but more protracted in others. We tested whether annual variation in migration timing was related to 3 indices of regional climatic conditions: the Pacific–North American index, multivariate El Niño–Southern Oscillation index, and North Atlantic Oscillation index. Climate indices explained relatively little of the variation in migration timing ($r^2 < 0.35$), but advances in spring migration and delays in autumn migration were associated with warm, wet conditions during positive phases of the climate indices. The strongest effects of climatic conditions on migration timing were found among short-distance migrants, with the largest changes in timing due to variation in the El Niño–Southern Oscillation and Pacific–North American indices. Linkages between the timing of movements and climatic conditions indicate that passerine birds on the Pacific coast exhibit phenotypic plasticity in their migration timing, but future studies based on experimental methods are needed to test alternative ecological mechanisms.

Keywords: autumn, climate indices, flycatcher, phenology, quantile regression, spring, thrush, timing of migration, warbler

Cambios a largo plazo en la fecha estacional de migración de las aves canoras en el corredor de vuelo del Pacífico

RESUMEN

La fenología estacional de los movimientos latitudinales es uno de los rasgos clave de la historia de vida de las aves migratorias. Usamos regresiones cuantiles para examinar los cambios a largo plazo en las fechas de migración de primavera y otoño en cinco especies de aves paserinas migratorias capturadas en una estación de anillado en el norte de California a lo largo de un período de 22 años desde 1987 hasta 2008. Nuestras cinco especies de estudio incluyeron tres migrantes de corta distancia: *Empidonax difficilis*, *Oreothlypis celata* y *Cardellina pusilla*, y dos migrantes de larga distancia: *Catharus ustulatus* y *Setophaga petechia*. La fecha mediana de migración se adelantó en primavera para 2 de las 5 especies (–2.5 días por década), pero se retrasó durante la migración de otoño para 3 de las 5 especies (+2.9 días por década). La duración del período de migración también se contrajo en algunas especies, pero se prolongó más en otras. Evaluamos si la variación anual en la fecha de migración estuvo relacionada con tres índices de las condiciones climáticas regionales: Pacífico/América del Norte, el índice multivariado El Niño/Oscilación del Sur y la Oscilación del Atlántico Norte. Los índices climáticos explicaron relativamente poco de la variación en la fecha de migración ($r^2 < 0.35$), pero los adelantos en la migración de primavera y las demoras en la migración de otoño estuvieron asociados con condiciones más cálidas y húmedas durante las fases positivas de los índices climáticos. Los efectos más fuertes de las condiciones climáticas sobre la fecha de migración fueron encontrados entre los migrantes de corta distancia, con los mayores cambios en fecha debidos a la variación en los índices de El Niño/Oscilación del Sur y Pacífico/América del Norte. Los vínculos entre las fechas de movimiento y las condiciones climáticas indican que las aves paserinas de la costa del Pacífico muestran plasticidad fenotípica en sus fechas de migración, pero se necesitan futuros estudios basados en métodos experimentales para evaluar mecanismos ecológicos alternativos.

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Palabras clave: atrapamoscas, curruca, fecha de migración, fenología, índices climáticos, otoño, primavera, regresión cuantil, zorzal

INTRODUCTION

Timing of migration is an important life-history trait for migratory birds, and a growing number of field studies have reported long-term changes in the seasonal timing of migratory movements in passerine birds (Gordo 2007, Rubolini et al. 2007, Bitterlin and Van Buskirk 2014). Changes in seasonal phenology may be due to adaptation via a genetic response to a changing environment, but they can be attributed to phenotypic plasticity if variation in timing is linked to environmental conditions (Jonzén et al. 2006, Gienapp et al. 2007). Understanding the patterns and mechanisms of change in timing is relevant to conservation because population declines have been linked to migration strategies of birds (Gilroy et al. 2016), and phenological mismatches with food resources can reduce the seasonal fecundity of migratory birds (Both et al. 2010, Jones and Cresswell 2010, Saino et al. 2011, Mayor et al. 2017).

Past studies of long-term changes in the timing of migratory movements of passerine birds have been limited in several ways. Early studies were often based on records of local experts or bird-watching groups who compiled first arrival dates as an easily recorded metric (Butler 2003, Ledneva et al. 2004, Murphy-Klassen et al. 2005, Swanson and Palmer 2009, DeLeon et al. 2011). Naturalist records are problematic because it is difficult to standardize for observer effort, and the demographic composition of bird populations is usually unknown. First arrival dates are variable and can be sensitive to environmental change (Mills 2005, Murphy-Klassen et al. 2005, Tøttrup et al. 2006b, Rubolini et al. 2007), but they also include anomalous outliers that reduce correlations with mean arrival dates (Sparks et al. 2005, Goodenough et al. 2015, Miles et al. 2017) or estimates of timing based on systematic sampling methods (Miller-Rushing et al. 2008b).

Past studies of migration timing have been mainly focused on the spring season, though autumn movements may show different patterns (Gallinat et al. 2015). Fitness consequences of early arrival in spring are likely linked to acquisition of a territory or mate, the number of nesting attempts in a breeding season, and seasonal declines in reproductive success (Both and Visser 2001). Potential fitness effects of changes in the timing of autumn migration are less clear but may be related to the timing of molt after the breeding season or to predation risk during migratory movements (Lank et al. 2003, Rohwer et al. 2005, Borowske et al. 2017). Early spring arrival coupled with later departure on autumn migration could lead to a longer breeding season for multi-brooded species (Jenni and Kéry 2003, Gordo and Sanz 2006, Van Buskirk et al. 2009, Zelt et al. 2017). Alternatively, advances in the timing of both spring and autumn migration might not lead to changes in the length of the breeding season (Cotton 2003, Thorup et al. 2007). In addition, autumn populations include juvenile birds, which may have different migration strategies than adults (Carlisle et al. 2005, Gill et al. 2014).

The main geographic focus of studies of migration timing has been flyways in Europe or eastern North America where latitudinal migrants cross a series of ecological barriers, including the Mediterranean Sea, the Sahara, and the Gulf of Mexico (Rubolini et al. 2007, Delmore et al. 2012, Bitterlin and Van Buskirk 2014, Cohen et al. 2017). By contrast, the coastlines of the Pacific Flyway provide a more contiguous corridor for migratory movements and may offer better opportunities for wind-assisted migration (Butler et al. 1997). Many migratory passerines in western North America also have the unusual strategy of molt migration, with early departure from breeding sites, feather molt during an extended stopover in the Mexican monsoon region during late summer, and then completion of migration to nonbreeding sites (Rohwer et al. 2005, Carlisle et al. 2009). Population trends for migratory birds in western ecosystems have been relatively stable (Sauer and Link 2011), but long-term advances in migration arrival combined with delays in spring green-up have recently led to increased phenological mismatch for western birds (Mayor et al. 2017).

Phenological studies have sought to identify the key life-history traits that are associated with changes in timing and to determine which climate indices or other environmental correlates are likely to be the strongest drivers of changes in migration phenology. Short-distance migrants often have earlier passage dates, show greater changes in migration timing, and are more responsive to ecological conditions, whereas long-distance migrants are more constrained in the timing of events in their annual cycle (Hagan et al. 1991, Gienapp et al. 2007, Rubolini et al. 2007; but see Jonzén et al. 2006). Large-scale climate indices can be better predictors of ecological processes than local weather conditions (Hallett et al. 2004), but the choice of an appropriate index is not always clear-cut (Knudsen et al. 2007). In northern Europe, migratory birds usually advance spring arrival with increased temperatures and precipitation that are associated with positive phases of the North Atlantic Oscillation index (NAO; Gordo 2007). Among North American birds, changes in the timing of migration have sometimes been linked to NAO or other climate indices (MacMynowski and Root 2007,

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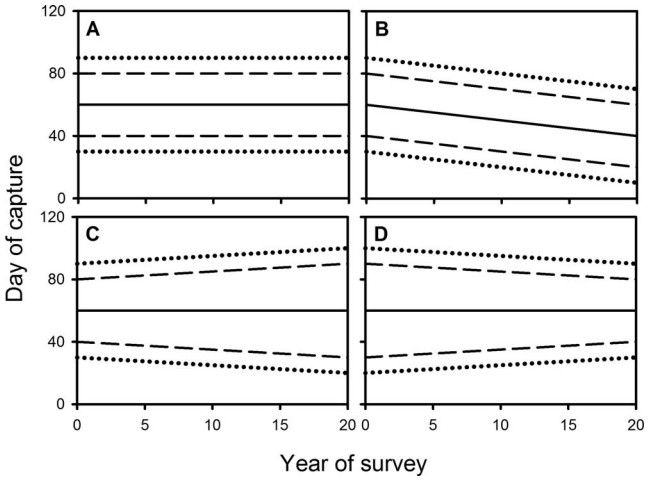


FIGURE 1. Hypothetical scenarios for long-term changes in migration timing: (**A**) no change across all quantiles; (**B**) equal advances across all quantiles; (**C**) protracted migration, in which advances in first arrivals are coupled with delays in later stages of migration; and (**D**) compressed migration, in which delays in first arrivals are coupled with advances in later stages of migration. Solid lines represent 0.50 quantile or median migration dates, dashed lines 0.25 and 0.75 quantiles, and dotted lines 0.10 and 0.90 quantiles.

Miller-Rushing et al. 2008a), but in many cases the relationships have been weak or absent (Marra et al. 2005, Wilson 2007, Van Buskirk et al. 2009, DeLeon et al. 2011).

We examined long-term changes in the migration timing of 5 passerine species at a stopover site in northern California, USA, during a 22 yr period. The present study builds upon past work in 5 ways. First, we investigated changes in migration timing during both the spring and autumn seasons. Second, using birds captured with systematic mist netting at an established banding station, we investigated long-term changes in migration timing. We standardized field effort within and among years, which facilitated comparisons between seasons and among species. Third, we analyzed our capture data with quantile regression to look at changes in different segments of the migration period and in its total duration (Cade and Noon 2003, Knudsen et al. 2007). We predicted that the seasonal timing of migration could change in 4 possible ways (Figure 1): (1) no changes in any quantiles, the *null model* (Wilson 2007); (2) equal changes among all quantiles, leading to *advances or delays in timing* without a change in the duration of the migration period (Tøttrup et al. 2006b, Thorup et al. 2007); (3) differential changes among quantiles whereby advanced first arrivals are coupled with no changes or delays in later stages, leading to a *prolonged migration period* (Van Buskirk et al. 2009, Hedlund et al. 2015, Miles et al. 2017); or (4) differential changes whereby delayed first arrivals are coupled with advancement of later stages, leading to a *compressed migration period* (Martín et al. 2014). Fourth, we examined variation in migration timing in relation to 3 climate indices that affect regional ecological conditions, including one of the first tests of the Pacific–North American index (PNA) as a possible correlate of migration timing. Warm, wet climatic conditions result in faster growth and higher abundance of invertebrate prey (Polis et al. 1997, Studds and Marra 2011), which we predicted would advance the timing of spring migration but delay the timing of autumn migration. Last, we compiled phenological data from available long-term studies to compare rates and patterns of change in the timing of migration at sites across North America.

METHODS

Study Site

Over a 22 yr period (1987–2008), we conducted systematic mist-net sampling and bird banding at Coyote Creek Field Station (hereafter "Coyote Creek"), Santa Clara County, California (37.4365°N, 121.9277°W), a riparian restoration site operated by the San Francisco Bay Bird Observatory. Habitat at the field station included remnant and restored riparian woodlands surrounding a water-overflow channel. Understory vegetation and canopy cover increased in the first decade after the restoration site was established, but habitat structure remained unchanged thereafter, during the second decade of our project. Coastal areas of northern California have a Mediterranean climate, with most rainfall and plant growth occurring from November to March, followed by a dry period of plant senescence from April to October.

Study Species

We investigated 5 species of migratory passerines that were passage migrants but did not breed at Coyote Creek: Pacific-slope Flycatcher (*Empidonax difficilis*), Swainson's Thrush (*Catharus ustulatus*), Orange-crowned Warbler (*Oreothlypis celata*), Yellow Warbler (*Setophaga petechia*), and Wilson's Warbler (*Cardellina pusilla*). All 5 species are small-bodied Neotropical migrants that use forest habitats and riparian thickets during migration. Their diet is mainly insectivorous (occasionally supplemented with nectar or fruits by Swainson's Thrushes and Orange-crowned Warblers). The 5 species are socially monogamous, with a male-territorial breeding system, and usually produce a single brood per season, with occasional double-brooding in some populations in coastal California. Changes in population size can affect estimates of migration timing (Miller-Rushing et al. 2008a), but these 5 species consistently had high numbers of seasonal captures at Coyote Creek.

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Foreign recoveries of banded individuals were relatively rare ($\leq$6 recoveries species^{-1}) but indicated that our 5 study species followed coastal migration pathways. A total of 11 band recoveries were all reported within 200 km of the Pacific coast, but up to 2,000 km north and 140 km south of Coyote Creek (San Francisco Bay Bird Observatory personal communication). To determine breeding and nonbreeding ranges for our 5 study taxa, we used subspecies designations based on plumage and range in coastal California.

Pacific-slope Flycatchers and Cordilleran Flycatchers (*E. occidentalis*) are closely related species that were considered conspecific until 1989 (Lowther et al. 2016). Based on a coastal range and subtle differences in bill morphology, wing shape, and plumage (Pyle 1997), our study population consisted primarily of Pacific-slope Flycatchers, whereas Cordilleran Flycatchers are an inland species found east of Coyote Creek to the Rocky Mountains. Three subspecies of Pacific-slope Flycatchers have been described, but the main subspecies captured in our study was *difficilis*. The breeding range of *difficilis* spans the Pacific coast of North America, and the nonbreeding range includes Baja California and the northern Pacific coast of Mexico.

Swainson's Thrushes breed broadly across northern and northwestern North America, and their nonbreeding range spans from Mexico to South America (Mack and Yong 2000). Swainson's Thrushes captured at Coyote Creek had dorsal plumage with reddish tones and were part of the *ustulatus* group ("russet-backed thrushes") that breed from southeastern Alaska to northern California. Geolocator studies indicate that coastal populations tend to winter in the northern part of their nonbreeding range in Mexico and Central America, whereas birds from inland populations migrate to South America (Delmore et al. 2012, Cormier et al. 2013).

Orange-crowned Warblers have a broad breeding distribution across North America (Gilbert et al. 2010). The main subspecies captured at Coyote Creek was *lutescens*, identified by a lack of contrast between head and upperparts. We also captured a few individuals of the *orestera* subspecies, which have a gray head that contrasts with a yellowish-olive body. The breeding range of *lutescens* is coastal areas of northern California to Alaska, whereas the nonbreeding range is centered in central California and coastal Mexico.

Three groups with 43 subspecies have been described for Yellow Warblers (Lowther et al. 1999). We mainly captured birds from the *aestiva* group at Coyote Creek, based on their yellow crown feathers and small body size (Pyle 1997). Birds from the *aestiva* group breed across most of North America, with a nonbreeding range spanning western Mexico through coastal areas east of the Andes in northern South America (Boulet and Gibbs 2006).

Wilson's Warblers breed across northern North America. Their nonbreeding range includes the southern United States through Central America (Ammon and Gilbert 1999). Three subspecies have been described, but the main subspecies captured at Coyote Creek was *chryseola*, identified by a bright yellow forehead with an orange tinge (Pyle 1997). Genetic and stable isotope data indicate that *chryseola* breeds along the Pacific slope region and coastal California, with a nonbreeding range that includes western Mexico (Paxton et al. 2007, Ruegg et al. 2014). Wilson's Warblers are also unusual in being a "leap-frog" migrant in which northern breeding populations tend to winter at the southern limits of the nonbreeding range.

The geographic distributions of western passerines are poorly known compared to migratory birds in other flyways (Carlisle et al. 2009). Based on current knowledge, all 5 of our study species breed in coastal areas of northern California to Alaska. Pacific-slope Flycatchers, Orange-crowned Warblers, and Wilson's Warblers were considered *short-distance migrants* because their nonbreeding ranges include the southern United States and Mexico, whereas Swainson's Thrushes and Yellow Warblers were considered *long-distance migrants* because they winter in Central America and northern South America.

Study Area and Field Methods

Staff at the San Francisco Bay Bird Observatory directed a year-round banding station at Coyote Creek throughout the 22 yr study period. A standardized protocol for mist-net sampling was established in 1987 with multiple lines of mist nets that sampled an area of approximately 10–14 ha. Net lines consisted of 3 permanent transects with 7–9 nets, 5 permanent transects with 2–3 nets, and a variable number of permanent and temporary single nets. Nets were opened 30 min before local sunrise and left open for 5 hr, weather permitting. To control for variable effort among years, we used capture data only from the subset of nets that were regularly operated every 1–3 days (Barton 2012). Data were not available from spring 1999, spring 2002, and autumn 2000 (Barton 2012).

Observatory staff and trained volunteers captured and banded birds with uniquely numbered metal bands issued by the U.S. Geological Survey. Birds were identified to species by plumage and morphometrics and were aged and sexed when possible (Pyle 1997). All birds were aged as immature (HY: hatch-year) or adult (AHY: after-hatch-year) by patterns of skull pneumatization and molt. Aging of birds by skull patterns was not conducted consistently in the early years of the banding program but was regularly recorded after 1995. The 3 species of warblers are dichromatic and were reliably sexed by plumage. Monomorphic flycatchers and thrushes were not sexed.

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TABLE 1. Median dates of migration and 4–8 wk periods for climate indices used to model long-term changes in the migration timing of 5 passerine species at Coyote Creek Field Station, California, USA, 1987–2008.

Species	Median date of spring migration	Climate index [a]			Median date of autumn migration	Climate index [a]		
		MEI	PNA	NAO		MEI	PNA	NAO
Pacific-slope Flycatcher	May 10	March–April	March	April–May	September 7	July–August	August–September	July
Swainson's Thrush	May 17	March–April	March	May	September 23	July–August	September–October	July
Orange-crowned Warbler	Apr 23	March–April	March	April–May	October 2	July–August	September–October	Aug
Yellow Warbler	May 21	March–April	March	May–June	September 19	July–August	September–October	July
Wilson's Warbler	May 9	March–April	March	April–May	September 13	July–August	September	July

[a] MEI = multivariate El Niño–Southern Oscillation index, NAO = North Atlantic Oscillation index, PNA = Pacific–North American index.

Climate Indices

We selected 3 climate indices that represented integrated measures of regional variation in weather patterns in western North America from 1987 to 2008. We obtained information on the first, the Multivariate El Niño–Southern Oscillation index (MEI), from the Physical Sciences Division of the Earth System Research Laboratory at the National Oceanic and Atmospheric Administration (NOAA; http://www.esrl.noaa.gov/psd). We obtained data on the other 2 climate indices, PNA and NAO (see above), from the Climate Prediction Center at NOAA (http://www.cpc.ncep.noaa.gov). Climate indices describe environmental conditions at a continental or hemispheric scale (Hallett et al. 2004). Here, we focus on the regional effects of the 3 indices for the Pacific Flyway of western North America, which encompassed the breeding, stopover, and nonbreeding sites used by our 5 study species.

MEI assesses long-term climatic dynamics that typically last 9–12 mo (El Niño) or 1–3 yr (La Niña), with a 3–5 yr periodicity (NOAA 2011). MEI has the greatest impact on the continental climate of North America during winter but also affects a small region in the west during summer. Positive phases of MEI (i.e. El Niño conditions) are associated with wetter-than-average winters in northwestern Mexico and the southwestern United States, and with wetter and warmer winters in northwestern South America. Positive phases of MEI are also associated with wetter-than-average summers in the Intermountain West. Climatic dynamics of MEI can have a large effect on ecological conditions encountered by migratory animals on the Pacific Flyway (Polis et al. 1997).

PNA assesses short-term climatic dynamics of ~2 wk (Feldstein 2000, Cash and Lee 2001) and has the greatest impact on climate in North America during spring, autumn, and winter. Positive phases of PNA are associated with warmer-than-average temperatures in Alaska, western Canada, the extreme western United States, and Baja California, but with cooler-than-average temperatures in northern Mexico. PNA can be influenced by the El Niño–Southern Oscillation, with correlations between the positive phases of both indices. PNA has not been modeled previously as a covariate for variation in the timing of bird migration.

NAO, which also assesses short-term climatic dynamics of ~2 wk (Feldstein 2003, 2007), has the greatest impact on climate in North America during spring and winter but also affects a small, confined region in north-central North America during summer. Positive phases of NAO are associated with warmer-than-average springs in the western United States, Baja California, and northwestern Mexico, warmer-than-average summers in the Pacific Northwest and Intermountain West, and warmer-than-average winters in Mexico and the extreme southwestern United States. Moreover, positive phases of NAO are associated with drier-than-average springs and winters in California. The timing of spring arrival advances during positive phases of the NAO for migratory birds in eastern North America (MacMynowski and Root 2007, Van Buskirk et al. 2009) and northern Europe (Gienapp et al. 2007, Gordo 2007).

We used the 22 yr median migration date for each species in spring and autumn to select a 1–2 mo period of climate data to use in our analyses (Table 1). We selected months when we expected climatic conditions to affect departure dates from nonbreeding or breeding sites, or movement rates along migration routes in the Pacific Flyway. For climatic effects prior to migration, we used average climate indices for the 8 wk period prior to the median migration date, which included MEI and NAO during summer and MEI and PNA during winter. For climate effects during migration, we used average climate indices for the 4 wk period surrounding the median migration date, which included NAO in spring and PNA in autumn. If a focal period spanned 2 mo, we averaged monthly indices (PNA and NAO) or used the 2 mo average (MEI).

Statistical Analyses

We divided the year into two 5 mo periods: February–June for spring and July–November for autumn. We dropped January and December from our analyses to exclude the occasional bird that spent a nonbreeding season at Coyote

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TABLE 2. Total numbers of individuals and demographic composition by age and sex classes for 5 passerine species at Coyote Creek Field Station, California, USA, 1987–2008.

		Age class [a]			Sex class [b]		
Species	Total	HY	AHY	U	M	F	U
			Spring migration				
Pacific-slope Flycatcher	401	–	99%	1%	–	–	100%
Swainson's Thrush	2,439	–	100%	<1%	–	–	100%
Orange-crowned Warbler	686	–	100%	<1%	43%	35%	22%
Yellow Warbler	246	–	100%	–	57%	34%	9%
Wilson's Warbler	1,258	–	100%	<1%	58%	33%	9%
			Autumn migration				
Pacific-slope Flycatcher	5,411	97%	2%	<1%	–	–	100%
Swainson's Thrush	558	47%	41%	12%	–	–	100%
Orange-crowned Warbler	627	55%	15%	31%	37%	24%	39%
Yellow Warbler	1,534	67%	14%	18%	28%	21%	51%
Wilson's Warbler	445	56%	26%	18%	60%	22%	19%

[a] HY = hatch-year or immature, AHY = after-hatch-year or adult, U = unknown age.
[b] M = male, F = female, U = unknown sex.

Creek. We used the first capture or recapture of an individual bird per season as the migration date and discarded our few within-season recaptures. Thus, changes in migration timing or in the duration of the migration period were determined by the passage of different birds through the stopover site and were not due to changes in the duration of stopover for an individual. We had limited evidence of local breeding at the study site but excluded any females captured with brood patches and any HY birds from our analyses of spring migration. We report the age and sex composition of our sample of captured birds, but our data were too sparse for separate analyses by demographic class.

MacMynowski et al. (2007) reported preliminary analyses of migration timing for a subset of our study species during the first half of our time series (1983–1997) but focused on first arrival dates during spring and did not control for sampling effort. Here, we used quantile regression to model long-term changes in migration timing for both the spring and autumn seasons (Cade and Noon 2003, Knudsen et al. 2007). We used quantile regression with 0.10, 0.25, 0.50, 0.75, and 0.90 quantiles to evaluate long-term changes in the timing of spring and autumn migration over our 22 yr study period. To control for annual variation in number of captures, we weighted our quantile regressions by the number of individuals captured per season–year combination. We used the "x-y pair" method with 10,000 replicates in the "boot.rq" function of package "quantreg" to bootstrap confidence intervals for model parameters in our quantile regression analyses. To calculate long-term changes in the duration of the migration period, we calculated the difference in number of days between the 0.10 and 0.90 quantiles for 1987 and 2008 as the 2 endpoints of our 22 yr time series. Quantile regression models were fit to capture data with functions of the "quantreg" package in R 2.12.0 (R Development Core Team 2010, Koenker 2011).

To test for phenotypic plasticity in migration timing, we modeled our capture data vs. the 3 climate indices. In a first step, we used linear regression to test for any long-term changes in our climate indices. We then used multiple regression with backward elimination of variables to evaluate the relationships between the median timing of migration and the climate indices. To control for annual differences in the number of captures, we weighted regressions by the number of individuals captured per season–year combination. Starting models included all 3 climate indices during spring and autumn. Model selection was based on Akaike's Information Criterion adjusted for small sample size (AIC_c). We considered alternative models equally parsimonious if $\Delta AIC_c \leq 2$. Models that differed by a single parameter could be within $\Delta AIC_c \leq 2$; therefore, we assessed significance with the unconditional 85% confidence intervals for model-averaged coefficients for each climate index (Arnold 2010). Model selection and model-averaging across alternative models were conducted with tools of the "AICcmodavg" package (Mazerolle 2011).

We compared results from our study with published estimates of long-term trends in migration timing for passerines in North America. We included papers reporting first arrival date, median or mean arrival date, or last departure date based on either captures or observations.

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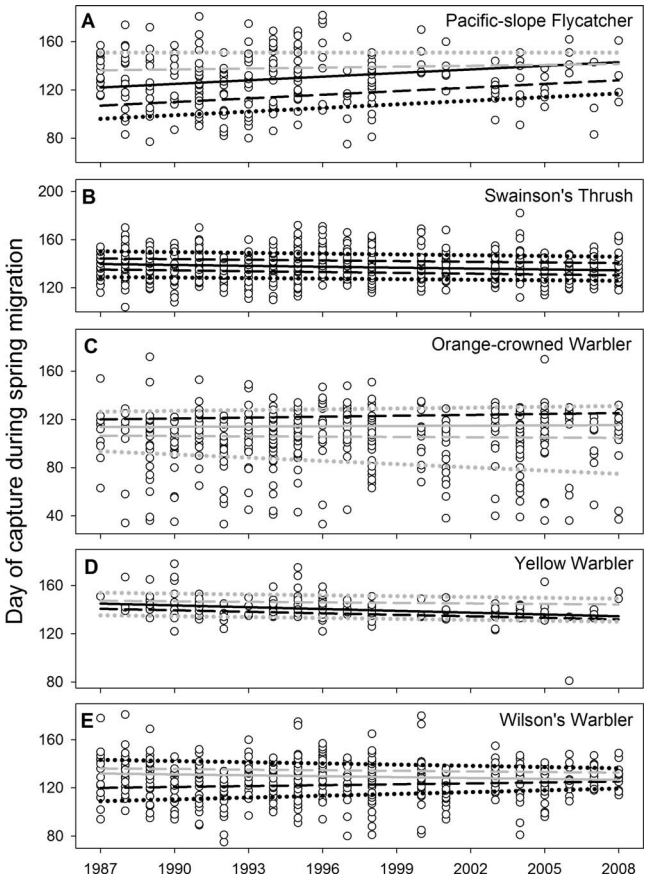


FIGURE 2. Quantile regression of the timing of spring migration (day 121 = May 1) for 5 passerine species captured with systematic mist-net sampling at Coyote Creek Field Station, California, USA, 1987–2008. Circles indicate first capture dates of individual birds per season. Solid lines represent 0.50 quantile or median migration dates, dashed lines 0.25 and 0.75 quantiles, and dotted lines 0.10 and 0.90 quantiles. Slopes significantly different from zero are black, and nonsignificant slopes are gray.

RESULTS

Mist-net Captures

We captured a total of 5,030 and 8,575 individual birds in spring and autumn over the 22 yr sampling period (Table 2). In spring we captured 246–2,439 individuals species^{-1}. In autumn we captured 445–5,411 individuals species^{-1}. Numbers of captures per species varied by season: we captured 4.4× more Swainson's Thrushes and 2.8× more Wilson's Warblers during spring migration, but we captured 13.5× more Pacific-slope Flycatchers and 6.2× more Yellow Warblers during autumn migration. We captured a similar number of Orange-crowned Warblers during both migration seasons.

Birds captured in spring were nearly all aged as adults (AHY), with a few unknown-age birds. Sex ratios in the 3 species of warblers tended to be male biased (F:M = 1:1.2–1.7; Table 2). Age and sex ratios varied among species in autumn. Pacific-slope Flycatchers were the most abundant species in autumn, but almost all captures were immature birds (97% HY), with relatively few adults (2% AHY). A majority of warblers captured in autumn were also immature birds (55–67% HY), with male-biased sex ratios among the subset of known-sex birds (F:M = 1:1.3–2.8; Table 2). Autumn captures of Swainson's Thrushes had a more balanced age ratio with similar percentages of immature (47% HY) and adult birds (41% AHY).

Timing of Migration

Median date of passage was earlier in spring for the 3 short-distance migrants: Pacific-slope Flycatchers, Orange-crowned Warblers, and Wilson's Warblers (April 23–May 10) but was 1–3 wk later for the 2 long-distance migrants: Swainson's Thrushes and Yellow Warblers (May 17–21; Table 1). Similarly, the timing of passage during autumn migration tended to be 1–2 wk earlier among short-distance migrants (September 7–13) than among long-distance migrants (September 19–23), with the exception of Orange-crowned Warblers (October 2).

We found long-term changes in migration timing that varied among the 5 study species and between the 2 migration seasons. Long-term changes were not uniform among the 5 quantiles that described spring or autumn migration (Figures 2 and 3). The rate of change in first arrival dates often differed from the median arrival date and other quantiles (Table 3). Considering median arrival dates for the 5 study species, the timing of spring migration was significantly advanced in Swainson's Thrushes and Yellow Warblers but delayed in Pacific-slope Flycatchers (median: –2.5 days decade^{-1}, range: –5.0 to +10.0), whereas the timing of autumn migration was delayed in Pacific-slope Flycatchers and Yellow Warblers but advanced in Swainson's Thrushes (median: +2.9 days decade^{-1}, range: –1.1 to +5.7).

In the 2 long-distance migrants, we detected slopes that were significantly different from zero but were similar among the different quantiles for timing of spring migration. Advances among the different quantiles led to long-term changes in seasonal phenology but not in the duration of migration for Swainson's Thrushes (–1.5 to –2.5 days decade^{-1}) and Yellow Warblers (–1.4 to –5.0 days decade^{-1}; Figure 2B, 2D). Patterns of change were more variable among the 3 species of short-distance migrants. Advances in first arrivals combined with delays in later stages led to an increased duration of spring migration of +10.6 days decade^{-1} for Orange-crowned Warblers (Figure 2C). By contrast, delays in first arrival combined with advances or little change in later stages led to decreased duration of spring migration for Pacific-slope Flycatchers (–9.5 days decade^{-1}) and Wilson's Warblers (–8.0 days decade^{-1}; Figure 2A, 2E).

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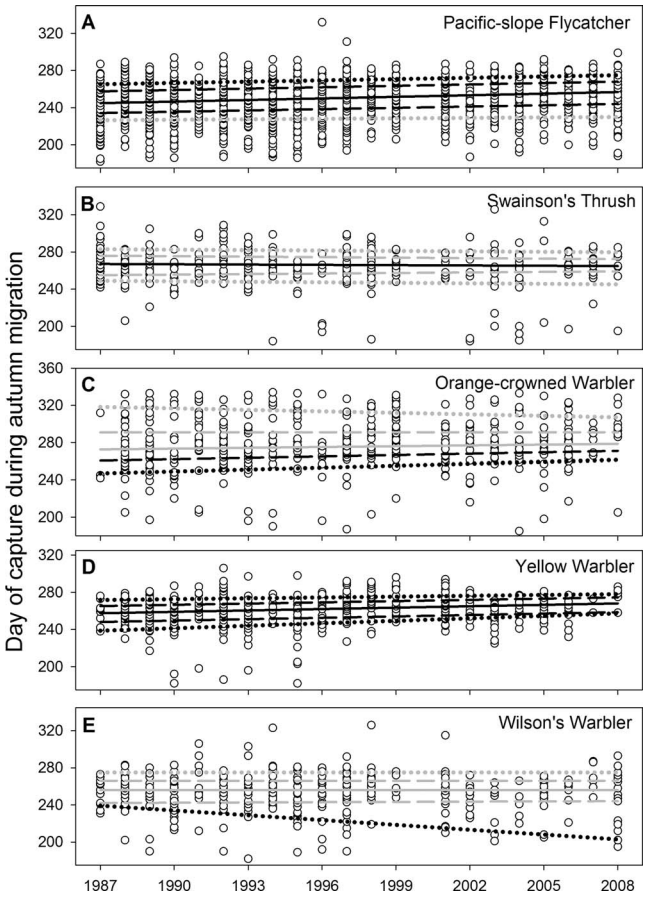


FIGURE 3. Quantile regression of the timing of autumn migration (day 274 = October 1) for 5 passerine species captured with systematic mist-net sampling at Coyote Creek Field Station, California, USA, 1987–2008. See caption of Figure 2 for descriptions.

Patterns of migration timing differed between spring and autumn. Overall, the duration of the autumn migration period averaged 12 days longer than the period of spring migration across our 22 yr study period. Timing of autumn migration was delayed by +3.0 to +8.9 days decade^{-1} in at least 4 quantiles for HY birds in Pacific-slope Flycatchers and Yellow Warblers (Table 3 and Figure 3). Delays of +5.0 to +6.9 days decade^{-1} were significant in 2 quantiles for Orange-crowned Warblers, leading to a decrease in the duration of the migration period of −11.7 days decade^{-1}. On the other hand, advances in the timing of first arrival combined with little changes in later stages led to an increased duration of the autumn migration period by +16.5 days decade^{-1} for Wilson's Warblers, which were largely due to an advance of −17.3 days decade^{-1} in the 0.10 quantile (Figure 1C). Timing of autumn migration showed relatively little change for Swainson's Thrushes, but advances of −1.1 days decade^{-1} were significant for the 0.50 quantile.

Climate Indices

We tested for relationships between migration timing and 3 climate indices: MEI, PNA, and NAO. Two climate indices exhibited long-term directional changes during our 22 yr study period. All monthly combinations of the autumn PNA shifted from negative to positive phases ($\beta = 0.07–0.11$, $r^2 = 0.27–0.40$, $P \leq 0.01$). By contrast, only the August NAO shifted from positive to negative phases ($\beta = -0.05$, $r^2 = 0.21$, $P = 0.03$). The other climate indices did not change significantly during the study period ($\beta = -0.06$ to −0.01, $r^2 = 0.01–0.14$, $P \geq 0.08$). Moreover, climate indices for our 5 mo migration seasons were not correlated ($r = -0.34$ to 0.42, $P \geq 0.05$).

TABLE 3. Slope coefficients (β, SE, and *P* values) from a quantile regression describing long-term changes in the timing of migration (days per decade) for 5 passerine species at Coyote Creek Field Station, California, USA, 1987–2008. Quantiles include the median date of capture (0.50), the interquartile range (0.25 and 0.75), and the 80% confidence interval (0.10 and 0.90). Negative slope coefficients indicate advances in migration timing, whereas positive slope coefficients indicate delays.

	0.10			0.25			0.50			0.75			0.90		
Species	β	SE	*P*≤	β	SE	*P*≤	β	SE	*P*≤	β	SE	*P*≤	β	SE	*P*≤
Spring migration															
Pacific-slope Flycatcher	+10.0	4.2	0.017*	+10.0	2.4	0.001***	+10.0	2.1	0.001***	+2.5	1.4	0.076	±0.0	3.2	1.000
Swainson's Thrush	−1.5	0.4	0.001***	−2.2	0.9	0.016*	−2.5	0.3	0.001***	−1.8	0.8	0.017*	−2.1	0.6	0.001***
Orange-crowned Warbler	−8.9	7.0	0.209	−0.8	2.6	0.750	+0.8	1.2	0.527	+2.5	0.8	0.001**	+2.2	1.6	0.154
Yellow Warbler	−2.5	2.9	0.384	−4.2	0.8	0.001***	−5.0	1.0	0.001***	−1.4	2.3	0.528	−2.4	2.3	0.305
Wilson's Warbler	+5.0	1.1	0.001***	+2.5	0.6	0.001***	−2.5	1.5	0.105	−1.7	1.2	0.171	−3.3	0.6	0.001***
Autumn migration															
Pacific-slope Flycatcher	+1.7	1.1	0.146	+4.7	0.5	0.001***	+5.7	0.9	0.001***	+5.0	0.3	0.001***	+4.6	0.5	0.001***
Swainson's Thrush	−1.8	1.7	0.289	+2.0	1.6	0.216	−1.1	0.5	0.032*	−1.8	1.8	0.338	−1.6	1.5	0.307
Orange-crowned Warbler	+6.9	2.6	0.007**	+5.0	1.7	0.004**	+2.9	2.2	0.193	±0.0	4.5	1.000	−5.4	5.0	0.280
Yellow Warbler	+8.9	0.6	0.001***	+5.0	1.1	0.001***	+5.0	1.0	0.001***	+4.4	1.1	0.001***	+3.0	1.2	0.012*
Wilson's Warbler	−17.3	3.7	0.001***	+0.9	3.8	0.812	±0.0	2.2	1.000	±0.0	1.9	1.000	±0.0	2.4	1.000

* $P < 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

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TABLE 4. Model selection results for alternative models of median dates of spring migration vs. 3 different climate indices for 5 passerine species at Coyote Creek Field Station, California, USA, 1987–2008.

Model [a]	*K*	Dev	ΔAIC_c [b]	w_i	r^2
Pacific-slope Flycatcher					
MEI + PNA	4	131.3	0.0	0.84	0.33
MEI + NAO + PNA	5	130.9	3.3	0.16	0.34
Swainson's Thrush					
NAO	3	97.1	0.0	0.79	0.01
MEI + NAO	4	96.9	3.0	0.18	0.02
MEI + NAO + PNA	5	96.8	6.5	0.03	0.03
Orange-crowned Warbler					
PNA	3	123.5	0.0	0.54	0.19
NAO + PNA	4	120.9	0.6	0.39	0.29
MEI + NAO + PNA	5	120.7	4.0	0.07	0.29
Yellow Warbler					
MEI	3	123.8	0.0	0.61	0.14
MEI + NAO	4	121.9	1.3	0.33	0.22
MEI + NAO + PNA	5	121.5	4.5	0.06	0.24
Wilson's Warbler					
NAO	3	115.3	0.0	0.73	0.14
NAO + PNA	4	114.6	2.4	0.22	0.17
MEI + NAO + PNA	5	113.9	5.3	0.05	0.20

Notes: *K* is the number of model parameters, Dev is the model deviance, ΔAIC_c is the change in Akaike's Information Criterion corrected for small sample size, w_i is the Akaike model weight, and r^2 is the coefficient of determination.

[a] Climate indices: MEI = multivariate El Nino–Southern Oscillation index, PNA = Pacific–North American index, NAO = North Atlantic Oscillation index. Timing of migration was modeled vs. variation in climate indices for the 8 wk period preceding the median migration date or the 4 wk period centered on the median migration date (see Table 2).

[b] Minimum AIC_c: Pacific-slope Flycatcher = 141.9, Swainson's Thrush = 104.6, Orange-crowned Warbler = 131.0, Yellow Warbler = 131.3, Wilson's Warbler = 122.8.

TABLE 5. Model selection results for alternative models of median dates of autumn migration vs. 3 different climate indices for 5 passerine species at Coyote Creek Field Station, California, USA, 1987–2008.

Model [a]	*K*	Dev	ΔAIC_c [b]	w_i	r^2
Pacific-slope Flycatcher					
PNA	3	134.0	0.0	0.77	0.11
MEI + PNA	4	133.7	2.8	0.19	0.12
MEI + NAO + PNA	5	133.6	6.2	0.04	0.13
Swainson's Thrush					
NAO	3	139.2	0.0	0.67	0.05
NAO + PNA	4	138.2	2.1	0.24	0.09
MEI + NAO + PNA	5	136.8	4.2	0.08	0.15
Orange-crowned Warbler					
PNA	3	137.1	0.0	0.77	0.27
NAO + PNA	4	136.9	2.8	0.19	0.28
MEI + NAO + PNA	5	136.6	6.0	0.04	0.29
Yellow Warbler					
PNA	3	139.7	0.0	0.73	0.06
MEI + PNA	4	138.9	2.3	0.23	0.10
MEI + NAO + PNA	5	138.9	5.8	0.04	0.10
Wilson's Warbler					
MEI	3	133.6	0.0	0.79	0.16
MEI + NAO	4	133.4	2.9	0.18	0.17
MEI + NAO + PNA	5	133.4	6.4	0.03	0.17

Notes: *K* is the number of model parameters, Dev is the model deviance, ΔAIC_c is the change in Akaike's Information Criterion corrected for small sample size, w_i is the Akaike model weight, and r^2 is the coefficient of determination.

[a] Climate indices: MEI = multivariate El Nino–Southern Oscillation index, PNA = Pacific–North American index, NAO = North Atlantic Oscillation index.

[b] Minimum AIC_c: Pacific-slope Flycatcher = 141.4, Swainson's Thrush = 146.7, Orange-crowned Warbler = 144.5, Yellow Warbler = 147.1, Wilson's Warbler = 141.0.

Median timing of migration was significantly associated with the regional climate indices, but a relatively low proportion of the variance was explained by climate indices in the spring ($r^2 < 0.34$; Table 4) and autumn seasons ($r^2 < 0.29$; Table 5). Significant relationships between migration timing and the climate indices were mostly found among the 3 short-distance migrant species, Pacific-Slope Flycatcher, Orange-crowned Warbler, and Wilson's Warbler ($r^2 = 0.12–0.35$). Migration timing was not related to climate indices for the 2 long-distance migrant species, Swainson's Thrush and Yellow Warbler ($r^2 < 0.15$).

Parameter estimates from top-ranked models indicated that spring migration was advanced in response to positive phases of the climate indices (Figure 4A–4C), whereas autumn migration tended to be delayed, at least for PNA (Figure 4D–4F). Advances in timing of spring migration were associated with warm, wet conditions during positive phases of the climate indices, indicated by negative slopes for 5 of 6 significant coefficients (Figure 4A–4C). One exception to the general pattern of advances was a delay in the timing of spring migration associated with positive indices of PNA for adult Pacific-slope Flycatchers (+5.7 days SD^{-1}; Figure 4B). We detected fewer relationships between the timing of autumn migration and the 3 climate indices (Figure 4D–4F). Delays in the timing of autumn migration were associated with positive values of PNA for 3 of 5 species (Figure 4E). Unexpectedly, advances in the timing of autumn migration were associated with positive values of MEI for Wilson's Warblers (–2.4 days SD^{-1}; Figure 4D). Timing of autumn migration was not associated with NAO for any of the 5 passerine species (Figure 4F).

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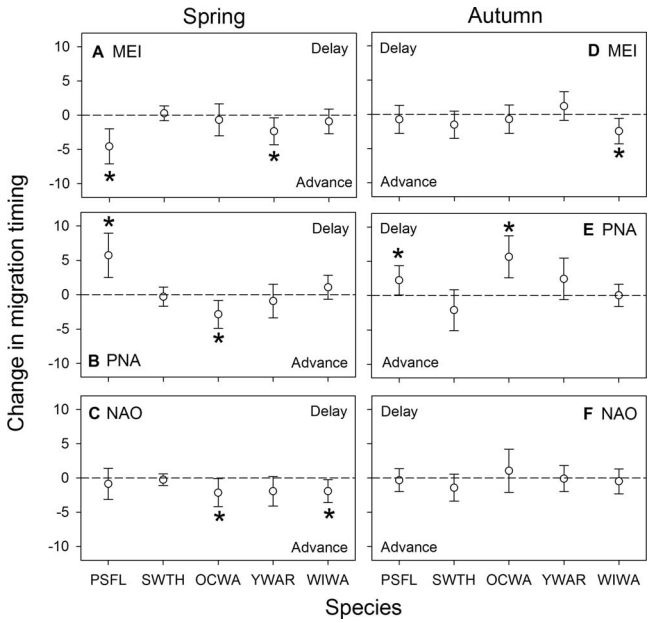


FIGURE 4. Model-averaged estimates of changes in timing during spring and autumn migration vs. climate indices at Coyote Creek Field Station, California, USA, 1987–2008. Changes in migration timing are reported in days per SD of the climate index ± unconditional 85% confidence interval (CI), and asterisks indicate CIs that do not include zero. Abbreviations: PSFL = Pacific-slope Flycatcher, SWTH = Swainson's Thrush, OCWA = Orange-crowned Warbler, YWAR = Yellow Warbler, and WIWA = Wilson's Warbler; MEI = multivariate El Niño–Southern Oscillation index, PNA = Pacific–North American index, and NAO = North Atlantic Oscillation index.

Patterns and Rates of Change across Locations

We compiled estimates of long-term changes in migration timing for passerine birds in North America (Table 6). Overall, most birds have not shown temporal trends in changes in migration timing during spring (range: 40–88%) or autumn (range: 40–73%). Considering the subset of species with significant temporal trends, more are exhibiting advances (median: 39%, range: 13–47%, $n = 13$ locations) than delays (median: 3%, range: 0–20%) during spring migration. The opposite is true for autumn migration; more species are exhibiting delays (median: 37%, range: 18–60%, $n = 5$ locations) instead of advances (median: 9%, range: 0–15%). Our estimates of the rate of change for our study species at Coyote Creek indicated a median advance of –2.5 days decade^{-1} for spring migration (range: –5.0 to +10.0, $n = 5$ species) but a median delay of +2.2 days decade^{-1} for autumn migration (range: –1.1 to +5.7). Timing of migration in North America has been advancing in spring at median rates ranging from –0.2 to –4.4 days decade^{-1} ($n = 13$ studies), whereas studies of autumn migration have reported delays with median rates ranging between +0.8 and +3.0 days decade^{-1} ($n = 5$ studies).

DISCUSSION

We investigated long-term changes in migration timing in 5 species of migratory birds captured at a coastal stopover site on the Pacific Flyway and used standardized methods for systematic mist netting to directly compare patterns and rates of change among species and between seasons. Our study resulted in 3 major findings. First, we found evidence of long-term changes in migration timing in birds captured at the Coyote Creek banding station. The general patterns were advances in timing of spring migration but delays in autumn migration. Use of quantile regression allowed us to model the total distribution of passage times. First arrival and median arrival dates showed different patterns of change, with variation among species in expansion or contraction of migration periods. Thus, our empirical results for 5 species of migratory passerines were consistent with 3 hypothetical scenarios for possible changes in migration timing (Figure 1B–1D) but did not support the null model (Figure 1A). Second, up to one-third of the annual variation in migration timing was explained by climate indices, which suggests that migration timing is phenotypically plastic in western passerines. Variations in migration timing were most strongly affected by climate indices associated with regional conditions on the Pacific coast (MEI and PNA), whereas a third index for the North Atlantic was less important (NAO). Finally, migration distance affected responses of these species to variation in climatic conditions. Three species of short-distance migrants had earlier passage dates, more variable changes in migration timing, and stronger responses to climatic variation. By contrast, 2 species of long-distance migrants had small but consistent changes in migration timing but were not affected by variation in the 3 climate indices.

Long-term Changes in Migration Timing

Comparisons of migration timing could be affected by differences in migration strategies within or among species, or by the ecological barriers encountered by migratory birds in different flyways (Rohwer et al. 2005, Carlisle et al. 2009, Delmore et al. 2012). Methods can also be a factor if comparisons are based on first observed arrival dates instead of median dates of passage for captured birds, if studies differ in the start and duration of the time period, or depending on the analytical technique (Gordo 2007, Knudsen et al. 2007, Goodenough et al. 2015). Despite these possible sources of heterogeneity, the general patterns from our field site in California were consistent with past reports of seasonal timing of migration for passerines in North America.

Short-distance migrants had earlier passage dates than long-distance migrants at Coyote Creek, consistent with patterns reported from other banding stations in

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TABLE 6. Long-term studies of changes in the seasonal timing of migration for passerine birds in North America. Negative rates of change indicate advances in migration timing, and positive rates indicate delays.

Location	Start year	Years (*n*)	Data [a]	Metric [b]	Species (*n*) [c]	Percentage of species with a significant change in timing			Rate of change in timing (days decade^{-1}) [d]		Source
						Advance	None	Delay	Median	Range	
Spring migration											
Continental	2001	12	Obs	MAD	48	52%	46%	2%	−4.4	−17.5 to +7.2	Mayor et al. 2017
California	1987	22	Cap	MAD	5	40%	40%	20%	−2.5	−5.0 to +10.0	**This study**
Massachusetts	1932	62	Obs	FAD	~79	47%	49%	4%	−2.2	−17.1 to +3.2	Butler 2003
Massachusetts	1970	33	Obs	FAD	14	21%	79%	0%	−1.8	−7.8 to +3.4	Ledneva et al. 2004
Minnesota	1971	36	Obs	FAD	25	24%	76%	0%	−1.6	−7.8 to +3.4	Swanson and Palmer 2009
Wisconsin	1936	61	Obs	FAD	11	45%	45%	9%	−1.2	−3.0 to +2.3	Bradley et al. 1999
New York	1967	42	Obs	FAD	48	40%	56%	4%	−0.8	−4.1 to +2.5	DeLeon et al. 2011
New York	1967	45	Obs	FAD	33	39%	58%	3%	−0.7	−2.5 to +2.5	Zelt et al. 2017
Massachusetts	1970	33	Cap	MAD	32	25%	75%	0%	−0.7	−3.6 to +1.0	Miller-Rushing et al. 2008a
Illinois	1976	27	Obs	FAD	8	13%	87%	0%	−0.6	−8.6 to +2.4	Strode 2003
Ontario	1975	26	Cap	MAD	13	15%	85%	0%	−0.5	−4.1 to +2.1	Mills 2005
Manitoba	1939	63	Obs	FAD	39	15%	85%	0%	−0.5	−3.0 to +1.4	Murphy-Klassen et al. 2005
Pennsylvania	1961	40	Cap	MAD	32	13%	88%	0%	−0.5	–	Marra et al. 2005
South Dakota	1971	36	Obs	FAD	25	28%	64%	8%	−0.2	−3.3 to +2.5	Swanson and Palmer 2009
Autumn migration											
Rhode Island	1960	48	Cap	MAD	19	0%	63%	37%	+3.0	–	Smith and Paton 2011
California	1987	22	Cap	MAD	5	0%	40%	60%	+2.9	−1.1 to +5.7	**This study**
New York	1967	45	Obs	LDD	33	9%	73%	18%	+1.1	−5.2 to +6.6	Zelt et al. 2017
Massachusetts	1969	47	Cap	MAD	37	11%	62%	27%	+1.0	−5.2 to +2.6	Stegman et al. 2017
Ontario	1975	26	Cap	MAD	13	15%	46%	38%	+0.8	−4.4 to +5.8	Mills 2005

[a] Cap = captures, Obs = observations.
[b] FAD = first arrival date, MAD = mean or median arrival date, LDD = last departure date.
[c] Number of migratory passerine species.
[d] Median and range for rate of change in timing for all migratory passerines. Rates for Butler (2003) are based on the subset of passerine species with significant trends.

North America (Hagan et al. 1991, Mills 2005, Van Buskirk et al. 2009). Long-term changes in migration timing were heterogeneous among our 5 study species, but advances in spring, delays in autumn, and median rates of change of about 2–3 days decade^{-1} were consistent with past reports for other migratory passerines. Median changes of –2.5 days decade^{-1} in spring and +2.9 days decade^{-1} in autumn for migratory birds at Coyote Creek are among the fastest rates of change in phenology for any location in North America (spring: –0.2 to –4.4; autumn: +0.8 to +3.0; Table 6). In Europe, changes in timing have included advances of up to –2.7 days decade^{-1} for spring migration (Hüppop and Hüppop 2003, Stervander et al. 2005, Tøttrup et al. 2006a, Sparks et al. 2007) and delays of up to +1.6 days decade^{-1} for autumn migration (Cotton 2003, Tøttrup et al. 2006b, Sparks et al. 2007).

Mechanisms for Changes in Migration Timing

Coppack and Both (2002) proposed 3 alternative mechanisms to explain advances in the timing of spring migration: (1) birds could migrate for shorter periods if nonbreeding sites are closer to breeding sites, (2) birds could depart from nonbreeding sites earlier if feeding conditions are good, or (3) birds could increase the speed of spring migration. One drawback for phenological studies based on captures of passage migrants at a stopover site is that the sample population may be a heterogeneous mixture of birds from different demographic classes or sites (Kelly 2006, Ruegg et al. 2014). Thus, a fourth mechanism for changes in migration timing is that (4) different segments of a population may be using different migration strategies. All 4 mechanisms are plausible explanations for advances in spring migration and delays in autumn migration that we observed.

Breeding and nonbreeding ranges of migratory passerines have been expanding and shifting poleward in North America (Auer and King 2014, Princé and Zuckerberg 2015) and Europe (Potvin et al. 2016). For example, the *lutescens* subspecies of Orange-crowned Warblers has recently expanded its nonbreeding range northward into San Diego County in California (Unitt 2004), which may explain advances in the early stages of migration that led to a protracted period of spring migration. Timing of

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departure from breeding or nonbreeding grounds was unknown for the passage migrants in our study (Kelly 2006) but has the potential to determine variation in the timing of arrival at a stopover site (Ouwehand and Both 2017). Advances in departure on spring migration are related to precipitation and effects on food resources at nonbreeding sites (Studds and Marra 2011, Zuckerberg et al. 2015). Conversely, timing of departure on autumn migration can be related to timing of breeding and completion of the last nesting attempt (Mitchell et al. 2012). The duration of the migration period was shorter during spring than during autumn at Coyote Creek, which is consistent with faster movement rates of western passerines during spring migration (La Sorte and Fink 2017). Migration speed in eastern North America is related to temperature, with faster migration in warmer temperatures, especially among species with slower rates of movement (Marra et al. 2005, Hurlbert and Liang 2012).

Our sample of birds captured with systematic mist netting exhibited seasonal differences in relative abundance, as well as variation in age and sex ratios. For example, we captured 3–4 times more Swainson's Thrushes and Wilson's Warblers during spring migration, but 6 times more Yellow Warblers in autumn. In the case of Pacific-slope Flycatchers, we captured different segments of the population in the 2 seasons: adult birds that passed through in spring did not return by the same route in autumn, when we captured 97% immature birds. Delays in spring arrival led to compression of spring migration among adult flycatchers (Mayor et al. 2017, present study), whereas timing of autumn migration was delayed in HY birds. Seasonal variation in numbers of birds captured may be driven by changes in migration behavior or routes (Delmore et al. 2012, La Sorte et al. 2014). Age ratios are often strongly biased toward immature birds among captures of autumn migrants at coastal banding stations (Ralph 1971, Taylor et al. 1994), presumably because adults use different migration routes and are unavailable for capture. Western birds use coastal sites at low elevations during spring migration but switch to more inland routes at higher elevations during autumn migration (La Sorte et al. 2014), which may be associated with a molt migration strategy (Rohwer et al. 2005, Wiegardt et al. 2017). Finally, long-term changes in migration timing could also be driven by individual strategies among birds of different age classes. Changes in migration timing among Black-tailed Godwits (*Limosa limosa*) were due to earlier arrival among new recruits, whereas individual arrival dates of experienced breeders remained highly consistent (Gill et al. 2014).

Sex-specific variation in migration strategies could also play a role in migration timing. Spring captures of warblers had a male-biased sex ratio at Coyote Creek, and male warblers usually precede females northward on spring migration (Francis and Cooke 1986, Otahal 1994, 1995). Thus, climate change might be predicted to have a greater effect on the timing of migration for males than for females. Earlier movements of males but not of females can result in a protracted period of spring migration (Hedlund et al. 2015), which we observed among Orange-crowned Warblers. Conversely, a similar rate of change in both sexes could lead to shifts in timing but not in the duration of migration (Bauböck et al. 2012), which we observed in Yellow Warblers.

Passage migrants at Coyote Creek could also have been a heterogeneous mixture of birds from different breeding or nonbreeding sites. In Wilson's Warblers, populations in the southern part of the nonbreeding range have earlier timing of spring migration (Ruegg et al. 2014). On the other hand, Yellow Warblers from northern breeding sites and Orange-crowned Warblers and Common Yellowthroats (*Geothypis trichas*) from southern breeding sites have earlier passage dates during autumn migration (Kelly 2006). Most of our study species have nonbreeding ranges that span a latitudinal gradient of environmental conditions. Climatic conditions in Mexico follow a north–south gradient of dry to moist, and El Niño or La Niña events tend to affect ecological conditions in the northern part of the range. Bird populations from separate breeding and nonbreeding populations may be exposed to different ecological conditions, and changes of timing for different subsets of a migratory population might help explain our observations of compressed and protracted migration periods.

Climate Indices and Migration Distance

Timing of migration was phenotypically plastic among migratory birds at Coyote Creek because timing was affected by regional indices of climatic conditions. Up to one-third of the variation in migration timing was explained by the 3 climate indices that we tested ($r^2 =$ 0.01–0.34, present study), which is comparable to estimates from other studies of avian migration in North America ($r^2 = 0.18$–0.46, MacMynowski and Root 2007; $r^2 = 0.13$–0.21, Miller-Rushing et al. 2008a). The climate indices with the greatest effect on migration timing at our study site were MEI and PNA, which have relatively short-term effects (about 1–3 yr) on the regional climatic conditions on the Pacific coast. We found that the timing of spring migration was advanced during phases of climate indices associated with higher temperatures and rainfall along the migration route in the Pacific Flyway and at nonbreeding sites in Mexico. Our results agree with advances in spring migration among passerines in northern Europe that are commonly associated with warm, wet conditions during positive phases of NAO (Gordo 2007).

Annual variation in the climate indices had less effect on the timing of autumn migration at Coyote Creek, but we

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found that warm, wet conditions tended to lead to delays in autumn passage. Wilson's Warbler was the only species in which climate indices led to advances in autumn migration; but this species is also unusual in being a "leap-frog" migrant in which northern breeding populations have earlier migration dates (Kelly 2006). NAO had less effect on migration timing for western passerines at our study site than the other 2 indices of climate change. Changes in migration timing for eastern passerines are sometimes linked to NAO (MacMynowski and Root 2007, Wilson 2007, Miller-Rushing et al. 2008a), but more often the relationship between migration timing and NAO have been weak or absent for birds in North America (Marra et al. 2005, Wilson 2007, Van Buskirk et al. 2009, DeLeon et al. 2011). We recommend use of MEI and PNA for future tests of climatic conditions in relation to the seasonal phenology of western birds.

The relative effect of climate indices on migration timing also differed between short- and long-distance migrants. The 3 species of short-distance migrants arrived earlier in spring migration and departed later in autumn migration, showed greater long-term changes in migration timing, and had the strongest relationships between migration timing and climatic conditions. By contrast, the 2 species of long-distance migrants arrived later in spring, showed less long-term change in migration timing, and had timing unaffected by climatic conditions. Our results agree with previous findings that long-distance migrants may be less sensitive than short-distance migrants to weather conditions on the migratory path (Hüppop and Hüppop 2003, Stervander et al. 2005, Gienapp et al. 2007, MacMynowski and Root 2007). Two hypotheses may account for the observed patterns. First, phenological cues may differ as a function of migration distance, with migration timing affected by climate in short-distance migrants but by photoperiod or endogenous cues in long-distance migrants (Hagan et al. 1991). Alternatively, both groups of birds may be sensitive to variation in climatic conditions, but local conditions may be a better predictor of conditions elsewhere in the migration route for short-distance migrants, and less reliable as cues for long-distance migrants (Van Buskirk et al. 2009, Senner 2012).

Conclusions

We have presented evidence of long-term changes in the migration timing of birds at a stopover site in California that were weakly associated with regional climate indices, but the causal relationships with ecological drivers remain unknown. Better data on migratory behavior are needed to identify sites where ecological conditions are likely to affect migration timing, but our understanding of the distributions, routes, and migration strategies of western birds remains incomplete (Carlisle et al. 2009). Patterns of migratory connectivity are starting to emerge with new data from population genetics (Boulet and Gibbs 2006, Ruegg et al. 2014), stable isotopes (Rohwer et al. 2005, Kelly 2006, Paxton et al. 2007), and movement tracks from birds with geolocators (Delmore et al. 2012, Cormier et al. 2013).

Like many long-term studies of bird migration, our study used observational approaches to document long-term changes in seasonal phenology and test the effects of climatic conditions. Experimental methods are needed to better understand underlying mechanisms and ecological drivers of variation in migration timing. For example, food supplementation at nonbreeding sites can lead to earlier departure on spring migration (Bridge et al. 2010, Danner et al. 2015). Conversely, variation in breeding strategies can affect the timing of molt and departure on autumn migration (Mitchell et al. 2012, Borowske et al. 2017). Finally, it is unclear whether long-term changes in the timing or duration of migration are affecting population dynamics of western birds (Carlisle et al. 2009, Mayor et al. 2017). Birds that experience delays or advances may be more vulnerable to trophic mismatches, whereas compression in migration timing may increase vulnerability to environmental perturbations. Future studies should examine the potential effects of range dynamics on the timing of migration, the ecological mechanisms driving annual variation in migratory phenology, and the consequences of changes in timing for population viability.

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Ethics statement: The field project was conducted under permits for scientific research on wild birds, including federal banding permits from the USGS Bird Banding Lab and state permits from the California Department of Fish and Wildlife. Capture and marking procedures were conducted in compliance with the Guidelines to the Use of Wild Birds in Research.

Author contributions: G.G.B. and B.K.S. conceived the project. G.G.B. supervised fieldwork during later years of the project, handled data management, and analyzed the long-term data. B.K.S. and G.G.B. prepared the manuscript.

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