

STOPOVER ECOLOGY OF FIVE SPECIES OF MIGRATORY SONGBIRDS AT A
COASTAL SITE IN THE PACIFIC FLYWAY

by

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Abstract

The migratory period is a critical time for birds. Population declines in long-distance migratory birds have been associated with trophic mismatches among climate change, timing of food availability, and timing of migratory movements. Studies on migratory songbirds have been limited to eastern North America and Europe, and migration strategies of birds may differ along the Pacific flyway. We evaluated the stopover ecology of five species of migratory songbirds at a coastal site in northern California. We found variation in changes in timing of spring migration, but consistent changes in timing of autumn migration over a 22-year period. Timing of spring migration advanced for Swainson's Thrushes (*Catharus ustulatus*) and Yellow Warblers (*Setophaga petechia*), was compressed for Pacific-slope Flycatchers (*Empidonax difficilis*) and Wilson's Warblers (*Cardellina pusilla*), but was protracted for Orange-crowned Warblers (*Oreothlypis celata*). In contrast, timing of autumn migration was delayed for Pacific-slope Flycatchers, Orange-crowned Warblers, and Yellow Warblers, but was protracted for Wilson's Warblers. Warm, wet conditions were associated with advanced spring migration, and warm, dry conditions were associated with delayed autumn migration. Changes in timing of migration related to climate conditions were strongest for Pacific-slope Flycatchers and Orange-crowned Warblers. Stopover duration of our five study species was longer than songbirds in eastern flyways, and on average, was longer in spring than autumn. Pacific-slope Flycatchers and Yellow Warblers had longer stopovers in spring, whereas Swainson's Thrushes and Wilson's Warblers stopped had longer stopovers in autumn. Birds captured at low body mass had longer stopovers in spring and autumn. Migratory birds in western North America may have different migration strategies because of differences in climate and geography, but more study is needed to discover migratory routes and compare our results to other stopover sites along the Pacific flyway. Understanding differences in migration strategies of different populations of the same species are important in directing conservation efforts, especially in light of ongoing climate change.

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Dedication

I dedicate my thesis to migratory birds. I am continuously fascinated by and compelled to understand the complexity of your lives, and this study has fueled this passion.

Chapter 1 - Introduction

The migratory period is a critical time for birds. Migration is physiologically stressful, and mortality rates can be high compared to other parts of the annual cycle (Sillett and Holmes 2002). Migration timing and variation in routes have been associated with changing climate, food availability, and geographic barriers (Stutchbury et al. 2009, Bridge et al. 2010, Studds and Marra 2011). Carry-over effects from migration to other parts of the annual cycle can affect timing of arrival on breeding sites, reproductive success, and annual survival rates (Møller 1994, Lozano et al. 1996, Hasselquist 1998, Calvert et al. 2009, McGowan et al. 2011).

Long-distance migratory birds are declining, and ongoing declines have been associated with mismatches caused by climate change and timing of food availability (Both et al. 2006, 2010, Jones and Cresswell 2010, Saino et al. 2011). A growing number of studies have assessed migratory strategies world-wide, but many have focused on birds in Europe and eastern North America. While we have gained tremendous insight to migration strategies of birds, birds in western North America may have different migration strategies compared to those of eastern North America (Kelly and Hutto 2005). Birds in western North America, especially coastal migrants, have restricted geographic ranges to the extreme west, often consist of different subspecies, and have complex migration strategies, including molt-migration (Butler et al. 2002, Rohwer et al. 2005, Pyle et al. 2009), variation in routes among different populations (Paxton et al. 2007), and leapfrog or elliptical patterns of migration (Bell 1997, Butler et al. 1996, Hutto 2000, Kelly et al. 2002). Last, Pacific coastal migrants have fewer geographic barriers that are prominent in the interior west and eastern North America, such as the Atlantic Ocean, Gulf of Mexico, and Great Lakes.

The goal of this study was to investigate the stopover dynamics for five species of migratory songbirds over a 22-year period at a stopover site in northern California. My thesis is divided into four chapters. Here, I introduce general knowledge on bird migration as a study system. In chapter two, I examine long-term changes in timing of migration related to climatic conditions, and describe the age and sex composition of each of the five species in spring and autumn. In chapter three, I contrast three quantitative methods used to estimate stopover duration, examine variation in stopover duration among species and between seasons, and assess

how body mass at first capture affects stopover duration. In chapter four, I synthesize the main results of my study and their implications for conservation of migratory birds.

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Chapter 2 - Ecological correlates of long-term changes in the seasonal phenology of migratory songbirds

Gina G. Barton and Brett K. Sandercock

Abstract

Climate change has had widespread impacts on the seasonal phenology and geographic distributions of plants and animals. One hypothesized mechanism driving declines of long-distance migratory birds is mismatches between changes in climate and timing of food availability during migration. We examined the changes in timing of spring and autumn migration in five species of migratory songbirds, and the response of migration timing to regional climate conditions over a 22-year period in northern California. Our project is one of the first studies of migratory timing on the Pacific coast, and we found heterogeneous changes between seasons in the timing of migration, with greater variability in spring than in autumn. In spring, timing of migration advanced and the migratory period became compressed or protracted. In autumn, we found mostly delays in timing of migration. Responses of timing of migration to regional climate conditions were relatively consistent among five songbird species. Advances in timing of spring migration were most often associated with warm, wet conditions, and delays in timing of autumn migration were most often associated with warm, dry conditions. Variation in the timing of migration was most often associated with El Niño Southern Oscillation and Pacific/North American climate indices, with the strongest effects in migration timing for Pacific-slope Flycatchers (*Empidonax difficilis*) and Orange-crowned Warblers (*Oreothlypis celata*). Regional climate conditions were key drivers for phenological events for western songbirds, and may be increasingly important because of potential changes in the intensity and periodicity of key climate indices.

Introduction

Ecological impacts of climate change are evident in a diverse range of organisms. Climate change has impacted geographic distributions and the seasonal phenology of life history events of plants and animals. Geographic distributions have shifted poleward for many butterflies and birds (Parmesan et al. 1999, Hitch and Leberg 2007, Doswald et al. 2009, Visser

et al. 2009). Seasonal phenology has generally advanced in the spring, including the timing of leaf emergence, flowering, fruiting, arthropod emergence, and migration and breeding of birds (Bradley et al. 1999, Peñuelas et al. 2002, Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003). Rates of change in seasonal phenology can vary among trophic levels (Parmesan 2007), which may lead to mismatches between the timing of life history events, such as migratory movements and peak food availability (Visser et al. 2006, Jones and Cresswell 2010). Migratory birds may be particularly susceptible to phenological mismatches if the effects of climate change differ among latitudes, with greater rates of change projected to occur at higher latitudes (IPCC 2007). Many populations of long-distance migratory birds are declining, and ongoing declines have been associated with mismatches caused by changes in climate and timing of food availability (Both et al. 2006; 2010, Jones and Cresswell 2010, Saino et al. 2011).

A growing number of long-term studies have evaluated the effects of climate change on timing of migration movements, and have mainly focused on birds in eastern North America (Miller-Rushing et al. 2008, Van Buskirk et al. 2009) and Europe (Hüppop and Hüppop 2003, Jonzén et al. 2006). Timing of spring migration has generally advanced among songbirds in these regions (Jonzén et al. 2006, Thorup et al. 2007, Van Buskirk et al. 2009). Further, advances in timing of spring migration have been associated with positive phases of the North Atlantic Oscillation climatic index (Hüppop and Hüppop 2003, Jonzén et al. 2006, Miller-Rushing et al. 2008). Past studies have been limited in scope in three ways. First, previous studies have investigated spring migration but few have assessed changes in timing of autumn migration (Jenni and Kéry 2003, Sparks et al. 2007, Van Buskirk et al. 2009). Second, mean passage dates (or median) or first arrival dates have been the main metrics used to quantify changes in migration timing, but fail to account for potential changes in the duration of the migratory period (Cotton 2003, Hüppop and Hüppop 2003, Miller-Rushing et al. 2008). Last, most studies have pooled differences in age and sex classes although differential migration is common in migratory birds (Francis and Cooke 1986), and different age and sex classes may vary in their responses to climate conditions (Saino et al. 2004, Balbontín et al. 2009).

We examined long-term changes in the timing of migration in five species of songbirds over a 22-year period at a stopover site in northern California. Our study is one of the first long-term analyses in the Pacific flyway examining both spring and autumn migration. We use quantile regression as a new approach for examining changes in timing of migration over the

entire migratory period, which improves upon estimates of changes based on first arrival dates (<1%) or central tendency alone (50%; Kovács et al. 2012). We tested for four hypothetical patterns of change in timing of migration (Fig. 2.1): (1) no changes in the timing of migration among all quantiles, (2) equal changes in the timing of migration among all quantiles, leading to overall advances in timing of migration, (3) differential changes in the timing of migration with advances in first arrivals coupled with delays in later stages leading to a prolonged migratory period, or (4) differential changes in the timing of migration with delays in first arrivals coupled with advances in later stages leading to a compressed migratory period. Last, we examine the response of timing of migration in relation to three regional climate indices, including the first test of the Pacific/North American climate index. Warm, wet climate conditions have been found to result in greater abundances and faster growth rates of insects (Polis et al. 1997, Bale et al. 2002, Studds and Marra 2011). We predicted that phases of climate indices associated with warm, wet conditions would result in advances in timing of spring migration, but delays in timing of autumn migration.

Methods

Study Site

We conducted systematic mist-net sampling and banding at the Coyote Creek Field Station (hereafter, Coyote Creek), a riparian restoration site of the San Francisco Bay Bird Observatory (hereafter, SFBBO), over a 22-year period from 1987 to 2008. Coyote Creek is located in Santa Clara County, California (37°28'N, 122°03'W), and the habitat includes remnant and restored riparian woodlands surrounding a water overflow channel. Understory vegetation and canopy cover generally increased for the first decade after establishment, but then remained constant from the mid-1990s to the end of our study (SFBBO, *unpublished reports*). Coastal areas of California have a Mediterranean climate with most rainfall and plant growth from November to April and a dry period of plant senescence from May to October.

Study Species

We investigated five migratory songbird species which are passage migrants that do not breed at Coyote Creek and had the greatest number of seasonal captures: 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*). To determine breeding and nonbreeding ranges for our study taxa, we used subspecies designations based on plumage and range of these species in coastal California.

The breeding range of Pacific-slope Flycatchers includes southeastern Alaska to southern California, and their nonbreeding range includes southern Baja California and western Mexico (Lowther 2000). Cordilleran Flycatchers (*E. occidentalis*), a closely related species, were considered conspecific prior to 1989 (AOU checklist). Our study population consisted primarily of Pacific-slope Flycatchers because this species breeds along the Pacific coast, whereas Cordilleran Flycatchers are an inland species found east of Coyote Creek to the Rocky Mountains. Of three described subspecies and ranges, the subspecies captured in our study was *difficilis*.

Swainson's Thrushes breed from Alaska through Canada to western and northeastern United States, and their nonbreeding range includes central Mexico through South America (Mack and Yong 2000). Banding and genetic data suggest that Pacific coast populations of Swainson's Thrush (*ustulatus* group) breed from coastal southeastern Alaska to southern California, and their nonbreeding range includes Mexico through Central America (Ruegg and Smith 2002).

Orange-crowned Warblers breed from Alaska through Canada to the western United States, and their nonbreeding range includes western and southern United States through Mexico (Gilbert et al. 2010). Of four subspecies, based on morphology and range, the main subspecies primarily captured was *lutescens*, with lack of contrast between the yellowish-olive head and body. We also captured a few *orestera*, which have a head that contrasts with yellowish-olive body.

Yellow Warblers breed in most of North America, and their nonbreeding range includes southwestern United States and western Mexico through Central America and northern South America (Lowther et al. 1999). Three groups of subspecies have been described, and based on range we captured birds from the *aestiva* group.

Wilson's Warblers breed from Alaska and Canada through western United States, and their nonbreeding range includes southern United States through Mexico and Central America (Ammon and Gilbert 1999). Genetic and stable isotope data suggest that Wilson's Warblers that migrate along the Pacific coast breed along the Pacific slope region and coastal California and

the nonbreeding range includes western Mexico (Clegg et al. 2003, Paxton et al. 2007). Three subspecies have been described, and based on plumage the subspecies captured was *chryseola* with a bright yellow forehead with an orange tinge.

Our five study species were Neotropical migrants that share overlapping ranges, foraging behavior, food preferences, and breeding behavior (Table 2.1). Swainson's Thrushes and Yellow Warblers are intercontinental migrants that travel to South America, whereas Pacific-slope Flycatchers, Orange-crowned Warblers, and Wilson's Warblers are intracontinental migrants that winter in Mexico and Central America. Offsite recoveries of banded individuals were rare with 0–6 recoveries per species, but were consistent with coastal migration pathways for the five species. A total of 11 band recoveries were all within 200 km of the Pacific coast and up to 2000 km north and 140 km south of Coyote Creek (SFBBBO, *unpublished data*).

Field Methods

San Francisco Bay Bird Observatory staff directed year-round systematic mist-netting and banding at Coyote Creek throughout the study period. Standardized mist-net sampling was established in 1987, and net lines consisted of three permanent transects of 7–9 nets, five permanent transects of 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 five hours, weather permitting. The sampled area of Coyote Creek was ~10–14 ha over the 22-year period. To control for variable effort among years, we took capture data from a standardized subset of days from 1987 to 1998 to eliminate potential biases caused by unequal number of sampling days among years and within seasons (Appendix A). We limited our capture sample to a core set of nets that were operated an average of three days per week from 1987 to 2008, and discarded captures from any additional sampling. We did not include data from Spring 1999 and 2002 because nets were not operated over the entire spring period, and we lack information from Autumn 2000 because banding data were lost for this season.

Observatory staff and trained volunteers captured and banded birds with uniquely numbered metal bands issued by the United States Geological Survey. Birds were identified to species by plumage and morphometrics, aged by skull pneumatization and patterns of feather molt, and sexed by plumage in dichromatic species (Pyle et al. 1987, Pyle 1997). Aging birds by skull pneumatization was inconsistent in early years but was regularly recorded after 1995.

Pacific-slope Flycatchers were the most difficult species to identify but were distinguished from other *Empidonax* species based on plumage, wing shape, and bill morphology.

Climate Data

We selected three climate indices representing integrated measures of regional variation in weather patterns in western North America from 1987 to 2008. We obtained climate index data for the Pacific/North American and the North Atlantic Oscillation from the Climate Prediction Center of the National Oceanic and Atmospheric Association (hereafter, NOAA; www.cpc.ncep.noaa.gov). We obtained the Multivariate El Niño/Southern Oscillation Index from NOAA's Earth System Research Laboratory Physical Sciences Division (www.esrl.noaa.gov/psd). Regional descriptions of climate indices are restricted to western North America, which encompass breeding, migration and nonbreeding sites for our five study species.

The Pacific/North American index (hereafter, PNA) assesses short-term climatic dynamics of ~2 weeks (Feldstein 2000, Cash and Lee 2001). PNA 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, extreme western United States and Baja California, and cooler than average temperatures in the northern half of Mexico. Positive phases of PNA are also associated with wetter than average springs and winters along the Pacific coast of Canada and northwestern United States, but drier than average autumns and winters in southwestern Canada and winters in the Pacific Northwest. PNA can be influenced by the El Niño/Southern Oscillation (hereafter, ENSO), with correlations between the positive phases of both indices.

The North Atlantic Oscillation (hereafter, NAO) also assesses short-term climatic dynamics of ~2 weeks (Feldstein 2003, 2007). NAO has the greatest impact on climate in North America during spring and winter, but also impacts a small, confined region in summer in northwestern to north-central United States and south-central Canada. Positive phases of NAO are associated with warmer than average springs in northwestern Mexico, Baja California and the western United States, warmer than average summers in the Pacific Northwest and intermountain west, and warmer than average winters in Mexico and the extreme southwestern United States.

Additionally, positive phases of NAO are associated with drier than average springs and winters in California and wetter than average springs and summers in extreme western Canada.

The Multivariate El Niño/Southern Oscillation Index (hereafter, MEI) assesses long-term climatic dynamics that typically last 9–12 months (El Niño) or 1–3 years (La Niña), with a 3- to 5-year periodicity (NOAA 2011). MEI has the greatest impact on the continental climate of North America during winter, but also impacts a small region in the west during summer. Positive phases of MEI, or El Niño conditions, are associated with wetter than average winters in northwestern Mexico and the southwestern United States and wetter and warmer than average winters in northwestern South America. Positive phases of MEI are also associated with wetter than average summers in the intermountain west.

We used the 22-year median migration date for each songbird species in spring and autumn to select the one- to two-month period of climate data to use in our analyses (Table 2.2). We selected months when we expected climate to affect departure dates from nonbreeding or breeding sites or to affect migration rates along migration routes. For climatic effects prior to migration, we used average climate indices for the eight-week period prior to the median migration date, which included summer MEI and NAO and winter MEI and PNA. For climate effects during migration, we used average climate indices for the four-week period surrounding the median migration date, which included spring NAO and autumn PNA. When the period spanned two months, we averaged monthly indices (PNA, NAO), or we used the two-month averages (MEI).

Statistical Analyses

Our five study species of songbirds were passage migrants at Coyote Creek, and we divided the year into two six-month periods: January–June for spring and July–December for autumn. We used the first capture per season as the migration date of each individual, and discarded within-season recaptures. To facilitate comparisons of age composition between hatching-year (HY) and after-hatching-year (AHY) birds, we pooled second-year (SY) or after-second-year birds (ASY) with AHY birds when <35% of birds were aged as SY or ASY. When <1% of birds were sexed, we pooled birds of known and unknown sex.

Statistical analyses were conducted with Program R (ver. 2.12.0, R Development Core Team 2010). We used package *quantreg* for quantile regression of timing of migration (ver.

4.71, Koenker 2011) and package AICcmodavg for model selection and model-averaging across climate models (ver. 1.13, Mazerolle 2011). We used quantile regression with 0.10, 0.25, 0.50, 0.75, and 0.90 quantiles to evaluate changes in timing of spring and autumn migration over the 22-year period, and weighted the regression by the number of individuals captured per seasonal period each year (Cade and Noon 2003). We report age and sex composition, but capture data were not adequate for separate analyses by demographic class. We used the ‘xy’ bootstrap method with 10,000 replications for hypothesis testing and to construct SEs. To calculate long-term changes in duration of migration over two decades, we calculated the difference in number of days between the 0.10 and 0.90 quantiles for 1987 and 2008 as the endpoints of our 22-year time series.

We used linear regression to assess long-term changes in climate indices. We used backward elimination multiple regression to evaluate the relationship between climate indices and median timing of migration, and weighted the regression by the number of individuals captured per seasonal period each year. Starting models included all three climate indices for both spring and autumn. We used Akaike’s Information Criterion adjusted for small sample size (AIC_c) for model selection, and considered models $\Delta AIC_c \leq 2$ to be equally parsimonious (Burnham and Anderson 2002). To assess the overall effects of each climate index on timing of migration, we model-averaged the slope estimates of each climate index for all models. Models that differed by one parameter could be within $\Delta AIC_c \leq 2$, therefore we used unconditional 85% confidence intervals on the model-averaged slope estimates of each climate index to assess parameter significance (Arnold 2010).

Results

Captures

We captured a total of 5,165 and 8,640 individual birds in spring and autumn over the 22-year period (Table 2.3). In spring, we captured 250 to 2,442 individuals per species. In autumn, we captured 67% more birds and from 445 to 5,413 individuals per species. In spring, we captured over four times more Swainson’s Thrushes and over two times more Wilson’s Warblers, but in autumn, we captured over 12 times more Pacific-slope Flycatchers and six times

more Yellow Warblers. We captured similar numbers of Orange-crowned Warblers in both seasons.

In spring, most birds captured were AHY birds ($\geq 95\%$), and sex ratios were generally male-biased (F:M = 1:1.3–1.7, Table 2.3). In autumn, age and sex ratios varied. Pacific-slope Flycatchers were the most abundant species in autumn and a majority of captures (97%) were of HY birds. Similarly, most warblers captured in autumn were HY birds (50–67%), and captures of Wilson’s Warblers were male-biased (F:M = 1:2.8, Table 2.3). Swainson’s Thrushes had the highest percentage (41%) of AHY birds captured during autumn migration.

Timing of Migration

We found long-term changes in the timing of migration that differed among the five study species and between the two seasons (Table 2.4, Fig. 2.2). Timing of spring migration significantly advanced 1.5–5.0 days per decade in at least two quantiles for Swainson’s Thrushes and Yellow Warblers. Differential changes in spring migration with delays in first arrivals combined with advances in later stages led to a decreased duration of spring migration of 8.4 days per decade for Wilson’s Warblers and 12.7 days per decade for Pacific-slope Flycatchers. In contrast, advances in first arrivals combined with delays in later stages led to an increased duration of spring migration of 37.8 days per decade for Orange-crowned Warblers. Our empirical results support all four of the hypothetical scenarios for predicted changes in migratory strategies (Fig. 2.1).

Patterns of timing of migration differed between spring and autumn, with duration of autumn migration averaging seven days longer than the duration of spring migration across the 22-year period. Timing of autumn migration was consistently delayed in all five quantiles for two species and in four quantiles for one species. Delays in timing of autumn migration of 1.7–8.9 days per decade were significant in at least four quantiles for HY Pacific-slope Flycatchers and Yellow Warblers, and delays of 2.1–6.7 days per decade were significant in two quantiles for Orange-crowned Warblers (Table 2.4, Fig. 2.3). Advances in first arrivals combined with little changes in later stages led to an increased duration of autumn migration by 16.5 days per decade for Wilson’s Warblers, but largely a result of an advance of 17.3 days per decade in the 0.10 quantile (Fig. 2.1c). Timing of autumn migration advanced 1.1–1.8 days per decade for Swainson’s Thrushes, but the advancement was only significant in the 0.50 quantile.

Climate

Two climate indices exhibited long-term directional changes during the 22-year period. All month combinations of the autumn PNA shifted from negative to positive phases ($\beta = 0.07\text{--}0.11$, $r^2 = 0.27\text{--}0.40$, $P \leq 0.01$). In contrast, only the August NAO shifted from positive to negative phases ($\beta = -0.05$, $r^2 = 0.21$, $P = 0.03$). Other climate indices did not change significantly during the study period ($\beta = -0.05\text{--} -0.01$, $r^2 = 0.01\text{--}0.13$, $P \geq 0.09$). Climate indices for our 6-month migratory seasons were not correlated ($r = -0.34\text{--}0.42$, $P \geq 0.054$).

Median timing of migration was associated with different regional climate indices, and a relatively low proportion of the variance in timing of migration was explained by climate indices in spring (1–39%, Table 2.5) and autumn (5–17%, Table 2.6). In spring, the top models for effects of climate on timing of migration included MEI and PNA for Pacific-slope Flycatchers, NAO for Swainson’s Thrushes and Wilson’s Warblers, NAO and PNA for Orange-crowned Warblers, and MEI and NAO for Yellow Warblers. In autumn, the top models for effects of climate on annual variation in timing of migration included PNA for Pacific-slope Flycatchers, Orange-crowned Warblers and Yellow Warblers, NAO for Swainson’s Thrushes, and MEI for Wilson’s Warblers.

In spring, most species showed similar responses in timing of migration to regional climate indices. For most species, advances in timing of spring migration were associated with positive phases of climate indices, indicated by negative slopes. The greatest change in timing of spring migration was delays in response to climate conditions for Pacific-slope Flycatchers (+6.4 days per SD of winter PNA, Fig. 2.4). Similarly, advances in timing of spring migration were associated with positive indices of winter MEI for Pacific-slope Flycatchers and Yellow Warblers (-2 to -5 days per SD). Advances in timing of spring migration were associated with positive indices of spring NAO for all five species and were significant for Wilson’s Warblers (-1.9 days per SD). Advances in timing of spring migration were associated with positive indices of winter PNA for Orange-crowned Warblers (-3.8 days per SD). In contrast, delays in timing of spring migration were associated with positive indices of winter PNA for Pacific-slope Flycatchers.

In autumn, most species showed similar responses in timing of migration to regional climate indices. The greatest response of changes in timing of autumn migration was delays in response to climate conditions for Orange-crowned Warblers (+5.0 days per SD of autumn PNA,

Fig. 2.4). Advances in timing of autumn migration were associated with positive indices of summer MEI for all species except Yellow Warblers and were significant for Wilson's Warblers (-2.4 days per SD). Generally, advanced timing of autumn migration was associated with positive indices of summer NAO, but was not significant for any species. In contrast, delayed timing of autumn migration was associated with positive indices of autumn PNA for all species except Swainson's Thrushes and was significant for HY Pacific-slope Flycatchers and Orange-crowned Warblers (+2 to +5 days per SD).

Discussion

Our field study is the first comprehensive analysis of long-term changes in both spring and autumn migration timing for songbirds in the western United States. We found evidence of long-term changes in timing of migration of five migratory songbirds. Patterns of change in timing of migration were heterogeneous between seasons and among species, but were related to regional climate conditions. In spring, we found advances in timing of migration for Swainson's Thrushes and Yellow Warblers, protracted migration for Orange-crowned Warblers, and compressed migration for Pacific-slope Flycatchers and Wilson's Warblers. Previous studies have reported advances in timing of spring migration among different species (Cotton 2003, Sparks et al. 2005, Beaumont et al. 2006, Jonzén et al. 2006, Thorup et al. 2007). However, many of these studies used first arrival date as the metric for change in timing, but the <1% tail of migratory timing is not representative of the whole population. For example, MacMynowski et al. (2007) used first arrival date to analyze the first 13–15 years of our time series. Our results for long-term changes in spring migration were generally opposite to their conclusions, but we included 7–9 more years of data, had better controls for sampling effort, and used quantile regression to consider the entire period of migration. In general, our results for spring timing are consistent with past research during the spring migratory period, which also found advances in timing and protracted migration among different species of migratory songbirds (Ahola et al. 2004, Mills 2005, Jonzén et al. 2006, Van Buskirk et al. 2009).

In contrast to spring migration, changes in timing of autumn migration were largely homogeneous among our study species, including delays in timing of migration in Pacific-slope Flycatchers, Orange-crowned Warblers and Yellow Warblers, but protracted migration in Wilson's Warblers. Past studies have reported heterogeneous changes in timing of autumn

migration among species including delays (Sparks et al. 2007, Chambers 2008), advances (Cotton 2003, Tøttrup et al. 2006, Chambers 2008), and protracted migration (Van Buskirk et al. 2009), or no evidence of change in timing (MacMynowski and Root 2007, Péron et al. 2007).

We considered three possible explanations for the different patterns of phenological change we found among our study species and seasons. First, changes in latitudinal geographic ranges of the breeding or nonbreeding sites could result in variation in changes of timing of migration at a stopover site during migration. For example, a northward shift in the nonbreeding range of a temperate species closer to a stopover location may result in the appearance of advances in spring migration at the same stopover location. Range expansions could also result in the appearance of protracted migration if migratory individuals originate from a larger latitudinal range, thus extending the duration of migration at a stopover location. Geographic ranges of our five study species and potential shifts are poorly understood. However, geographic ranges have shifted poleward in many taxa (La Sorte and Thompson 2007, Visser et al. 2009, Zuckerberg et al. 2011), and shifts have been associated with both a warming climate and changes in land use (La Sorte and Thompson 2007, Hockey et al. 2011). For some migratory bird species in North America and in Africa, there is growing evidence that nonbreeding ranges are expanding or will expand in the future (La Sorte and Thompson 2007, Doswald et al. 2009, Zuckerberg et al. 2011). Links among range shifts, expansions, or contractions and timing of migration require further study.

Second, age- and sex-specific variation in migratory strategies could result in intra- and inter-seasonal differences in timing of migration. Inter-seasonal differences in patterns of migration could be related to age-specific variation in migratory strategies. In Pacific-slope Flycatchers, for example, we found compressed migration among adults in spring but delays in autumn among hatching-year birds. Variation in patterns of change between early and late migrants within a season could also be due to sex-specific strategies. At Coyote Creek, male Orange-crowned Warblers and Wilson's Warblers migrate northward earlier than females (Otahal 1994, 1995). If it is advantageous for males but not females to migrate earlier, we could have advances in early migrants but little change in late migrants, resulting in a protracted spring migration, similar to the patterns we observed in Orange-crowned Warblers.

Last, environmental factors at the area of origin may affect migration timing. Rainfall may increase food abundance causing advances in departure from nonbreeding sites (Studds and

Marra 2011). If a species has multiple nonbreeding sites and changes in environmental conditions vary among sites, then birds may advance or delay departures from nonbreeding sites or alter migration rates. Thus, we may see differential changes of timing for different subsets of a migratory population, leading to compressed or protracted migration. Our three explanations are nonexclusive and different combinations could potentially result in complex patterns of timing of migration.

Although patterns of change in migratory timing were heterogeneous among our five study species, we found relatively consistent responses of migration timing to regional climate conditions. Unsurprisingly, the Pacific/North American index was the climatic index with the greatest effect on changes in timing for Pacific-slope Flycatchers and Orange-crowned Warblers. These two species had opposite responses in spring, which may result from different regional weather patterns in Mexico affected by PNA during winter. Autumn indices of PNA trended toward positive phases in the latter years of our study, but may still be an important index to consider when assessing how western migratory birds are affected by regional climate conditions. Interactions between the PNA and ENSO may also be important given associations of ENSO with timing of songbird migration in both spring and autumn.

Timing of spring migration advanced with phases of climate indices that were associated with warm, wet conditions at potential nonbreeding sites and along the spring migration route, which is consistent with previous studies. Advances in timing of spring migration were associated with warm, wet conditions of the North Atlantic Oscillation index in the United States (MacMynowski and Root 2007, Wilson 2007, Miller-Rushing et al. 2008) and the El Niño Southern Oscillation index in California (MacMynowski et al. 2007). Associations of timing of spring migration to climate conditions resulting from the ENSO index in the eastern United States were less clear, likely because weather patterns resulting from ENSO phases vary across Central and South America, resulting in drier than average conditions in some regions but wetter than average conditions in other regions. Spatial heterogeneity in climate effects could cause the differences in responses of migration timing across the United States, because birds originating from wetter areas may have better local environmental conditions that allow for earlier departure and thus earlier migration (Studds and Marra 2011).

Delays in timing of autumn migration were associated with phases of climate indices resulting in warm, dry conditions at potential breeding sites and along the autumn migration

route. Delays in autumn migration associated with warmer climatic conditions are consistent with long-term studies in the eastern United States, although those studies only reported associations with NAO (MacMynowski and Root 2007, Van Buskirk et al. 2009). We found no significant changes in timing associated with NAO, possibly because NAO may have a greater impact on birds migrating in eastern flyways than the Pacific coast.

Gaps in our understanding of the ecology of migrants complicate interpretation of changes in migratory timing and assessment of the long-term effects on migratory birds (Faaborg et al. 2010). We lack basic information on geographic ranges and connectivity, the causal factors affecting timing of migration, and whether change or lack of change in timing of migration are detrimental for all species. Tools such as stable isotopes have been used to investigate population structure of Wilson's Warblers and Swainson's Thrushes at nonbreeding sites (Ruegg and Smith 2002, Clegg et al. 2003, Kelly et al. 2005) and along migration pathways (Paxton et al. 2007). However, we still lack distributional information for many common species of songbirds. We found that timing of migration was associated with regional climate indices, but the causal relationships remain unknown. Assessing individual weather variables that are incorporated into climate indices may help identify specific factors that are driving changes in migratory timing. Sampling arthropod abundance in relation to departure dates or migration rates may help to understand if food, climate, or both affect the timing of migration. Most long-term studies, including this study, have used observational approaches to examine changes in migratory timing and experimental protocols are needed for a better mechanistic understanding. One experimental study showed that food supplementation resulted in earlier departure from nonbreeding sites by Dark-eyed Juncos (*Junco hyemalis*, Bridge et al. 2010), and field studies with similar protocols are needed for insectivorous birds (Studds and Marra 2011).

Last, it is unclear if change in the duration of migration is detrimental for a given species. Birds that show compression of migration timing may be most vulnerable to environmental perturbations if their migration window is more limited. Key information needed for a better understanding of variation in timing of migration should focus on variation in geographic ranges of migratory species, causal factors resulting in changes in migration timing, and how variation in migration timing affects population viability.

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Table 2.1. Life history traits of five migratory species of songbirds captured at Coyote Creek Field Station, California, 1987–2008.

Species	Migration distance	Habitat	No. of broods	Diet
Pacific-slope Flycatcher <i>Empidonax difficilis</i>	Intracontinental	forest	usu. 1, occ. 2	Insects
Swainson's Thrush <i>Catharus ustulatus</i>	Intercontinental	forest, riparian	usu. 1, occ. 2	Insects, fruits in autumn
Orange-crowned Warbler <i>Oreothlypis celata</i>	Intracontinental	early-successional forest, shrub	usu. 1, occ. 2 in central/inner coastal CA	Insects, occ. fruit, nectar, tree sap
Yellow Warbler <i>Setophaga petechia</i>	Intercontinental	shrub, riparian	1	Insects
Wilson's Warbler <i>Cardellina pusilla</i>	Intracontinental	shrub	usu. 1, occ. 2 in central/inner coastal CA	Insects

Table 2.2. The 22-year median migration date and months of climate indices used for models of five migratory species of songbirds captured at Coyote Creek Field Station, California, 1987–2008.

Species	Spring				Autumn			
	Median migration date	MEI	NAO	PNA	Median migration date	MEI	NAO	PNA
Pacific-slope Flycatcher	10 May	Mar/Apr	Apr/May	Mar	7 Sep	Jul/Aug	July	Aug/Sep
Swainson's Thrush	17 May	Mar/Apr	May	Mar	23 Sep	Jul/Aug	July	Sep/Oct
Orange-crowned Warbler	22 Apr	Mar/Apr	Apr/May	Mar	4 Oct	Jul/Aug	Aug	Sep/Oct
Yellow Warbler	21 May	Mar/Apr	May/Jun	Mar	19 Sep	Jul/Aug	July	Sep/Oct
Wilson's Warbler	9 May	Mar/Apr	Apr/May	Mar	13 Sep	Jul/Aug	July	Sep

MEI = Multivariate El Niño Southern Oscillation Index, NAO = North Atlantic Oscillation, PNA = Pacific/North American.

Table 2.3. Total number of individual birds and percentages of different age and sex classes for migratory songbirds captured during spring and autumn migration at Coyote Creek Field Station, California, 1987–2008.

Species	Total	HY	AHY	Unknown age	Male	Female	Unknown sex
<i>Spring</i>							
Pacific-slope Flycatcher	419	4%	95%	1%	-	-	100%
Swainson's Thrush	2442	<1%	100%	<1%	-	-	100%
Orange-crowned Warbler	792	3%	97%	<1%	42%	33%	24%
Yellow Warbler	250	<1%	100%	-	56%	34%	10%
Wilson's Warbler	1262	-	100%	<1%	58%	33%	9%
<i>Autumn</i>							
Pacific-slope Flycatcher	5413	97%	2%	<1%	-	-	100%
Swainson's Thrush	558	47%	41%	12%	-	-	100%
Orange-crowned Warbler	690	50%	15%	34%	38%	23%	39%
Yellow Warbler	1534	67%	14%	18%	28%	21%	51%
Wilson's Warbler	445	56%	26%	18%	60%	22%	19%

HY = hatching year, AHY = after hatching year.

Table 2.4. Slopes (β), SE, and P for quantiles of timing of migration (days per decade) at Coyote Creek Field Station, California 1987–2008. Negative slopes indicate advances in timing of migration.

Species	Quantile														
	0.10			0.25			0.50			0.75			0.90		
	β	SE	$P \leq$	β	SE	$P \leq$	β	SE	$P \leq$	β	SE	$P \leq$	β	SE	$P \leq$
<i>Spring</i>															
Pacific-slope Flycatcher	10.0	4.5	0.028*	10.0	2.5	0.001***	10.0	2.2	0.001***	0.5	1.6	0.742	-3.3	4.7	0.475
Swainson's Thrush	-1.5	0.4	0.001***	-2.2	0.9	0.009**	-2.5	0.3	0.001***	-1.8	0.8	0.024*	-2.3	0.6	0.001***
Orange-crowned Warbler	-36.3	7.6	0.001***	-11.7	5.8	0.046*	-1.3	0.9	0.179	2.5	0.7	0.001***	3.3	2.1	0.112
Yellow Warbler	-2.5	2.5	0.314	-4.2	0.8	0.001***	-5.0	1.0	0.001***	-2.1	2.3	0.352	-2.0	3.1	0.514
Wilson's Warbler	5.0	1.0	0.001***	2.5	0.5	0.001***	-2.5	1.6	0.113	-1.7	1.3	0.184	-3.8	0.6	0.001***
<i>Autumn</i>															
Pacific-slope Flycatcher	1.7	1.1	0.141	4.7	0.4	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	0.290	2.0	1.5	0.181	-1.1	0.6	0.047*	-1.8	2.0	0.376	-1.6	1.5	0.286
Orange-crowned Warbler	6.7	2.6	0.011*	4.0	2.0	0.047*	2.1	2.0	0.287	-2.2	5.0	0.654	4.0	5.7	0.481
Yellow Warbler	8.9	0.6	0.001***	5.0	1.2	0.001***	5.0	1.0	0.001***	4.4	1.2	0.001***	3.0	1.2	0.011*
Wilson's Warbler	-17.3	3.8	0.001***	0.9	4.3	0.833	0	2.1	1.000	0	1.9	1.000	0	2.3	1.000

Notes: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Table 2.5. Comparison of climate models associated with spring median migration dates at Coyote Creek Field Station, California, 1987–2008.

Species	K	Dev	ΔAIC_c	w_i	r^2
Pacific-slope Flycatcher					
MEIw + PNAw	4	130.8	0.0	0.85	0.39
MEIw + NAOsp + PNAw	5	130.6	3.5	0.15	0.39
Swainson's Thrush					
NAOsp	3	97.1	0.0	0.79	0.01
MEIw + NAOsp	4	96.9	3.0	0.18	0.02
MEIw + NAOsp + PNAw	5	96.8	6.5	0.03	0.03
Orange-crowned Warbler					
PNAw	3	143.0	0.0	0.65	0.12
NAOsp + PNAw	4	141.4	1.6	0.30	0.19
MEIw + NAOsp + PNAw	5	141.3	5.0	0.05	0.20
Yellow Warbler					
MEIw	3	124.0	0.0	0.60	0.15
MEIw + NAOsp	4	122.0	1.1	0.34	0.23
MEIw + NAOsp + PNAw	5	121.6	4.4	0.07	0.24
Wilson's Warbler					
NAOsp	3	115.3	0.0	0.73	0.14
NAOsp + PNAw	4	114.6	2.4	0.22	0.17
MEIw + NAOsp + PNAw	5	113.8	5.3	0.05	0.20

Notes: K = number of parameters, Dev = deviance, ΔAIC_c = change in Akaike's Information Criterion corrected for small sample size, w_i = Akaike weight, r^2 = coefficient of determination. MEIw = Mar/Apr; NAOsp = Apr/May, May, or May/Jun; PNAw = Mar. Minimum AIC_c : Pacific-slope Flycatcher = 141.4, Swainson's Thrush = 104.6, Orange-crowned Warbler = 150.5, Yellow Warbler = 131.5, and Wilson's Warbler = 122.8.

Table 2.6. Comparison of climate models associated with autumn median migration dates at Coyote Creek Field Station, California, 1987–2008.

Species	<i>K</i>	Dev	ΔAIC_c	w_i	r^2
Pacific-slope Flycatcher					
PNAa	3	134.0	0.0	0.77	0.11
MEIsu + PNAa	4	133.7	2.8	0.19	0.12
MEIsu + NAOsu + PNAa	5	133.6	6.2	0.04	0.13
Swainson's Thrush					
NAOsu	3	139.2	0.0	0.67	0.05
NAOsu + PNAa	4	138.2	2.1	0.24	0.09
MEIsu + NAOsu + PNAa	5	136.8	4.2	0.08	0.15
Orange-crowned Warbler					
PNAa	3	146.6	0.0	0.79	0.16
MEIsu + PNAa	4	146.5	3.0	0.18	0.16
MEIsu + NAOsu + PNAa	5	146.4	6.5	0.03	0.17
Yellow Warbler					
PNAa	3	139.7	0.0	0.73	0.06
MEIsu + PNAa	4	138.9	2.3	0.23	0.10
MEIsu + NAOsu + PNAa	5	138.9	5.8	0.04	0.10
Wilson's Warbler					
MEIsu	3	133.6	0.0	0.79	0.16
MEIsu + NAOsu	4	133.4	2.9	0.18	0.17
MEIsu + NAOsu + PNAa	5	133.4	6.4	0.03	0.17

Notes: See footnote of Table 2.5 for definition of column headings. MEIsu = Jul/Aug; NAOsu = Jul or Aug; PNAa = Aug/Sep, Sep, or Sep/Oct. Minimum AIC_c : Pacific-slope Flycatcher = 141.4, Swainson's Thrush = 146.7, Orange-crowned Warbler = 154.0, Yellow Warbler = 147.1, and Wilson's Warbler = 141.0.

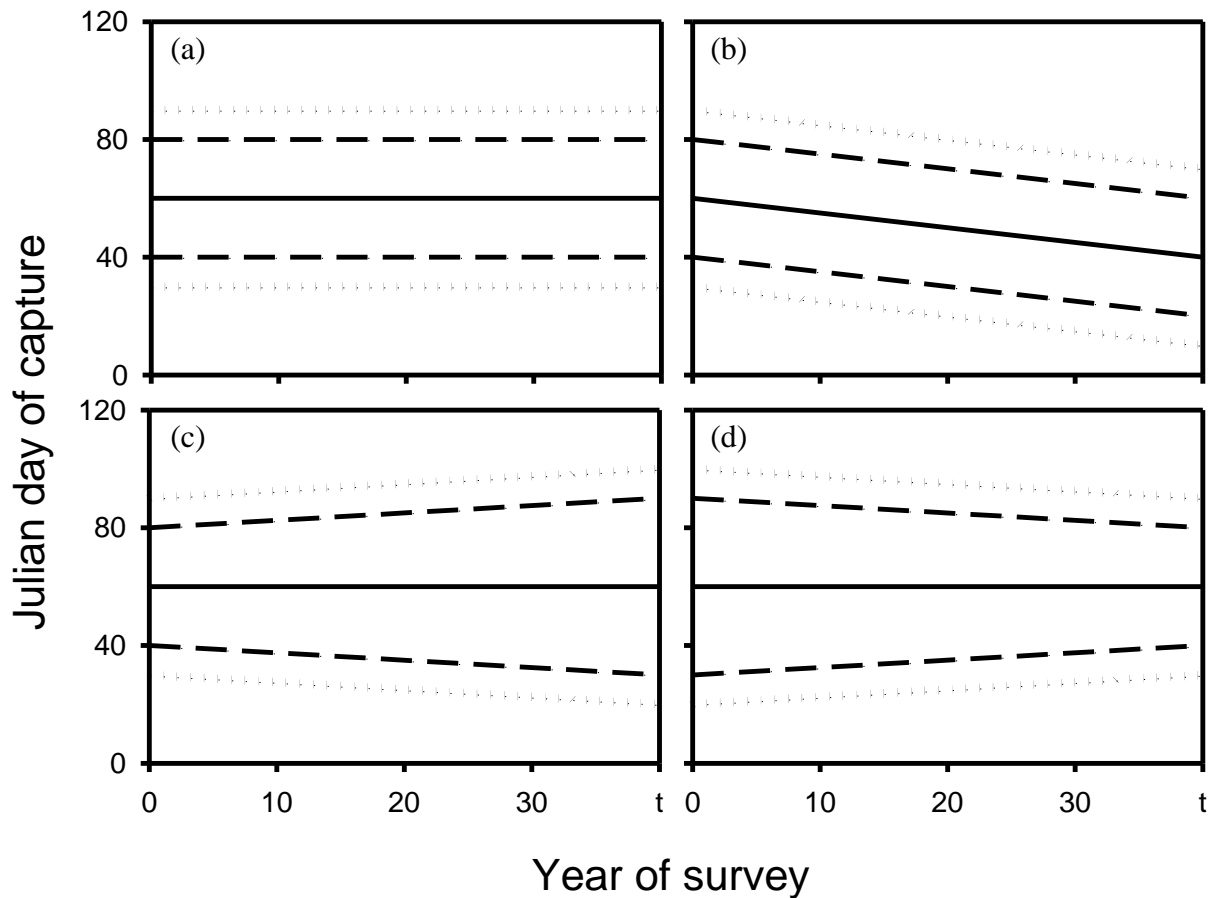


Figure 2.1. Hypothetical patterns of migratory dynamics resulting from long-term changes in timing of migration with (a) no change across all quantiles, (b) equal advances across all quantiles, (c) protracted migration with advances in first arrivals coupled with delays in later stages of migration, and (d) compressed migration with delays in first arrivals coupled with advances in later stages of migration. Solid lines are the 0.50 quantile or median migration dates, dashed lines are the 0.25 and 0.75 quantiles, and dotted lines are the 0.10 and 0.90 quantiles.

Figure 2.2. Quantile regression of timing of spring migration for five species of migratory songbirds captured during systematic mist-net sampling at Coyote Creek Field Station, California, 1987–2008. Open circles are first capture dates of individual birds per season. Solid lines are the 0.50 quantile or median migration dates, dashed lines are the 0.25 and 0.75 quantiles, and dotted lines are the 0.10 and 0.90 quantiles. Slopes significantly different from zero are black and non-significant slopes are grey. Julian day 121 = 1 May.

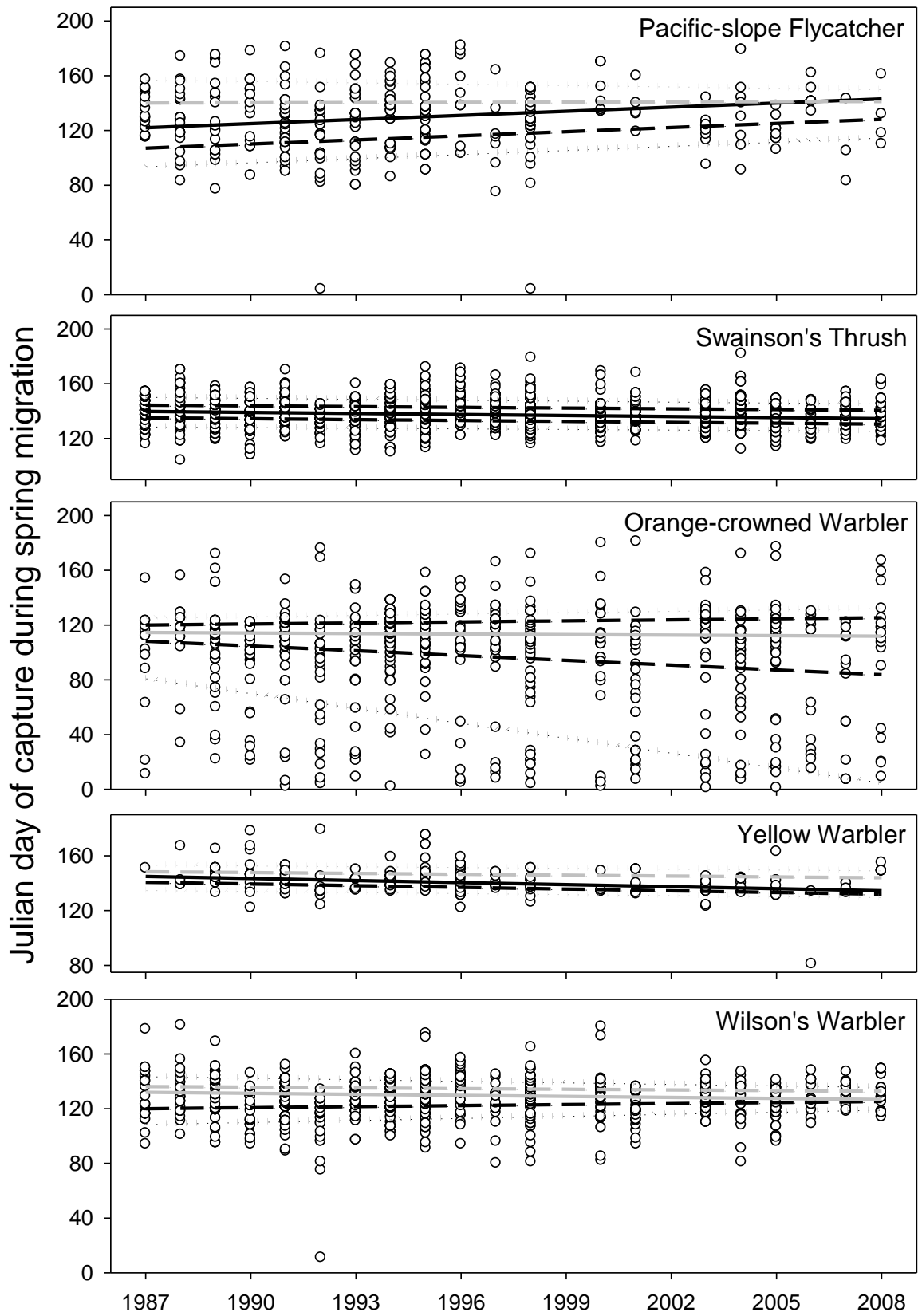
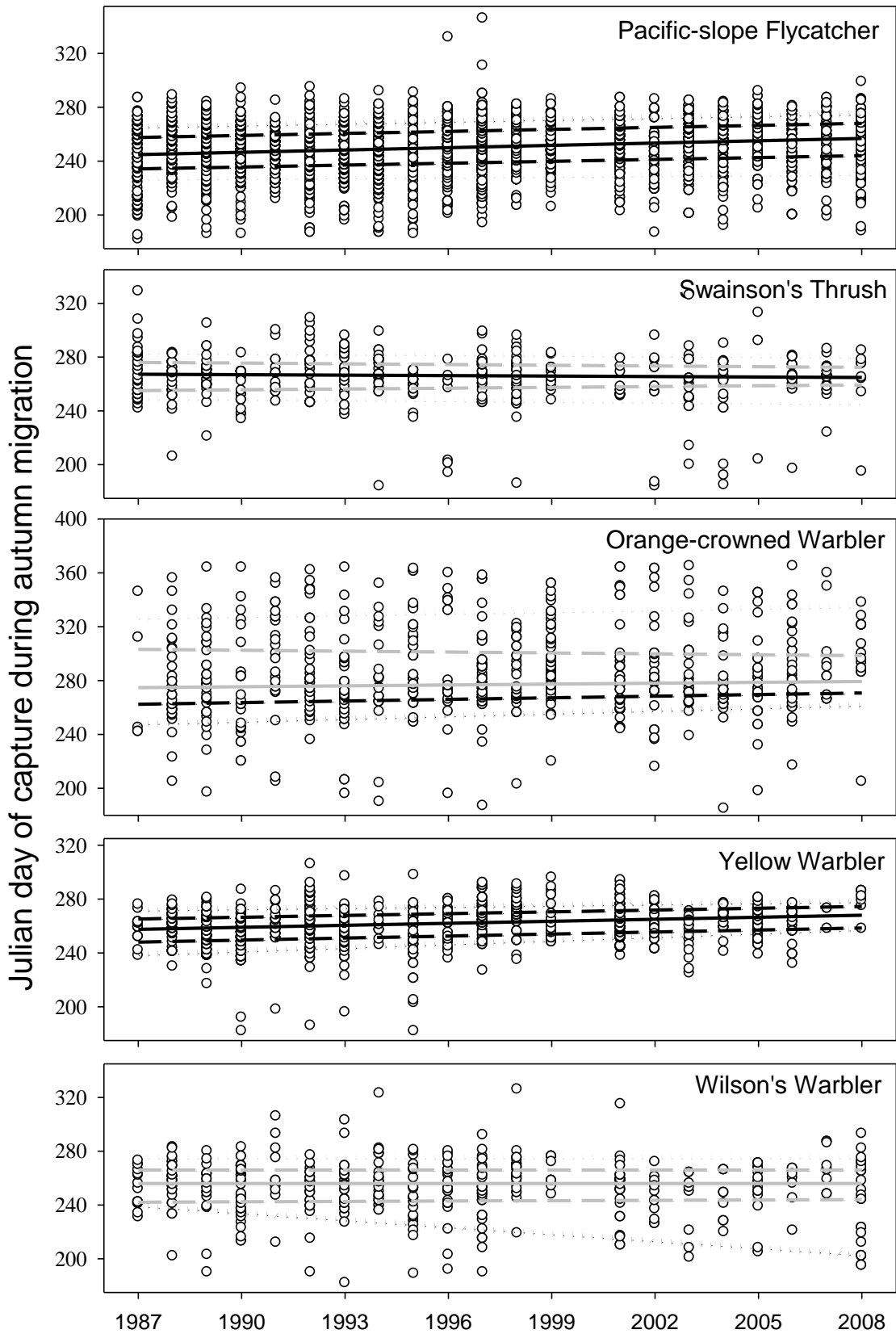


Figure 2.3. Quantile regression of timing of autumn migration for five species of migratory songbirds captured during systematic mist-net sampling at Coyote Creek Field Station, California, 1987–2008. See caption of Figure 2.2 for descriptions. Julian day 274 = 1 Oct.



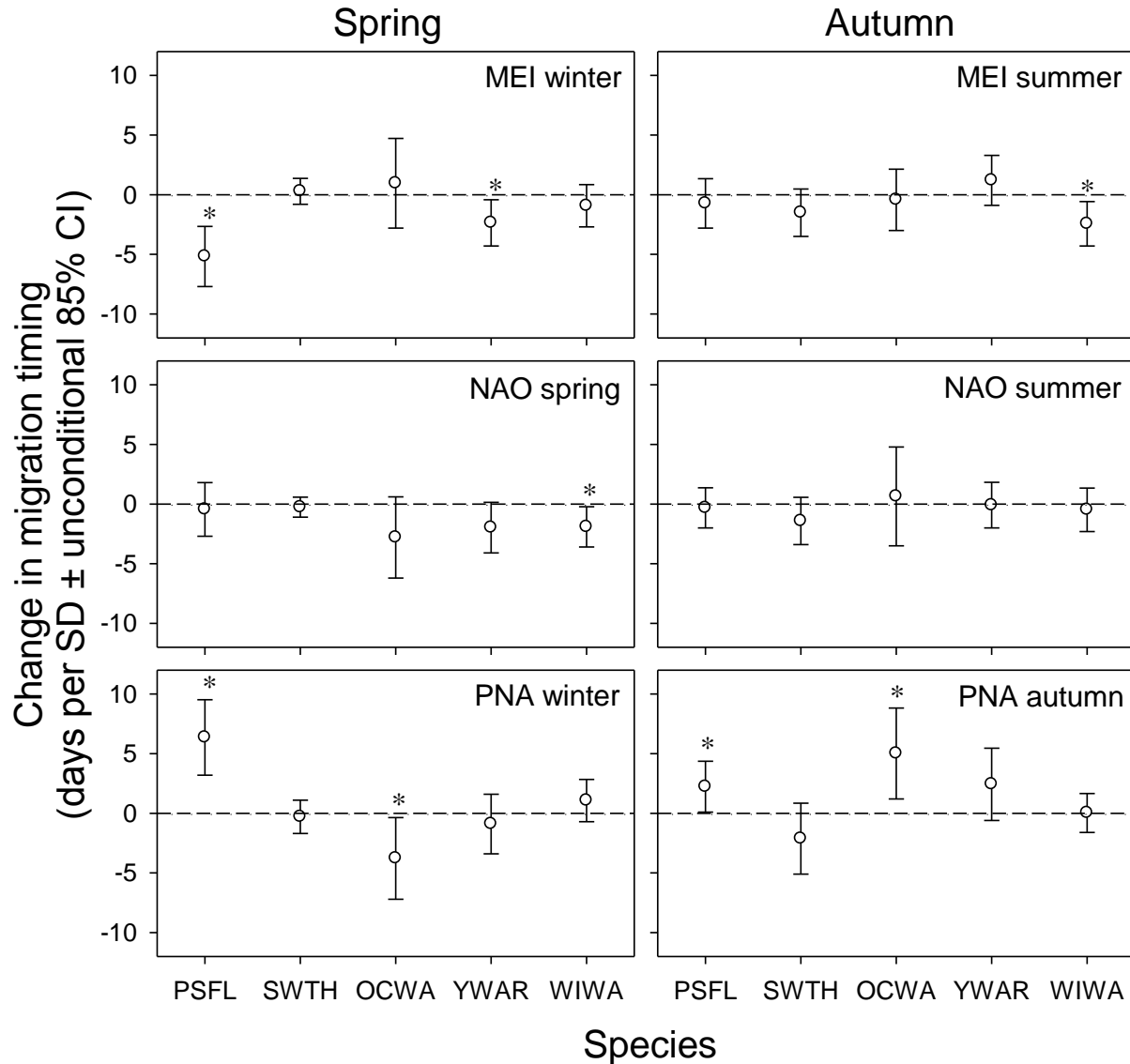


Figure 2.4. Model-averaged estimates in spring and autumn in days per SD of the climate index \pm unconditional 85% confidence intervals of climate indices at Coyote Creek Field Station, California, 1987–2008. Negative numbers indicate advances in timing of migration. Asterisks (*) denote slope \pm unconditional 85% CI that do not include zero. Acronyms include: MEI = Multivariate El Niño/Southern Oscillation Index, NAO = North Atlantic Oscillation, PNA = Pacific/North American, PSFL = Pacific-slope Flycatcher, SWTH = Swainson’s Thrush, OCWA = Orange-crowned Warbler, YWAR = Yellow Warbler, WIWA = Wilson’s Warbler.

Chapter 3 - Estimation of stopover duration for five species of migratory songbirds in northern California

Abstract

The migratory period is a critical stage of the annual cycle for latitudinal migrants, and conditions during migration and at stopover sites can affect stopover dynamics. We compared stopover duration in spring and autumn for five species of migratory songbirds using a 12-year mark-recapture dataset collected in northern California. We used three methods to estimate stopover duration for migratory songbirds: minimum stopover duration, Cormack-Jolly-Seber models, and Pradel temporal symmetry models. We also examined how body mass at first capture affected stopover duration as an individual covariate. Stopover duration was longer in spring than autumn, but varied among species. Pacific-slope Flycatchers (*Empidonax difficilis*; 25.7 days) and Yellow Warblers (*Setophaga petechia*; 20.0 days) had longer stopovers in spring than in autumn (7.8 days, 9.3 days), whereas Swainson's Thrushes (*Catharus ustulatus*; 5.5 days) and Wilson's Warblers (*Cardellina pusilla*; 5.3 days) had shorter stopovers in spring than in autumn (8.7 days, 14.3 days). Orange-crowned Warblers (*Oreothlypis celata*) had similar stopovers in both seasons (spring: 33.1 days, autumn: 31.5 days). Birds with a greater body mass at first capture had consistently shorter stopover durations. Birds migrating along the Pacific coast may use different migratory strategies than birds in eastern flyways, and variation in migration routes and molt strategies of populations may affect stopover duration of species across North America. Future investigations should determine migration routes and rates of migration to better understand dynamics at stopover sites.

Introduction

The migratory period is a critical stage of the annual cycle for latitudinal migrants, because much of the time is spent resting and refueling at stopover sites. Migration is physiologically stressful and mortality can be high (Sillert and Holmes 2002). Conditions at stopover sites, including food availability, climate conditions, and predation rates, can affect stopover dynamics, including rates of fat deposition and duration of stay at a stopover site (Rguibi-Idrissi et al. 2003, Newton 2006, Péron et al. 2007, Arizaga et al. 2008). Growing evidence shows that carryover effects from events during migration may also be widespread.

Events during spring migration can affect timing of arrival at breeding sites and subsequent reproductive success (Møller 1994, Lozano et al. 1996, Hasselquist 1998, Calvert et al. 2009). Understanding stopover ecology is also critical for conservation. Loss or changes in habitat quality at stopover sites can affect population viability of migratory animals (McGowan et al. 2011). Moreover, estimates of stopover duration can be critical for estimating population size from counts of flocks of migratory birds at stopover sites (Cohen et al. 2009).

A growing number of studies have evaluated stopover dynamics of birds during migration, but two challenges hinder comparisons of stopover dynamics of songbirds among different flyways – one ecological and one methodological. First, geographic barriers to migration differ dramatically around the world. Latitudinal migrants that breed in northern Europe may face barriers that include the North Sea, Alps, Mediterranean Sea, and Sahara Desert (Morganti et al. 2011, Schmaljohann and Naef-Daenzer 2011). In eastern North America, barriers to latitudinal migration include the Great Lakes, Atlantic Ocean, and Gulf of Mexico. In contrast, latitudinal migrants along the Pacific flyway may encounter fewer barriers if they fly along coastal areas (Kelly and Hutto 2005).

The quantitative methods used to estimate stopover duration vary, and limitations of some methods may hamper comparisons. Previous studies have used three methods to estimate stopover duration for marked migratory birds. *Minimum stopover duration* is calculated as the time elapsed between first and last capture and has been the main method used for most birds (Yong et al. 1998, Carlisle et al. 2005, Gordo and Sanz 2006). Minimum stopover duration is biased because it only uses information for individuals captured more than once, discards information from birds recaptured multiple times between the first and last capture, and does not include probability of site use before first capture or after last capture (Fig. 3.1). *Cormack-Jolly-Seber models* (hereafter, CJS) are a mark-recapture approach that improves on minimum stopover duration. CJS and other mark-recapture approaches control for variation in the probability of encounter (p), which is often less than one, and incorporate all encounter information from individuals captured. CJS models are often used to estimate annual rates of apparent survival (ϕ) where ϕ is the product of true survival (S) and site fidelity (F). In analyses of daily stopover duration, S approaches one and $\phi \cong F$, or the probability of stopover site use (Sandercock 2006). Last, *Pradel temporal symmetry models* have a similar structure to CJS models but they also include the probability of site use before first capture, thus giving an

estimate of total stopover duration. Comparisons among the three estimators for two migratory songbirds in Switzerland found that estimates based on minimum stopover duration and CJS models were 38–51% lower than estimates from Pradel models (Schaub et al. 2001).

In this study, we used long-term data to investigate the stopover dynamics of five species of migratory songbirds at a coastal site in California. Our study is one of the first projects to estimate stopover duration for migratory songbirds on the Pacific flyway. We investigated potential biases among different estimates by comparing stopover duration estimated from minimum stopover duration, CJS models, and Pradel models. Last, we tested the effect of body mass at first capture on stopover duration and predicted that lean birds should stay longer at stopover sites if fat dynamics are important for successful migration.

Methods

Study Site

We conducted systematic mist-net sampling and banding at the Coyote Creek Field Station (hereafter, Coyote Creek), a riparian restoration site of the San Francisco Bay Bird Observatory, over a 12-year period from 1987 to 1998. Coyote Creek is located in Santa Clara County, California (37°28'N, 122°03'W), and the habitat consists of remnant and restored riparian woodlands surrounding a water overflow channel. Understory vegetation and canopy cover increased during the first decade after site establishment, but then remained constant from the mid-1990s to the end of our study (SFBBO, *unpublished reports*). Coastal areas of California have a Mediterranean climate with most rainfall and plant growth from November to April and a dry period of plant senescence from May to October.

Study Species

We investigated five species of migratory songbirds that were passage migrants at Coyote Creek and had the greatest number of seasonal captures: 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*). To determine breeding and nonbreeding ranges for our study taxa, we used subspecies designations based on plumage and range of these species in coastal California.

Pacific-slope Flycatchers breed along the Pacific coast of North America, and their nonbreeding range spans the Pacific coast of Mexico (Lowther 2000). Cordilleran Flycatchers (*E. occidentalis*), a closely related species, were considered conspecific prior to 1989 (AOU checklist). Our study population consisted primarily of Pacific-slope Flycatchers because this species breeds along the Pacific coast, whereas Cordilleran Flycatchers are an inland species found east of Coyote Creek to the Rocky Mountains. Of three described subspecies and ranges, the subspecies captured in our study was *difficilis*.

Swainson's Thrushes breed broadly across north and northwestern North America, and their nonbreeding range spans from Mexico to South America (Mack and Yong 2000). Banding and genetic data suggest that Pacific coast migrants of Swainson's Thrush from the *ustulatus* group breed from southeastern Alaska to southern California, and spend the nonbreeding season in the northern part of their nonbreeding range throughout Mexico and Central America (Ruegg and Smith 2002).

Orange-crowned Warblers have a broad distribution across North America. The main subspecies captured at Coyote Creek was *lutescens*, distinguished by a lack of contrast between the yellowish-olive head and body. We also captured a few *orestera*, which have a head that contrasts with yellowish-olive body. The range of *lutescens* spans the Pacific coast of North America in the breeding and nonbreeding season (Gilbert et al. 2010).

Three groups of subspecies have been described for Yellow Warblers, and based on range we captured birds from the *aestiva* group. Birds from the *aestiva* group breed in most of North America, and their nonbreeding range spans western Mexico through northern South America (Lowther et al. 1999).

Wilson's Warblers are found across northern North America, and their nonbreeding range includes southern United States through Central America (Ammon and Gilbert 1999). Three subspecies have been described, and based on plumage the subspecies captured was *chryseola* with a bright yellow forehead with an orange tinge. Genetic and stable isotope data indicate that *chryseola* breeds along the Pacific slope region and coastal California and the nonbreeding range includes western Mexico (Clegg et al. 2003, Paxton et al. 2007).

Our five study species were Neotropical migrants that share overlapping ranges, foraging behavior, food preferences, and breeding behavior (Table 3.1). Swainson's Thrushes and Yellow Warblers are intercontinental migrants that travel to South America, whereas Pacific-slope

Flycatchers, Orange-crowned Warblers, and Wilson's Warblers are intracontinental migrants that spend the nonbreeding season from the United States through Central America. Offsite recoveries of banded individuals were rare with 0–6 recoveries per species in a 22-year period, but were consistent with coastal migration pathways for the five species. A total of 11 band recoveries were all within 200 km of the Pacific coast and up to 2000 km north and 140 km south of Coyote Creek (SFBBO, *unpublished data*).

Field Methods

San Francisco Bay Bird Observatory staff directed year-round systematic mist-netting and banding at Coyote Creek for the 12-year period from 1987–1998. Standardized mist-net sampling was established in 1987, and net lines consisted of three permanent transects of 7–9 nets, five permanent transects of 2–3 nets, and a variable number of permanent and temporary single nets. Nets were operated every 1–2 days and were opened 30 min before local sunrise and left open for five hours, weather permitting. The sampled area of Coyote Creek was ~10–14 ha over the 12-year period. Standardized mist-netting was also conducted during the 10-year period from 1999 to 2008, but these data were not included because sampling effort was less consistent and was not comparable to earlier years. We did not include data from 1995 because sampling dates were lost.

Observatory staff and trained volunteers captured and banded birds with uniquely numbered metal bands issued by the United States Geological Survey. Birds were identified to species by plumage and morphometrics, aged by skull pneumatization and patterns of feather molt, and sexed by plumage in dichromatic species, and wing chord and mass were measured (Pyle et al. 1987, Pyle 1997). Pacific-slope Flycatchers were the most difficult species to identify but were distinguished from other *Empidonax* species based on plumage, wing shape, and bill morphology.

Statistical Analyses

Our five study species of songbirds were passage migrants at Coyote Creek, and we divided the year into two 6-month periods: January–June for spring and July–December for autumn. We created seasonal capture histories for each species by combining capture date for all years from 1987 to 1998. Within the 180-day period, we sampled 110–168 days in spring and

76–169 days in autumn. For days not sampled, we coded captures as zero, which reduced the probability of encounter but allowed us to combine years with different sampling schedules.

We used three methods to estimate stopover duration (Fig. 3.1). First, minimum stopover duration was calculated as the median of the difference between first and last day of capture for birds captured at least twice. Second, Cormack-Jolly-Seber (CJS) models estimate apparent survival (ϕ), the probability that an individual present at time i was present at time $i + 1$ and the probability of encounter (p ; Cormack 1964, Jolly 1965, Seber 1965). Last, Pradel (1996) models ($\phi\gamma$ -parameterization) estimate apparent survival (ϕ), seniority (γ), the probability that an individual present at time i was present at time $i - 1$, and the probability of encounter (p). Time intervals between capture occasions were one day. Daily variation in apparent survival (ϕ) and seniority (γ) is likely in migratory birds if timing of departure and arrival is affected by local environmental conditions like prevailing tail winds (Morganti et al. 2011, Schmaljohann and Naef-Daenzer 2011). Estimation of time dependence for these parameters requires considerable data but recaptures of migrants at stopover sites are often rare events (Morris et al. 2006). Accordingly, our starting model was a constant model without time-dependent variation in any of the three parameters ($\phi_c\gamma_cp_c$). We pooled age and sex classes for analyses of stopover dynamics but report the demographic composition for our samples. Few birds were aged as second-year or after-second-year birds ($\leq 33\%$), thus we report age classes as hatching-year and after-hatching-year.

We used Pradel models to assess how body mass at first capture affected apparent survival and seniority. Variation in wing chord was low (CV: 3.3–4.6%, $n = 5$ species), so we did not calculate residual body mass adjusted for body size. A few birds were outliers with body mass $> \pm 4SD$ of the mean, so we discarded these individuals as possible misidentified species or transcription errors, which made up $\leq 0.8\%$ of our samples. To test for differences of body mass at first capture between spring and autumn, we first tested for unequal variances between spring and autumn using a Bartlett's test, then used the appropriate t-test for equal or unequal variances. Our four candidate models were $\phi_{wt}\gamma_{wt}p_c$, $\phi_{wt}\gamma_cp_c$, $\phi_c\gamma_{wt}p_c$, and $\phi_c\gamma_cp_c$.

We used package RMark (ver. 2.1.0, Laake and Rexstad 2008) in Program [R] (ver. 2.14.2, R Development Core Team 2012) to construct models for Program MARK (ver. 6.1, White and Burnham 1999). We used the logit link for all models, but used the sine link for

$\phi_c \gamma_c p_c$ spring model for Yellow Warblers because the sine performs better if parameter estimates are close to the boundaries of 0 or 1. We imported models into MARK to run goodness-of-fit tests for CJS models using the median \hat{c} approach and to adjust \hat{c} to 1. Because goodness-of-fit tests are not available for Pradel models, we assumed minimal overdispersion and that $\hat{c} = 1$. We calculated stopover duration (\hat{d}) from CJS models as

$$\hat{d}_{CJS} = \frac{-1}{\ln(\hat{\phi})} \quad \text{eqn. 1}$$

where $\ln(\hat{\phi})$ is the natural log of the daily estimate of apparent survival. We calculated stopover duration from Pradel temporal symmetry models as (Schaub et al. 2001):

$$\hat{d}_{PTS} = \frac{-1}{\ln(\hat{\gamma})} + \frac{-1}{\ln(\hat{\phi})} \quad \text{eqn. 2}$$

Using the delta method, we calculated the variance of the estimates of stopover duration as (Seber 1982, Powell 2007):

$$\widehat{Var}(\hat{d}_{CJS}) = \widehat{Var}(\hat{\phi}) \left(\frac{1}{\hat{\phi} \ln^2(\hat{\phi})} \right)^2 \quad \text{eqn. 3}$$

and

$$\widehat{Var}(\hat{d}_{PTS}) = \widehat{Var}(\hat{\gamma}) \left(\frac{1}{\hat{\gamma} \ln^2(\hat{\gamma})} \right)^2 + \widehat{Var}(\hat{\phi}) \left(\frac{1}{\hat{\phi} \ln^2(\hat{\phi})} \right)^2 \quad \text{eqn. 4}$$

We used Akaike's Information Criterion adjusted for small sample size (AIC_c) for model selection to examine the effects of mass on stopover duration, and considered models $\Delta AIC_c \leq 2$ to be equally parsimonious (Burnham and Anderson 2002). To compare how body mass at first capture affected stopover duration, we took real parameter estimates from the model $\phi_{wt} \gamma_{wt} p_c$ using mass values within the range of observed masses.

Results

We captured a total of 5,500 and 9,415 individual birds for the 12-year period in spring and autumn, respectively (Table 3.2). The proportion of birds captured more than once within a season was low and ranged from 0.2 to 6.5%. We recaptured a greater proportion of individual birds in autumn (12.8%) than in spring (10.9%). In spring, most birds captured were AHY birds ($\geq 97\%$), and sex ratios were generally male-biased (F:M = 1:1.7–1.9; Table 3.2). In autumn, age and sex ratios varied. Pacific-slope Flycatchers were the most abundant species captured in autumn and a majority of birds (97%) were HY birds. Similarly, most warblers captured in

autumn were HY birds (50–70%), and captures of Wilson’s Warblers were male-biased (F:M = 1:2.9). Swainson’s Thrushes had the highest percentage (43%) of AHY birds captured during autumn migration.

Estimates of stopover duration differed among the three quantitative methods that we tested. Daily encounter probabilities (p) were low (0.002–0.13) and were more variable in spring than in autumn (Table 3.3). Median minimum stopover duration was 2.0–7.0 days, estimates from CJS models were 2.7–17.8 days, and estimates from Pradel models were 5.3–33.1 days. On average, stopover duration estimates from CJS models were two times longer (range: 0.8–4.5 times) than median minimum stopover duration, and estimates from Pradel models were two times longer (range: 1.8–2.0 times) than CJS models (Table 3.4). However, 95% CI of minimum stopover duration overlapped with both CJS and Pradel models (Fig. 3.2).

On average, estimates of stopover duration from Pradel models were 20% longer in spring than in autumn but varied by species (Table 3.4; Fig. 3.2). Stopover duration was 54–70% longer in spring than autumn for Pacific-slope Flycatchers (spring: 25.7 days, autumn: 7.8 days) and Yellow Warblers (20.0 days, 9.3 days), but was 58–170% shorter in spring than autumn for Swainson’s Thrushes (5.5 days, 8.7 days) and Wilson’s Warblers (5.3 days, 14.3 days). Stopover duration was similar between seasons for Orange-crowned Warblers (33.1 days, 31.5 days). Estimates of spring stopover duration were shortest for Swainson’s Thrushes (5.5 days) and Wilson’s Warblers (5.3 days). In autumn, three species had short estimates of stopover duration: Pacific-slope Flycatchers (7.8 days), Swainson’s Thrushes (8.7 days), and Yellow Warblers (9.3 days), and estimates were longest for Orange-crowned Warblers (31.5 days).

Body mass at first capture differed between seasons for all species except Wilson’s Warblers (Table 3.5). Swainson’s Thrushes were 23% heavier in autumn (35.7 g) than in spring (29.0 g), and Pacific-slope Flycatchers, Orange-crowned Warblers, and Yellow Warblers had $\leq 2.4\%$ body mass difference between seasons. Pradel models that included body mass at first capture as a covariate for ϕ and γ received 92–100% of the model weights in four of five species (Table 3.6). Body mass received less weight for Pacific-slope Flycatchers in spring (7–20%) and Orange-crowned Warblers in autumn (13–23%). Overall, stopover duration was longer for birds captured at a lighter body mass in spring and autumn (Fig. 3.3). Changes in stopover duration

related to mass tended to be greater for Swainson's Thrushes and Wilson's Warblers in autumn. The effects of mass on stopover duration were similar in both seasons for Pacific-slope Flycatchers, Orange-crowned Warblers, and Yellow Warblers.

Discussion

Our analyses provide some of the first estimates of stopover duration for migratory songbirds on the Pacific Flyway. Estimates of stopover duration differed among the three quantitative methods we used, with Pradel temporal symmetry models yielding the longest estimates of stopover duration. We found variation in stopover duration between seasons and among species. Pacific-slope Flycatchers and Yellow Warblers had a longer stopover duration in spring, whereas Swainson's Thrushes and Wilson's Warblers had a longer stopover duration in autumn. Stopover duration for Orange-crowned Warblers was similar between seasons and was longer than other species in both seasons. Last, we found that longer stopover duration was related to body mass at capture.

Comparisons of estimates of stopover duration from different methods suggest that the most widely used estimates of minimum stopover are biased low. Our stopover duration estimates using Pradel models were on average four times longer than minimum stopover duration, a difference comparable to estimates reported previously (0.6–5.0 times longer; Schaub et al. 2001, Carlisle et al. 2005, Arizaga et al. 2008, 2010). Estimates of ϕ and γ can be asymmetrical, but our sparse capture data precluded use of time-dependent models. Because our estimates for ϕ and γ were comparable to each other, estimates from constant Pradel models resulted in doubling of stopover duration, in which case \hat{d}_{CJS} may be closer to the 'true' stopover duration if the underlying distribution of arrival and departure dates is Poisson (Efford 2005). We had low encounter probabilities (p ; 0.002–0.034), which can produce underestimates of stopover duration (Salewski et al. 2007, Verkuil et al. 2010). Moreover, inestimable parameters, especially for time-dependent models, can result from small sample sizes and low sampling intensity (Morris et al. 2006). Studies with greater sampling intensity, such as increasing sampling days and collecting resight data, may increase parameter estimability for time-dependent models and may result in more accurate estimates of stopover.

Few comparative estimates exist, but stopover duration from Pradel models was longer at Coyote Creek than published estimates for the same or related species in spring and autumn

(Morris et al 2006; Table 3.4, Table 3.7). In contrast, stopover duration was similar (≤ 1 day difference) or longer when comparing minimum stopover duration, but was similar or shorter when comparing telemetry estimates, which are comparable to CJS estimates, and differences varied between seasons. Spring stopover duration was comparable to published estimates using minimum stopover duration and telemetry, but longer using Pradel models. In contrast, autumn stopover duration was longer at Coyote Creek than most published estimates regardless of method used, with the caveat that many of these comparisons are for minimum stopover duration which had large confidence intervals (Fig. 3.2). Published estimates using telemetry tended to be longer than our estimates using CJS, but use of telemetry may increase stopover duration (Warnock and Bishop 1998). Apparent differences in stopover duration among studies may vary depending on the method used to estimate stopover duration.

Spring migration in songbirds is usually faster and more synchronous than autumn migration (Franssen 1995, Stutchbury et al. 2009), and we predicted that stopover duration would be shorter in spring to reflect faster spring migration rates. Unexpectedly, we found seasonal differences in stopover duration with longer spring stopovers on average, but stopover duration varied among species. Few studies have made seasonal comparisons of stopover duration for songbirds. A few studies found longer autumn stopovers than spring (Lavee et al. 1991, Rguibi-Idrissi et al. 2003, Chernetsov and Mukhin 2006) or no difference between spring and autumn (Yong et al. 1998, Morris and Glasgow 2001, Seewagen et al. 2010). One study found longer spring stopovers, attributing it to refueling prior to crossing the Sahara Desert (Salewski and Schaub 2007).

The differences we found between seasons and among previous studies may reflect variation in migratory strategies among different flyways, species, or both. Strategies used by migratory songbirds in western North America may differ from other flyways (Kelly and Hutto 2005). Molt-migration is a common strategy used by western birds because of seasonal climate variation (Rohwer et al. 2003, Pyle et al. 2009), and birds migrating along the Pacific coast have few geographic barriers during migration compared to flyways in eastern North America or between Europe and Africa (Kelly and Hutto 2005, Morganti et al. 2011, Schmaljohann and Naef-Daenzer 2011). Moreover, seasonal differences in conditions along a migration route, such as wind and food availability, often results in elliptical migration routes (Newton 2008). The western U.S. has productive springs and dry autumns in coastal areas, such as the San Francisco

Bay area, and migration, especially in spring, is concentrated along riparian corridors. We could expect longer stopovers at Coyote Creek in both spring and autumn than other stopover sites in the eastern flyways. In spring, longer stopovers may result from competition for food because of a concentration of migrants along riparian corridors, and in autumn, longer stopovers may result from low food availability resulting from the dry season. Last, western warblers occupy a smaller nonbreeding geographic area relative to the breeding area, whereas eastern warblers occupy a larger nonbreeding area relative to the breeding area (Kelly and Hutto 2005). Greater competition at nonbreeding sites for western warblers could have a carry-over effect to migration, resulting in longer spring stopovers relative to the eastern flyways because of poor condition at departure from nonbreeding sites.

Variation in migratory movement patterns could drive seasonal differences in stopover duration. At coastal stopover sites in autumn juvenile birds are more common than inland sites, resulting in variation in stopover site use between seasons (Ralph 1981), and juvenile birds often have longer autumn stopovers than adults (Morris et al. 1996, Yong et al 1998, Rguibi-Idrissi et al. 2003). Species with elliptical migration routes, such as Semipalmated Sandpipers (*Calidris pusilla*) and Connecticut Warblers (*Oporornis agilis*), may have differential stopover site use between spring and autumn (Gratto-Trevor and Dickson 1994, Reed et al. 2003). Moreover, species with leapfrog migration patterns, such as Wilson's Warblers and Fox Sparrows (*Passerella iliaca*), and consequently different migration distances, may intermix at a stopover site within a season (Bell 1997, Kelly et al. 2002, Clegg et al. 2003). All five of our study species breed in California, and although one study suggests that migratory birds that breed near a stopover site have longer stopovers in autumn, it is unclear how this may affect stopover duration (Finch and Yong 2000). These variations in migration patterns can complicate interpretation of intra and interseasonal variation in stopover duration.

Differences in molt strategies may also drive seasonal variation. Molt is energetically demanding, and its timing in the annual cycle may affect body condition and stopover duration for the migratory period following molt. Two of our five study species, Pacific-slope Flycatchers and Yellow Warblers undergo annual or pre-alternate molts at nonbreeding sites, and both species had longer autumn stopovers than spring. In contrast, three other study species undergo annual molts at breeding sites and have a minimal or no pre-alternate molt. Swainson's Thrushes and Wilson's Warblers had shorter spring stopovers than autumn, but Orange-crowned

Warblers had similar stopovers in both seasons. Pacific-slope Flycatchers also tended to have the shortest autumn stopovers of our five species at Coyote Creek, which could reflect faster migration to arrive at nonbreeding sites to begin its annual molt. In Western Sandpipers (*Calidris mauri*), which molt at nonbreeding sites and time migration to avoid predation, longer stopovers were associated with increased predation risk from Peregrine Falcons (*Falco peregrines*; Ydenberg et al. 2004). Differences in molt strategies among species may cause variation in stopover duration of migratory birds.

This is the first study to assess stopover duration for a suite of species in spring and autumn in the Pacific flyway. Our comparisons combine 12 years of data, capturing annual variability and possibly giving more accurate estimates of stopover duration. With the development of light-level geolocators small and light enough to fit larger passerines, we have gained more information on the stopover ecology of songbirds (Stutchbury et al. 2009, 2011), but these tags require recovery to obtain data, which makes studies at a stopover site difficult. Previous studies suggest that birds may be able to adjust migration rates (Stutchbury et al. 2011), but more study is needed to determine what factors may cause a bird to alter its migration rate and how changes in migration rates affect stopover duration. While migration has been documented to have the highest mortality rates during the annual cycle (Sillett and Holmes 2002), the effects of variation in migration rates or stopover duration on migration mortality is poorly understood. We know little information about migration routes that songbirds use and how they vary among flyways and between seasons. Few studies in North America have assessed stopover dynamics of songbirds along a flyway, so adding a network of sites to determine routes, migration rates, and important stopover sites can help identify potential critical stopover habitats for migratory songbirds.

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Table 3.1. Life history traits of five migratory species of songbirds captured at Coyote Creek Field Station, California, 1987–1998.

Species	Migration distance	Habitat	No. of broods	Diet
Pacific-slope Flycatcher <i>Empidonax difficilis</i>	Intracontinental	forest	usu. 1, occ. 2	Insects
Swainson's Thrush <i>Catharus ustulatus</i>	Intercontinental	forest, riparian	usu. 1, occ. 2	Insects, fruits in autumn
Orange-crowned Warbler <i>Oreothlypis celata</i>	Intracontinental	early-successional forest, shrub	usu. 1, occ. 2 in central/inner coastal CA	Insects, occ. fruit, nectar, tree sap
Yellow Warbler <i>Setophaga petechia</i>	Intercontinental	shrub, riparian	1	Insects
Wilson's Warbler <i>Cardellina pusilla</i>	Intracontinental	shrub	usu. 1, occ. 2 in central/inner coastal CA	Insects

Table 3.2. Total number of individual birds captured, recaptured ≥ 1 times, and percentages of different age and sex classes for five species of migratory songbirds captured during spring and autumn migration at Coyote Creek Field Station, California, 1987–1998.

Species	Captures	Recaptured		Unknown		Unknown		sex
		≥ 1	HY	AHY	age	Male	Female	
<i>Spring</i>								
Pacific-slope Flycatcher	506	12	2.8%	96.6%	0.8%	-	-	100%
Swainson's Thrush	2619	543	0.1%	99.8%	0.1%	-	-	100%
Orange-crowned Warbler	794	130	1.1%	98.6%	0.3%	51%	30%	19%
Yellow Warbler	325	18	2%	98%	0%	60%	32%	8%
Wilson's Warbler	1256	116	0%	99.9%	0.1%	61%	35%	4%
<i>Autumn</i>								
Pacific-slope Flycatcher	6024	616	97%	2%	1%	-	-	100%
Swainson's Thrush	807	36	49%	43%	8%	-	-	100%
Orange-crowned Warbler	522	96	56.1%	18.4%	25.5%	37%	16%	47%
Yellow Warbler	1625	184	70.2%	17.4%	12.4%	26.95%	24.55%	48.55%
Wilson's Warbler	437	86	56%	27%	17%	62%	21%	17%

HY = hatching-year, AHY = after-hatching-year.

Table 3.3. Parameter estimates from CJS and Pradel temporal symmetry models for five species of migratory songbirds captured during spring and autumn migration at Coyote Creek Field Station, California, 1987–1998.

	CJS				Pradel					
	$\hat{\phi}$	SE($\hat{\phi}$)	\hat{p}	SE(\hat{p})	$\hat{\phi}$	SE($\hat{\phi}$)	$\hat{\gamma}$	SE($\hat{\gamma}$)	\hat{p}	SE(\hat{p})
<i>Spring</i>										
Pacific-slope Flycatcher	0.933	0.020	0.002	0.001	0.932	0.020	0.918	0.020	0.002	0.001
Swainson's Thrush	0.704	0.009	0.134	0.006	0.703	0.009	0.689	0.008	0.134	0.006
Orange-crowned Warbler	0.946	0.005	0.012	0.001	0.944	0.005	0.939	0.005	0.012	0.001
Yellow Warbler	0.915	0.022	0.007	0.002	0.914	0.022	0.893	0.021	0.007	0.002
Wilson's Warbler	0.691	0.022	0.048	0.006	0.690	0.022	0.680	0.021	0.048	0.006
<i>Autumn</i>										
Pacific-slope Flycatcher	0.780	0.007	0.041	0.002	0.771	0.006	0.778	0.006	0.041	0.002
Swainson's Thrush	0.799	0.025	0.017	0.003	0.794	0.024	0.796	0.024	0.017	0.003
Orange-crowned Warbler	0.943	0.005	0.019	0.002	0.940	0.005	0.937	0.005	0.019	0.002
Yellow Warbler	0.810	0.012	0.029	0.003	0.804	0.012	0.808	0.012	0.029	0.003
Wilson's Warbler	0.874	0.011	0.043	0.005	0.866	0.011	0.872	0.011	0.043	0.005

Table 3.4. Estimates of stopover duration using three methods for five species of migratory songbirds captured during spring and autumn migration at Coyote Creek Field Station, California, 1987–1998.

	\hat{d}_{min}		\hat{d}_{CJS}		\hat{d}_{PTS}	
	median	Q1–Q3	\bar{x}	SE	\bar{x}	SE
<i>Spring</i>						
Pacific-slope Flycatcher	5.0	1.8–15.3	14.3	4.4	25.7	5.2
Swainson's Thrush	3.0	1.0–5.0	2.8	0.1	5.5	0.1
Orange-crowned Warbler	4.0	2.0–26.0	17.8	1.6	33.1	1.9
Yellow Warbler	3.0	2.0–10.8	11.2	3.0	20.0	3.5
Wilson's Warbler	2.0	1.0–4.0	2.7	0.2	5.3	0.3
<i>Autumn</i>						
Pacific-slope Flycatcher	5.0	3.0–7.0	4.0	0.1	7.8	0.2
Swainson's Thrush	3.0	1.8–7.0	4.4	0.6	8.7	0.8
Orange-crowned Warbler	7.0	3.8–31.5	16.9	1.5	31.5	1.9
Yellow Warbler	4.0	3.0–7.0	4.8	0.3	9.3	0.4
Wilson's Warbler	6.0	3.0–9.8	7.4	0.7	14.3	0.9

Notes: Minimum stopover duration (\hat{d}_{min}) = max–min for birds recaptured within a season; Cormack-Jolly-Seber $\hat{d}_{CJS} = \frac{-1}{\ln(\hat{\phi})}$ where ϕ = daily probability of site fidelity, corrected for probability of encounter (p); Pradel temporal symmetry $\hat{d}_{PTS} = \frac{-1}{\ln(\hat{\gamma})} + \frac{-1}{\ln(\hat{\phi})}$ where ϕ = daily probability of site fidelity and γ = daily probability of presence in the population before first capture, corrected for probability of encounter (p). Q1 = 25% quartile, Q3 = 75% quartile.

Table 3.5. Body mass (g) at first capture ($\bar{x} \pm SD$) and *t*-test comparisons between seasons for five species of migratory birds captured in spring and autumn at Coyote Creek Field Station, California, 1987–1998.

Species	Spring			Autumn			<i>t</i> - test		
	n	\bar{x}	SD	n	\bar{x}	SD	<i>t</i>	<i>df</i>	<i>P</i> ≤
Pacific-slope Flycatcher	494	10.2	0.7	5950	10.4	0.9	6.4	626.7	0.001
Swainson's Thrush	2584	29.0	2.4	790	35.7	4.2	43.3	955.2	0.001
Orange-crowned Warbler	779	9.1	0.8	504	9.0	0.8	-2.6	1281	0.009
Yellow Warbler	316	9.6	0.9	1593	9.8	1.0	4.4	484.5	0.001
Wilson's Warbler	1220	7.4	0.6	429	7.5	0.8	1.5	609.4	0.148

Table 3.6. Comparison of Pradel models for the effects of body mass at first capture on stopover duration in spring and autumn at Coyote Creek Field Station, California, 1987–1998.

	$\phi_c \gamma_c P_c$ K=3	$\phi_{wt} \gamma_c P_c$ K=4	$\phi_c \gamma_{wt} P_c$ K=4	$\phi_{wt} \gamma_{wt} P_c$ K=5
<i>Spring ΔAIC_c</i>				
Pacific-slope Flycatcher	0.0	2.0	2.0	4.0
Swainson's Thrush	45.6	43.2	44.5	0.0
Orange-crowned Warbler	9.7	11.6	11.0	0.0
Yellow Warbler	407.9	10.3	10.5	0.0
Wilson's Warbler	7.8	9.7	9.7	0.0
<i>Spring w_i</i>				
Pacific-slope Flycatcher	0.536	0.196	0.196	0.073
Swainson's Thrush	0.000	0.000	0.000	1.000
Orange-crowned Warbler	0.008	0.003	0.004	0.985
Yellow Warbler	0.000	0.006	0.005	0.989
Wilson's Warbler	0.020	0.007	0.008	0.965
<i>Autumn ΔAIC_c</i>				
Pacific-slope Flycatcher	90.5	68.6	65.3	0.0
Swainson's Thrush	57.8	59.7	59.8	0.0
Orange-crowned Warbler	0.0	1.4	1.6	2.5
Yellow Warbler	27.6	24.0	23.0	0.0
Wilson's Warbler	9.0	7.0	6.0	0.0
<i>Autumn w_i</i>				
Pacific-slope Flycatcher	0.000	0.000	0.000	1.000
Swainson's Thrush	0.000	0.000	0.000	1.000
Orange-crowned Warbler	0.444	0.226	0.201	0.129
Yellow Warbler	0.000	0.000	0.000	1.000
Wilson's Warbler	0.010	0.027	0.046	0.916

Notes: K = number of parameters, ΔAIC_c = change in Akaike's Information Criterion corrected for small sample size, w_i = Akaike weight. Model notation includes: c = constant, wt = body mass.

Table 3.7. Estimates of stopover duration for selected songbirds from other studies using three different methods.

Season	Species	State	Method	Estimate (days)	Source
Spring	Traill's Flycatcher	ME	PTS	3.5	Morris et al. 2006
Spring	Swainson's Thrush	CR	MIN	2.0	Wilson et al. 2008
Spring	Swainson's Thrush	OH	TEL	3.7	Matthews and Rodewald 2010
Spring	Wilson's Warbler	CA	MIN	2.0	Otahal 1995
Spring	Wilson's Warbler	NM	MIN	2.5	Yong et al. 1998
Spring	Wilson's Warbler	ME	PTS	2.6	Morris et al. 2006
Autumn	Yellow-bellied Flycatcher	ME	MIN	2.7	Morris et al. 1996
Autumn	Traill's Flycatcher	ME	MIN	2.9	Morris et al. 1996
Autumn	Least Flycatcher	ME	MIN	3.1	Morris et al. 1996
Autumn	Dusky Flycatcher	NM	MIN	1.5	Finch and Yong 2000
Autumn	Dusky Flycatcher	ID	MIN	4.2	Carlisle et al. 2005
Autumn	Swainson's Thrush	ME	MIN	2.5	Morris et al. 1996
Autumn	Swainson's Thrush	NY	TEL	4.5	Seewagen and Guglielmo 2010
Autumn	Swainson's Thrush	CA	TEL	8.9	Tietz and Johnson 2007
Autumn	Swainson's Thrush	ME	PTS	3.3	Morris et al. 2006
Autumn	Orange-crowned Warbler	ID	MIN	2.0	Carlisle et al. 2005
Autumn	Yellow Warbler	ID	MIN	3.9	Carlisle et al. 2005
Autumn	Wilson's Warbler	ID	MIN	1.5	Carlisle et al. 2005
Autumn	Wilson's Warbler	NM	MIN	2.3	Yong et al. 1998
Autumn	Wilson's Warbler	ME	MIN	2.6	Morris et al. 1996
Autumn	Wilson's Warbler	CA	MIN	5.0	Otahal 1995
Autumn	Wilson's Warbler	ME	PTS	3.3	Morris et al. 2006

CR = Costa Rica; MIN = minimum, TEL = telemetry, PTS = Pradel temporal symmetry.

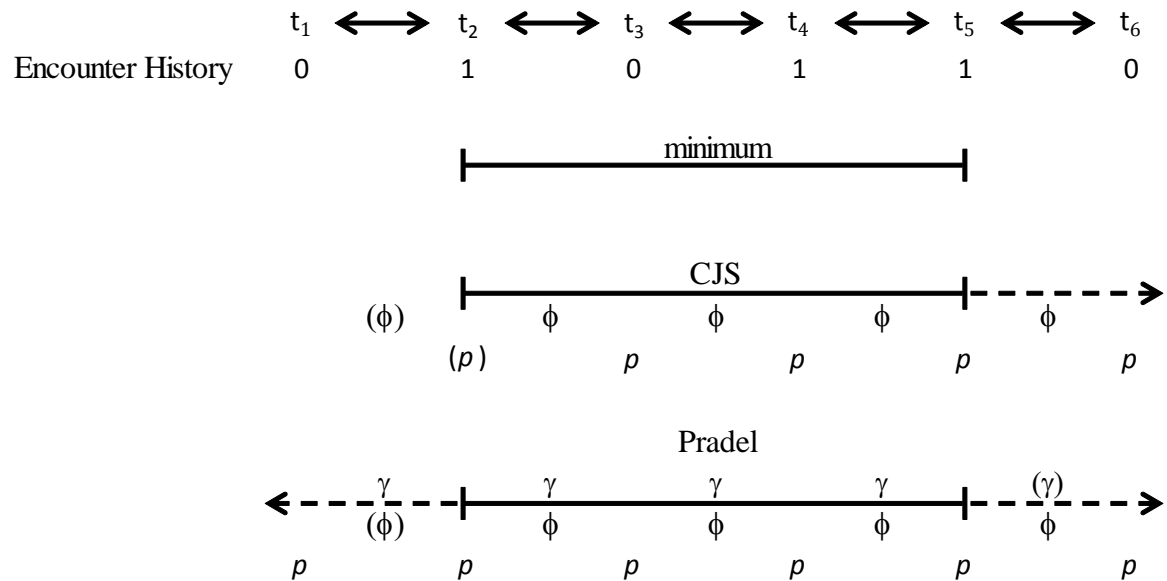


Figure 3.1. Comparison of methods used to estimate stopover duration for a sample encounter history. Minimum stopover duration is the difference between first and last day capture, ignoring other captures in between. Cormack-Jolly-Seber (CJS) models estimate the daily probability of site fidelity after first capture (ϕ), corrected for the probability of encounter (p). Pradel temporal symmetry survival and seniority models estimate the daily probability of site fidelity before last capture (γ). Parameters without parentheses are estimated for this capture record, but parameters in parentheses are estimated the model.

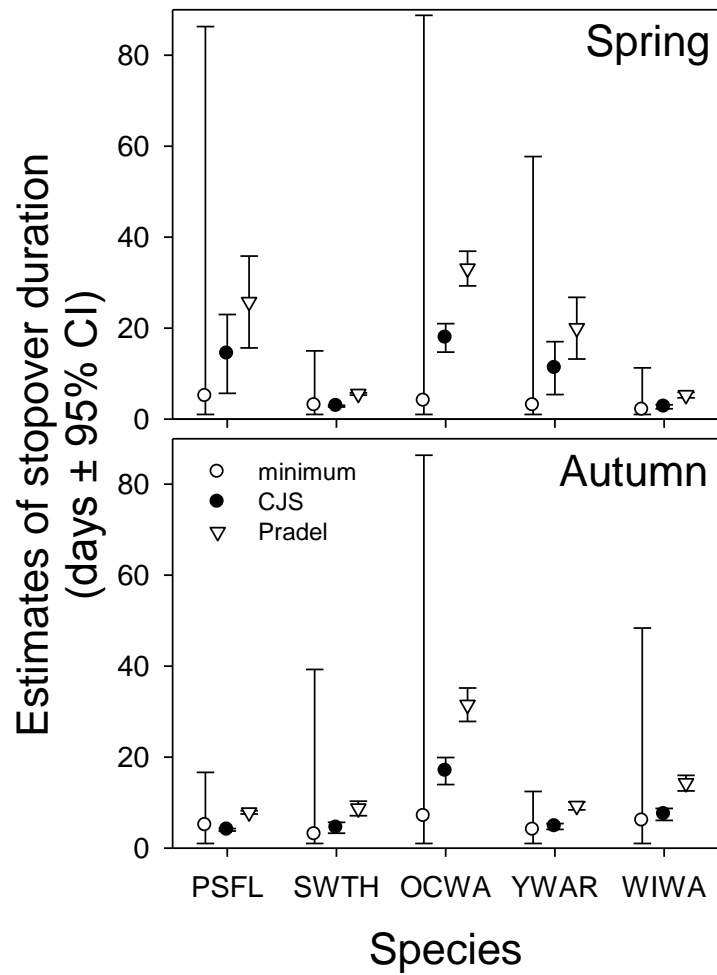


Figure 3.2. Estimates of stopover duration in spring and autumn using minimum stopover duration (median $\hat{d}_{min} \pm 95\% \text{ CI}$), Cormack-Jolly-Seber models (CJS) ($\hat{d}_{CJS} \pm 95\% \text{ CI}$), and Pradel temporal symmetry survival and seniority models ($\hat{d}_{PTS} \pm 95\% \text{ CI}$) for five species of migratory songbirds at Coyote Creek Field Station, California, 1987–1998. PSFL = Pacific-slope Flycatcher, SWTH = Swainson’s Thrush, OCWA = Orange-crowned Warbler, YWAR = Yellow Warbler, WIWA = Wilson’s Warbler.

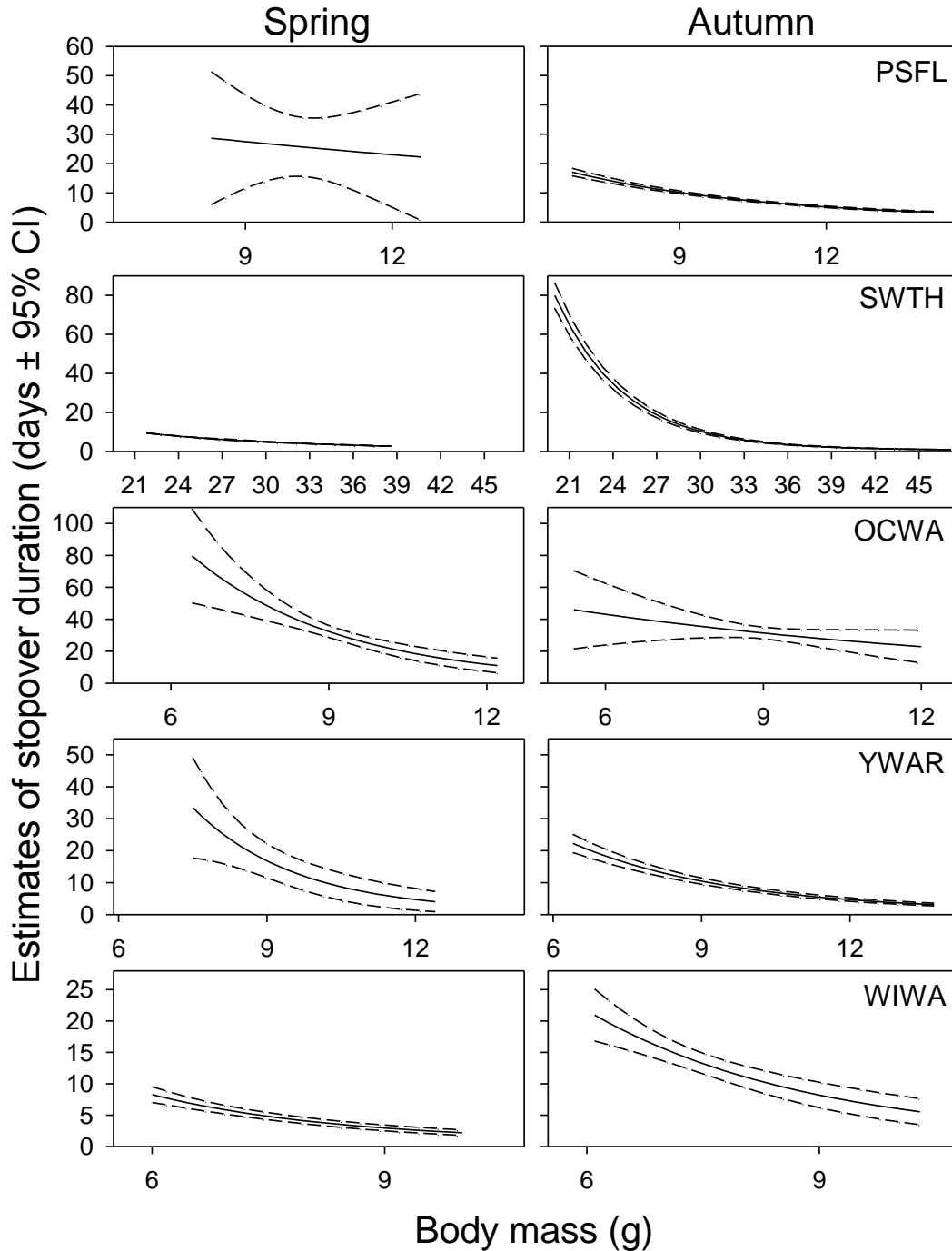


Figure 3.3. Real parameter estimates of spring and autumn stopover duration ($\hat{d}_{PTS} \pm 95\% \text{ CI}$) in relation to body mass for different body masses at first capture from the model $\phi_{wt}\gamma_{wt}p_c$ for five species of migratory songbirds at Coyote Creek Field Station, California, 1987–1998. PSFL = Pacific-slope Flycatcher, SWTH = Swainson’s Thrush, OCWA = Orange-crowned Warbler,

YWAR = Yellow Warbler, WIWA = Wilson's Warbler. Solid lines are mean stopover duration and dashed lines are 95% confidence intervals.

Chapter 4 - Conclusions

Field studies of migratory songbirds at stopover and nonbreeding sites are a growing area of ornithology, but stopover ecology of migratory songbirds is still poorly understood, and comparisons along the Pacific flyway are limited. We found that the stopover ecology of songbirds is complex in its timing, response to regional climate conditions, and stopover duration. Changes in migration timing varied among species in spring, but were consistently delayed in autumn. Previous studies have used primarily first arrival date or last departure date to measure changes in timing of migration, and in contrast to our results, reported advances in timing of spring migration but no consistent patterns in autumn migration. We conclude that it is important to examine the entire migratory period when assessing changes over time, because it is likely more representative of population patterns. Regional climate conditions were associated with timing of migration for some species in spring and autumn; wet, warm conditions were associated with advanced timing of spring migration, and dry, warm conditions were associated with delayed timing of autumn migration. Although changes in timing were associated with broad scale climate indices, causal factors driving these changes remain unknown.

Estimates of stopover duration varied seasonally and among species, and stopover length varied depending on the quantitative method used. We found that some species had longer stopovers in spring than autumn, while other species had longer stopovers in autumn than spring. Stopover duration for most of our study species was longer than published estimates from populations in eastern North America, which likely include different subspecies. Comparisons of estimates of stopover duration from the three different methods suggest that the most widely used estimate, minimum stopover duration, is biased low. Stopover duration from Pradel models was four times longer than minimum stopover duration. Estimates from constant Pradel models resulted in doubling of stopover duration, in which case estimates from CJS models may be closer to the true stopover duration if the underlying distribution of arrival and departure dates is Poisson. Moreover, low encounter probabilities, which are common in migration studies, can produce underestimates of stopover duration.

Variation in changes in timing of migration and variation in stopover duration among species could reflect differences in population composition, flyways, molt strategies, or changes in geographic ranges. Composition of populations using a stopover site may vary within and

between seasons. In autumn, four of our five study species had a juvenile-biased age ratio, thus delays in autumn timing may be representative of the juvenile population. Species with leapfrog migrations, such as Wilson's Warblers, which migrate different distances and therefore may have different migration strategies, may intermix at a stopover site. Evidence suggests that birds using the Pacific flyway have different migration strategies, such as molt-migration, which could explain differences between our results and results from previous studies from other flyways. How differences in molt strategies among species, such as timing of molt, may affect stopover ecology in songbirds is unclear. We also lack specific geographic range information for many subspecies, and few studies have examined temporal changes of geographic ranges at breeding or nonbreeding sites.

Future research should include development of a network of stopover sites along a flyway to determine if changes in timing of migration or stopover duration are similar along a flyway or if they vary in relation to breeding and nonbreeding sites. Increasing sampling intensity by sampling daily and including resighting or telemetry data would increase the precision of estimates of stopover duration, and would facilitate comparisons among studies. Future research should also examine the potential role of food, predation, climate, and other key ecological factors on the stopover ecology of migratory birds. Comparisons from a network of stopover sites across North America would help determine temporal and spatial variability of stopover ecology and may reveal important ecological factors driving this variability. Understanding variation in stopover ecology would help determine causes of population declines for migratory birds and prioritize conservation decisions for migratory songbirds, especially in the context of ongoing climate change.

Appendix A - Subsampling of mist-net data

Mist-netting effort was variable among years and months over the 22-year period. To control for potential biases arising from unequal sampling effort, we used a subsample of the complete dataset. From 1987 to 1998, nets were operated more frequently overall and the seasonal effort varied among months compared to 1999–2008 (Fig. A.1). Nets were opened on average 21.9 days per month, ranging 0–31 days per month. From 1999–2008, nets were operated systematically with less variable frequency among months. Nets were opened on average 11.0 days per month, ranging 0–15 days per month.

Overall sampling effort was greater in the first 12 years, so we took a subsample of the capture data from 1987–1998 that was similar to the 1999–2008 sampling effort. To control for annual and seasonal differences in effort, we selected the day that the core area was sampled, which was one day per week in 1987–1995, and selected days that were three and four days later, resulting in 0–2 days between sampled days. In 1996–1998, we restricted our sample days to that the core area was sampled, which was three days per week, resulting in 1–2 days between sampled days. The subsampled number of days nets were operated between the periods of 1988–1998 and 1999–2008 was similar (Fig. A.2). From 1987–1998, nets were open an average 11.4 days per month, ranging 0–14 days per month, and from 1999–2008, nets were opened an average 10.9 days per month, ranging 0–14 days per month.

We discarded years that we did not use for analyses (spring 1999 and 2002 and fall 2000), and data from 1995 were missing because we were unable to completely reconstruct the number of days nets were operated. During the period from 1987–2008, nets were opened an average of 11.9 days per month, ranging 0–14 days per month (Fig. A.2c). We used this subsample in our analyses of timing of migration.

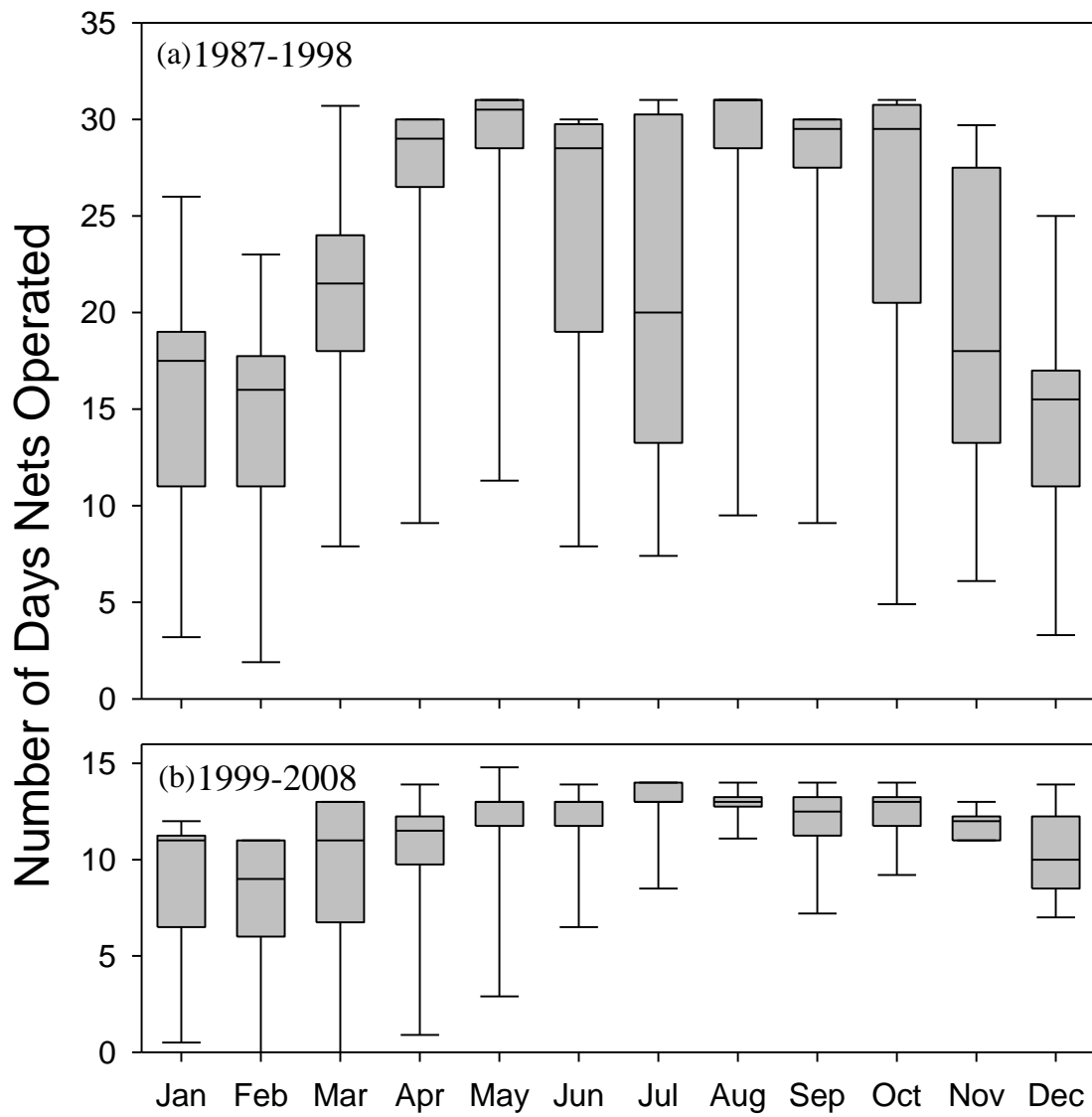


Figure A.1. Boxplots of the total number of days that nets were operated in (a) 1987–1998 and (b) 1999–2008 at Coyote Creek Field Station, California.

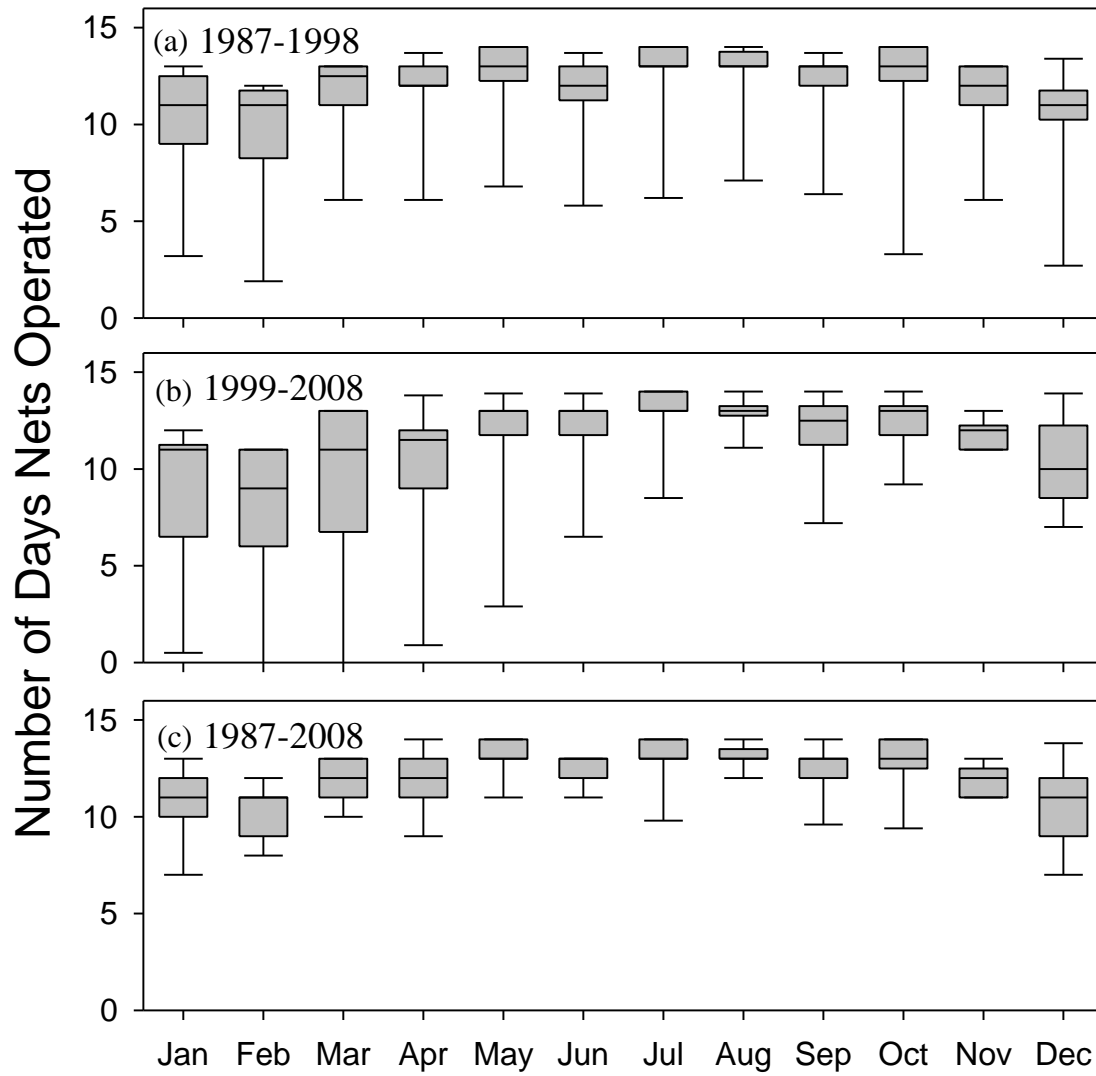


Figure A.2. Boxplots of the subsampled number of days that nets were operated in (a) 1987–1998, (b) 1999–2008, and (c) 1987–2008 at Coyote Creek Field Station, California.