Arnold Schwarzenegger
Governor

CLIMATE CHANGE AND THE TIMING OF SONGBIRD MIGRATION IN CALIFORNIA: FOCUS ON COASTAL CENTRAL AND NORTHERN REGIONS

PIER PROJECT REPORT

Prepared For:
California Energy Commission
Public Interest Energy Research Program

Prepared By:
Dena P. MacMynowski
Terry L. Root
Stanford University

March 2007
CEC-500-2007-010

California Climate Change Center
Report Series Number 2007-003

Prepared By:
Stanford University
Center for Environmental Science and Policy
Stanford Institute for International Studies
Dena P. MacMynowski
Terry L. Root
Stanford, California 94305-6055
Contract No. 500-02-004
Work Authorization No. MR-024

Prepared For:
California Energy Commission
Public Interest Energy Research (PIER) Program

Guido Franco
Contract Manager

Kelly Birkinshaw
Program Area Manager
Energy-Related Environmental Research

Laurie ten Hope
Office Manager
Energy Systems Research

Martha Krebs, Ph.D.
Deputy Director
ENERGY RESEARCH AND DEVELOPMENT DIVISION

B. B. Blevins
Executive Director

DISCLAIMER
This report was prepared as the result of work sponsored by the California Energy Commission. It does not necessarily represent the views of the Energy Commission, its employees or the State of California. The Energy Commission, the State of California, its employees, contractors and subcontractors make no warrant, express or implied, and assume no legal liability for the information in this report; nor does any party represent that the uses of this information will not infringe upon privately owned rights. This report has not been approved or disapproved by the California Energy Commission nor has the California Energy Commission passed upon the accuracy or adequacy of the information in this report.

Acknowledgments

We thank the California Energy Commission's PIER program for financial support of this research. We are grateful for the thousands of hours of time spent collecting information on bird arrivals in California by unnamed thousands of volunteers, interns, and scientists. Hand-written data was diligently sorted and entered by Lindsay D. Love and Brandon Root. Kathy Klimkiewicz of the Bird Banding Laboratory kindly assisted us with obtaining the raw banding station data. Grant Ballard and Geoff Geupel of PRBO Conservation Science generously contributed net hour and recapture data and provided constructive comments on the analysis.

Please cite this report as follows:

MacMynowski, D. P., and T. L. Root. 2007. *Climatic Change and the Timing of Songbird Migration in California: Focus on Coastal Central and Northern Regions.* California Energy Commission, PIER Energy-Related Environmental Research. CEC-500-2007-010.

Preface

The Public Interest Energy Research (PIER) Program supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

The PIER Program, managed by the California Energy Commission (Energy Commission), conducts public interest research, development, and demonstration (RD&D) projects to benefit California's electricity and natural gas ratepayers. The PIER Program strives to conduct the most promising public interest energy research by partnering with RD&D entities, including individuals, businesses, utilities, and public or private research institutions.

PIER funding efforts are focused on the following RD&D program areas:

- Buildings End-Use Energy Efficiency
- Energy-Related Environmental Research
- Energy Systems Integration
- Environmentally Preferred Advanced Generation
- Industrial/Agricultural/Water End-Use Energy Efficiency
- Renewable Energy Technologies
- Transportation

In 2003, the California Energy Commission's Public Interest Energy research (PIER) Program established the **California Climate Change Center** to document climate change research relevant to the states. This Center is a virtual organization with core research activities at Scripps Institution of Oceanography and the University of California, Berkeley, complemented by efforts at other research institutions. Priority research areas defined in PIER's five-year Climate Change Research Plan are: monitoring, analysis, and modeling of climate; analysis of options to reduce greenhouse gas emissions, assessment of physical impacts and of adaptation strategies, and analysis of the economic consequences of both climate change impacts and the efforts designed to reduce emissions.

The California Climate Change Center Report Series details ongoing Center-sponsored research. As interim project results, the information contained in these reports may change; authors should be contacted for the most recent project results. By providing ready access to this timely research, the Center seeks to inform the public and expand dissemination of climate change information; thereby leveraging collaborative efforts and increasing the benefits of this research to California's citizens, environment, and economy.

Climatic Change and the Timing of Songbird Migration in California: Focus on Coastal Central and Northern Regions is the final report for the Dynamic Ecosystem Modeling for California project (contract number 500-02-004, work authorization number MR-024) conducted by Stanford University.

For more information on the PIER Program, please visit the Energy Commission's website www.energy.ca.gov/pier/ or contract the Energy Commission at (916) 654-5164.

Table of Contents

Preface iii
Abstract vii
Executive Summary 1
1.0 Introduction 5
2.0 Spring Migration 7
2.1. Methods 7
2.1.1. Data Sources 7
2.1.2. Species Selection 9
2.1.3. Metrics of Migration 10
2.1.4. Climate Association 10
2.1.5. Migration Pattern 12
2.2. Results 13
2.2.1. Climate Variables 13
2.2.2. Climate Association 13
2.2.3. Trends in Phenology 14
2.2.4. Effort Analysis 14
2.2.5. Migration Patterns between Locations: Complete Migrants 15
2.2.6. Migration Patterns between Locations: Partial Migrants 16
2.2.7. Metrics of Arrival 18
2.2.8. Comparison with Early Twentieth Century Data 18
2.3. Discussion 18
3.0 Fall Migration 21
3.1. Introduction 21
3.2. Methods 21
3.2.1. Data Sources 21
3.2.2. Species Selection 22
3.2.3. Metrics of Migration 23
3.2.4. Climate Association 23
3.2.5. Migration Pattern 24
3.3. Results 24
3.3.1. Seasonal Migratory Patterns 24
3.3.2. Migratory Patterns of Age Classes 28
3.3.3. Migration Length 28
3.3.4. Trends in Phenology 28

3.3.5. Climate Variables 29
3.3.6. Climate Associations 29
3.4. Discussion 29
4.0 Summary and Conclusions 31
5.0 References 35

Appendix A. Spring Phenology Summary Statistics

Appendix B. Fall Phenology Summary Statistics

Appendix C. Fall Phenology Summary Statistics of Age-Differential Migration

List of Figures

Figure 1. Central and Northern California data sites 7
Figure 2. Comparison of Effort in NAB Regions 15
Figure 3. Comparison of four Neotropical migrant species 16
Figure 4. Spring distribution of partial migrants species at Station 2 17
Figure 5. Spring distribution of partial migrant species at Station 1 17
Figure 6. Fall locations of banding data 22
Figure 7. Seasonal distribution at all four stations 24
Figure 8. Seasonal distribution of four year-round species at Station 2 25
Figure 9. Seasonal distribution of three summer-only species 26
Figure 10. Seasonal distribution of three winter-only species 26
Figure 11. Seasonal distribution of 4 long-distance partial migrant species 27
Figure 12. Seasonal distribution of 4 short-distance partial migrant species 27

List of Tables

Table 1. Summary of species' spring data sources 11
Table 2. Summary of fall species data 23

Abstract

This study analyzed the spring and fall phenology of songbird species migrating through central and northern California. Using observational and banding data at multiple sites, the research team evaluated evidence for a change in arrival times being linked to either non-climatic or multi-scalar climatic explanations. The study incorporated three distinct temporal metrics of migration into its analysis. In the spring, of the 13 species with a change in arrival ($p<0.10$), 10 (77%) are likely or highly likely climate associates; the remainder are possibly climate associates. All species for which arrival is highly likely to be associated with climate are exhibiting changes ($p<0.10$, $n=5$) and all species lacking evidence for association between migration phenology and climate ($n=3$) exhibit no change. In contrast, during the fall, consistent, multi-site evidence of phenological change is lacking for most species examined. Only complete migrants ($n=7$) demonstrate multi-site associations with local/regional temperature or continental-scale climate. All other species lack widespread, consistent climatic associations with their fall arrival. All species exhibit a trend ($p<0.10$) in at least one metric of migration at one location; the majority ($n=11$) are earlier. Additionally, this study compared five indices of El Niño-Southern Oscillation (ENSO) with species' arrival times; the Multivariate ENSO Index (MEI) was the most consistent indicator of ENSO association.

Keywords: phenology, differential migration, climate change, North Atlantic Oscillation, Pacific Decadal Oscillation, El Niño Southern Oscillation, Pacific flyway

Executive Summary

Introduction

Global climate change is emerging as a significant, if not dominant, force in ecosystem change over the next several decades. Migrating birds are of particular concern, given their need of multiple habitats, which can be spread over large areas, such as wintering range in the Neotropics and breeding range in far northern temperate regions. Consequently, migratory activities have the potential to be disrupted in various ways by the diverse and asynchronous changes in ecosystems caused by climate change.

California is home to dozens of migratory bird species. It is also an integral part of the Pacific flyway as millions more birds pass through the state en route to, or returning from, breeding destinations further north.

Time is of the essence for migrating birds: it is critical for departures with favorable weather conditions, intersecting adequate resources to fuel further flight, and for spring migrants, ensuring that arrival on the breeding grounds is coincident with the flush of spring insects to feed offspring. This project focuses on the phenology (the timing of biological events) of migrant songbirds in California to: (1) understand if changes have already occurred in the timing of migration, and identify those changes; (2) identify relationships between phenology and multi-scale climatic factors; and (3) highlight species of concern. This study conducted analyses of spring and fall migration for songbirds observed or banded in coastal central and northern California.

Purpose

Although climate-related changes associated with the California marine ecosystem and western North American spring plant phenology have been documented, there are no assessments of phenological changes to land vertebrates along the Pacific coast of North America. Virtually all research on climatic change and songbird migration has been conducted in the central and eastern part of North America. The purpose of this study was to conduct the first detailed analysis of changes in migratory phenology in western North America.

Project Objectives

Spring and fall migratory phenology in California were analyzed to investigate whether:

- Changes in migratory phenology (that is, earlier or later arrival) are occurring.
- Regional and large-scale climate influences migratory phenology.
- Both short- and long-distance migrants are affected by climate.
- Western North American songbirds are responding similarly to climatic change as eastern North American species.

The research team investigated whether those species that do exhibit changes in arrival are more or less likely to have the timing of their arrival associated with multi-scale climatic variables than those species that are not exhibiting significant arrival changes. Two alternate,

non-climatic explanations for species' trends—that is, changes in reporting and changes in species' population sizes—are also evaluated.

The research team assessed two types of species' arrival data (banding and observation), two scales of species' arrival data (site-specific and regional), and two locations (inland and coastal) in central/northern California. For spring, 20–30 years of continuous data (1969–2003) on the arrival of 21 long-distance migrant songbird species were analyzed. For fall, 18 species of short- and long-distance migrant species were examined. The overarching goal was to investigate the cross-seasonal (that is, spring and fall) phenological changes in western North American terrestrial ecosystems and provide a basis for comparison with phenological changes identified in migrant songbirds in eastern North America.

Outcomes

Spring Migratory Phenology

Using correlation analysis, of the 13 species with a significant ($P<0.10$) change in arrival, 10 (77%) are likely or highly likely to be associated with temperature and a large-scale climate oscillation index (El Niño Southern Oscillation, ENSO; North Atlantic Oscillation, NAO; and/or Pacific Decadal Oscillation, PDO); the remainder are possibly climate associates. All species for which spring arrival is highly likely to be associated with climate are exhibiting changes (n=5) and all species lacking evidence for association between migration phenology and climate (n=3) exhibit no change. Migrants tend to arrive earlier in association with warmer temperatures, positive NAO indices, and stronger ENSO indices. Six species negatively correlate with ENSO at least at one location; four are correlated at two or more locations. Thirteen species' arrival is correlated with NAO at least at one location; 10 (77%) are negatively associated.

Fall Migratory Phenology

Twelve of 15 species exhibit a trend ($P\leq0.05$) in first or median arrival date at one location; the majority (n=8) are earlier. When age classes are separated, all significant arrival trends (n=5) of juveniles are earlier. A regionally consistent relationship between autumn migratory phenology and autumn climate (local and regional temperature, El Niño-South Oscillation, Pacific Decadal Oscillation) is not detected. In contrast to previous studies in eastern North America, advanced autumn phenology is detected. Examination of the seasonal arrival distribution of the 14 migrant species suggests that the conventional categories of "short" and "long" distance migrant may be too general to assess patterns in the intra-seasonal phenology of migrant species.

Conclusions

This multi-site analysis provides greater evidence that changes in western North American land ecosystems are already detectable with warming of less than a degree Celsius over the past century.

Earlier spring and autumn migratory phenology is occurring along the coastal Pacific flyway. Migrants in California whose arrival is likely or highly likely associated with climate constitute the majority of species that are exhibiting statistically significant trends towards earlier arrival. There is evidence for extensive phenological changes in California songbirds' migratory phenology—as well as differences between seasons, between species, between data sites, and

between metrics of migration. The spatial and temporal complexity of bird migration indicates the importance of using larger scales of research and multiple data sites to examine the extent of phenological changes across species' ranges and populations.

Recommendations

There are few analyses of species' responses to climatic change in western North America. This initial study detects differences between eastern and western songbird species, which are likely related to the prominent differences in ecosystems (such as aridity) across the continent. Therefore, there is a strong need for further research in California to detect, understand, and anticipate the ecosystem impacts from global warming.

Four general recommendations for future analysis and modeling of phenology under climatic change scenarios are made:

- Use multiple data sites in order to evaluate change over the scale of a region or species' range
- Develop multiple metrics of phenological change in order capture different aspects of a species' biology
- Create multi-factor assessments of change and association in order to synthesize results from multiple data sites and multiple climatic scales
- Include multiple trophic levels of analysis when possible

Future modeling efforts are encouraged to consider elements of phenological change at multiple spatio-temporal scales. In particular, cross-seasonal linkages (for example, spring, summer, autumn) are a fruitful area for further investigation to enhance understanding of how climatic change influences species' life history.

1.0 Introduction

Over the past decade, hundreds of studies have detected a signal of climatic change in plants and animals around the planet. *Phenology,* the timing of biological events, has been used as an indicator of ecosystem response to global warming and human influence on climate. There is widespread concern about asynchronous changes in spring phenology between nutrition levels as well as interest in the spatial relationships of changes. For instance, spring might be advancing due to warming temperatures, but migratory birds might be unable to alter the timing of their arrival to correspond to these changes. Consequently, the migrants could be out of time sync with the insect food sources for their offspring.

Furthermore, geographic differences in the effects of global warming can have serious consequences for species that rely on resources spread across a hemisphere. Migratory birds can be affected differently by changing conditions on their wintering grounds, migratory routes, and breeding ranges. Northern latitudes are warming more quickly, compared to sub-tropical and tropical latitudes—a situation that could lead to greater phenological changes on the breeding grounds compared to the more southerly migration route. These questions make migratory bird phenology a critical research area in evaluating the current and future impacts of climatic change.

For reasons detailed in the Methods section, for spring, the study focused on the phenology of Neotropical, long-distance species. Additional, but more limited, data on selected species of partial migrants are discussed. Data on fall species are more comprehensive; this study conducted analyses on multiple categories of resident and migratory species.

Over the past decade, there have been hundreds of studies to detect a signal of climatic change in plant and animal behavior (IPCC 2001; Parmesan and Yohe 2003; Root et al. 2003). Widespread changes in phenology, ranges, and abundance have been identified. Recently, a study applied the climatological framework of climatic change detection and attribution to attribute many species' phenological shifts to anthropogenic forcings on the atmosphere (Root et al. 2005).

For spring migration, the research extend the conceptual model of detection and attribution to test the hypothesis that changes in certain migratory bird species' spring phenology are best explained by recent climatic change. In summary, over 50% of the species analyzed have evidence of a change in arrival; the majority arrives earlier. The study considered evidence for three alternative hypotheses to explain these observed changes: (1) an increase in the number of birds (increasing species' populations), (2) an increase in reporting (increasing observer population), and (3) climatic-influences on species' arrival. Specifically, to assess evidence for the third hypothesis, the study examined the trend in arrival (detection) separately from species' association with climate at the local, regional, and continental scales. It then compared the results of a species' trend analysis with the likelihood of the species' climate association. The results substantiate the theory that climatic change is the best explanation for the observed changes in species' spring phenology.

This study conducted similar analyses for fall migrant species. In summary, there is limited association between species' arrival and climatic variables. Thus, the detection and attribution framework used for spring analyses is not applicable. However, the study was able to compare, in detail, the seasonal distribution of numerous species with different migratory/residency

characteristics. It also addressed long-standing questions on the phenology of juvenile and adult songbird migration along coastal California.

This analysis includes two other unique methodological elements. First, it frames each species' analysis with multiple data sites, multiple metrics of migration, and multiple scales of climate. The study does not rely on a single indicator or single dataset. Second, it uses two different types of data—banding station and regional observer networks—to conduct multiple scales of analysis and compare results over a region. Similarly, this study examines climate variables at the local, regional, and continental scales. Particularly, El Niño-Southern Oscillation (ENSO) is an important part of coastal California climate. This study compares six different indices of ENSO (e.g., Stenseth et al. 2003) to ascertain whether a particular index better captures terrestrial ecosystem conditions of importance to migratory birds.

Due to the differences in datasets, species, and analytic foci, the Methods, Results, and Discussion for spring and fall migration are presented separately. The final section offers overall conclusions, observations, and future directions.

2.0 Spring Migration

2.1. Methods

2.1.1. Data Sources

Spring songbird arrival data for coastal central and northern California came from two sources: the U.S. Bird Banding Laboratory, and the original records used to compile seasonal summaries published in *North American Birds* (NAB) and its associated preceding publications (i.e., *Field Notes, National Audubon Society Field Notes, American Birds*). Figure 1 illustrates the two regions and banding station locations of data.

Bird Banding Data

Initially, 35 California sites, which had 10,000+ birds banded over the past 50 years, were selected. Of these, 11 had sufficiently long-term data for further year-by-year, seasonal scrutiny. Since the banding data were obtained from the public record, there were no accompanying station-specific banding protocols, such as effort data (e.g., the number of nets used, the length of time that nets were open). Thus, the researchers developed filtering parameters to select locations, seasons, and years that are highly likely to have had data collected in a systematic, scientific manner. There was little ambiguity in selection: a location either had long-term, consistent data or it had obvious indicators of less serious, sporadic banding activity. Furthermore, most of the locations identified correspond with known current or historic bird observatories.

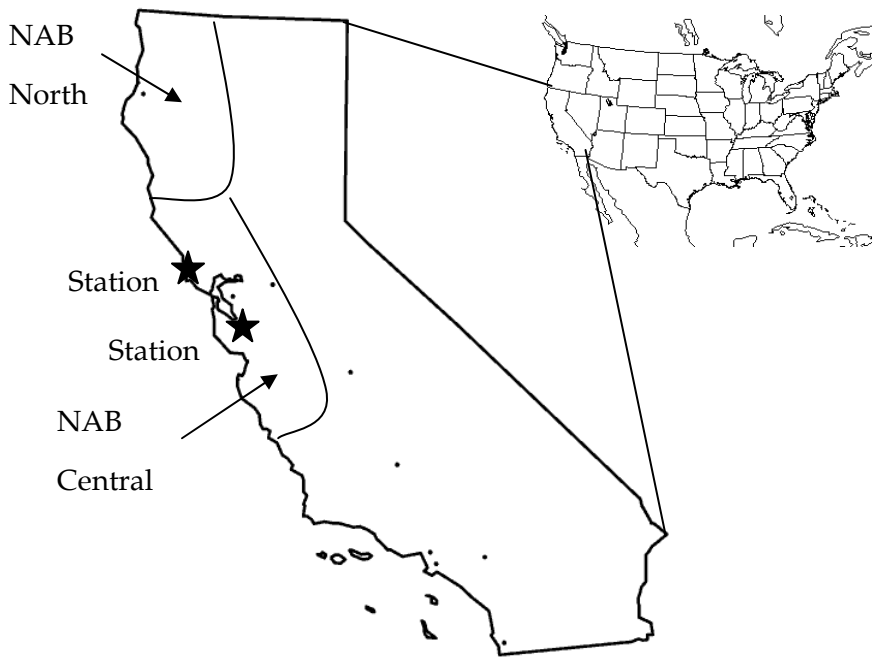

Figure 1. Central and Northern California data sites

The minimum spring banding season was defined as Julian day 45–160 (mid-February through early June). The minimum effort criteria for a banding season was banding at least one bird in a day with a three-day or less gap between birds banded for the duration of a season. For a continuous span of years to be analyzed further, it must have met the adequate season criteria for a minimum of 10 years with no gaps greater than three years between good seasons. Two banding data locations were selected that met these criteria. Data at Station 1 were available from 1985–1997 and at Station 2 from 1969–2002. Despite being in close proximity (less than 100 km, or 62 mile, apart), the stations have distinct migratory patterns, and thus, the species observations are considered independent.

G. Ballard and G. Geupel at PRBO Conservation Science provided recapture data (1971–2002) for the six species at banding Station 2. Recaptured birds at this location are mostly local residents (Grant Ballard, pers. comm.) and could affect results if they arrived earlier than the majority of new captures. Analyses were conducted with both sets of data (i.e., with and without recaptures). Accordingly, the local residents arrived slightly earlier, with the median of first arrival 1–5 days earlier than the dataset without recaptures. There were negligible differences in the median of arrival. There were no differences in the statistical significance of arrival trends for first arrival or the median of migration. Thus, given the minimal differences, and for consistency with banding Station 1, the results are reported using the USBBL dataset (no recaptures).

North American Birds Data

Since the late 1970s, birders have collected and reported sightings of species to county-level coordinators associated with the American Birding Association or the National Audubon Society. These observations have been compiled and summaries published in quarterly birding journals. The journals have undergone several association and name changes, from *American Birds* to *Field Notes* to, currently, *North American Birds.*

The north-central California editors have kept the hand-written records for the past 20 years in an assortment of approximately 20 binders and boxes. These records cover California from roughly San Luis Obispo northwards. The corresponding records for southern California were not made available for assessment. Researchers identified 25 candidate species and entered all of the hand-written records into spreadsheets for all years available. The older records were more extensive. As time has progressed, interest has shifted from recording and reporting regular arrivals to rarities. Some recent species records were completely unavailable. To accommodate early sighting of swallows, researchers defined the NAB season as beginning on February 1. For most species, this study's researchers have data from approximately 1979–1994 or 1979–2003.

The county-based records were divided into two geographic subsets: NAB Central and NAB North (Figure 1). NAB Central consists of coastal central California, including Alameda, Contra Costa, Marin, Monterey, Napa, San Benito, Santa Clara, Santa Cruz, San Francisco, San Mateo, Sonoma, and Solano counties. NAB North consists of coastal northern California, including Del Norte, Lake, Humboldt, Mendocino, Siskiyou, and Trinity counties. These divisions are based on geographic similarity, continuity, and differences in observer effort. To assess changes in effort, researchers summed the number of reports received each year for the species selected for this analysis (see species selection criteria below, and Results).

Individual Observers

At the outset of this project, researchers conducted a statewide search for local data, as might have been maintained by local birders or biologists (such data has been used elsewhere, with success, for this type of analysis). Researchers inquired with county-coordinators from *North American Birds* throughout the state. After much correspondence and examination of possible datasets, data were obtained from four individual sources; two of which are in coastal northern-central California (Berkeley and Santa Clara County). The central-northern California data will complement the previous data sources and provide an opportunity to compare collecting methods. The remaining two sources are located in southeastern California, on opposite slopes of the southern terminus of the Sierra Nevada (Inyo County and Indian Wells Valley).

This study obtained historical records of the spring arrival of 15 species in Berkeley, California, from the early 1900s to 1947. These data were published in a bar graph in the proceedings of the Cooper Ornithological Society in 1948. The specific year of observation is lacking; researchers only have a series of 10–34 arrival dates during the early part of the century. Even so, the mean of these data is a fortuitous benchmark for changes. The study assumed that the species arrival dates were from the author's own records of arrival in the area; however, they might include reports from other correspondents. Thus, the observation effort is much less than the NAB data and these data are subject to observer-effort bias. This report includes comparisons with the NAB and banding data, but adds a strong caveat in interpretation of the results.

For Inyo County and Indian Wells, there were nominally data for 21 species and 13 species, respectively. It was decided to disregard these data due to questions on observer consistency. Initial analyses showed extreme and inconsistent results, flags for changes in observer effort and, for Inyo County, confounding influences of elevation. For the Santa Clara County dataset, there are data on 22 species. Given time constraints, and the likely overlap between this dataset and the NAB data, this dataset was not included in the following analyses.

2.1.2. Species Selection

This study focused its analyses on long-distance Neotropical migrants for a few reasons. First, these species are of considerable conservation concern. Second, at banding stations and for observers, migrants will not be confused with resident birds of the same species during spring migration. Third, for the individual and network data, observers are keen to spot the new arrivals each year.

A special emphasis has been placed on evaluating the existence of over-wintering populations in central-northern California. While the vast majority of a species migrates south of the United States for the winter, for some species, a small number (1–20) birds might remain in coastal areas. This is much more of a problem in southern California, where vagrants from Mexico and small, irregular flocks of Neotropical species can occur in a given year. In the rest of California, overwintering Neotropical migrants are generally limited to less than 10 birds of a species and are particularly found in central coastal California. Researchers consulted several sources to identify species of concern in this regard.

In addition to the Neotropical migrants, there are several species that are either (1) partial migrants, or (2) complete migrants, but winter in California. These species do have migratory

populations that either reside in California or pass through the region, but are difficult to separate from the residents. In order to attempt to identify the migratory passage, researchers considered the seasonal distribution of individuals. This was possible with the highest abundance species that had distinct migratory phases at the banding stations, i.e., the migrants were discernable from wintering or breeding populations.

The species list was created by prioritizing the banding data and NAB data—the most thorough and complete data sources. To be included, a species had to have: (1) a minimum of five birds banded in a year, or one sighting per year for NAB data, (2) no more than a three-year gap between years with the minimum number of birds collected, (3) a continuous span of at least 10 years of viable years, and (4) two-thirds of the years within the continuous span must have data. Eight species met these criteria at the banding stations (five in common between both). Twenty species met these criteria from the NAB data (13 in common between central and northern California). Table 1 lists the species and their respective data sources.

2.1.3. Metrics of Migration

Researchers defined three metrics of migration to be used in trend and climate association analyses with the banding and NAB data: (1) first record of the season, (2) onset of continuous migration, and (3) median of the migratory period. Each metric has its particular benefits and weaknesses and captures a different ecological aspect of migration (see Discussion). The first record was simply the absolute first date of arrival; this applied to both the banding and NAB data. For the banding data, researchers defined the onset of continuous migration as the date on which there was no greater than a three-day gap between birds banded during the species' passage through the site. For the NAB data, researchers identified the two highest months of species' records and defined the median date of arrival within those two months as the onset of continuous migration. This study only considers the first part of the NAB season, because observer effort is expected to decline as the season progresses and first sightings have been made; for this dataset, researchers could only evaluate the two metrics of initial migratory passage. For the banding data, the median of the migratory period is the date on which 50% of the birds for that season have been banded. There is only one observation for the individual observer data: the first date of sighting.

2.1.4. Climate Association

Researchers calculated the Pearson correlation coefficient between the arrival date (for each migration metric) and climate at the local, regional, and continental scales. For the local scale, the study used monthly minimum and maximum temperatures recorded at the National Weather Service COOP weather station closest to the banding location: San Jose International Airport, California, (37°21′N, 121°54′W) for Station 1; and Petaluma, California, (38°15′W, 122°36′W) for Station 2. Researchers selected a centrally located COOP station for the NAB data: San Francisco International Airport (37°37′N, 122°23′W) for central California; and Eureka (40°49′N, 124°10′W) for Northern California. For the individual observer data, the study used San Jose International Airport for the Santa Clara County dataset, InyoKern (35°39′N, 117°49′W) for the Indian Wells dataset, and Independence (36°48′N, 118°12′W) for the Inyo County dataset. For the regional scale, researchers created monthly regional averages of mean temperature anomalies from the Historical Climatology Network. Researchers defined two regions: coastal, western California (30-50°N, 115-125°W); and the United States west of the Rocky Mountains (30-50°N, 105-125°W).

Table 1. Summary of species' spring data sources

	Weston 1948	BBL	NAB Central	NAB North
Vaux's Swift			X	X
Western Kingbird			X	X
Olive-sided Flycatcher	X		X	X
Black-headed Grosebeak	X	X	X	X
Lazuli Bunting	X		X	
Western Wood-Pewee	X		X	X
Western Tanager			X	X
Barn Swallow	X	X	X	X
Cliff Swallow	X		X	X
Northern Rough-winged Swallow			X	X
Warbling Vireo	X	X	X	X
Nashville Warbler			X	X
Orange-crowned Warbler	X	X	X	X
Black-throated Gray Warbler			X	X
MacGillvary's Warbler	X		X	X
Wilson's Warbler	X	X	X	X
Blue-grey Gnatcatcher			X	X
House Wren	X		X	X
Swainson's Thrush	X	X	X	
Western/Pacific-slope Flycatcher	X	X		
Chipping Sparrow	X			
Yellow Warbler	X	X		

At the continental scale, this study evaluated a species' association with the North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), and the El Niño-Southern Oscillation (ENSO). For NAO, researchers used a station-based index.[1] Because ENSO is such an important part of the California coastal climate, researchers compared five different indices of ENSO (e.g., Stenseth et al. 2003) to ascertain whether a particular index better captures terrestrial ecosystem conditions of importance to migratory birds. The study examined the Multi-variate ENSO Index (MEI), the Southern Oscillation Index (SOI), the North Pacific Index (NP), the N34 index, and transN index. Researchers then selected the most consistent index for further analyses (see Results).

For all of the associations, researchers examined only the index or monthly mean temperature for the month of arrival and the preceding month in order to minimize spurious associations. Climate conditions in these proximal months have the clearest possible link to conditions experienced immediately before departure from the wintering grounds and/or during migration.

For the banding and NAB data, researchers created a metric of likelihood of a species' association with climate using the associations with temperature and climate indices described above. To enhance the rigor of the analysis, researchers incorporated multiple scales of climate association *and* multiple data sites. The subjective probabilities are based upon the consistency of evidence for climate association at 2–4 data sites for each species. Due to the high correlation between temperatures at the local and regional scale, they are combined into one category.

Researchers defined four categories of association: (1) highly likely (statistically significant association ($p < 0.10$) of the same sign for both temperature and a climate index at *two or more* locations), (2) likely (statistically significant association of the same sign for both temperature and a climate index at *one* location), (3) possible (statistically significant association of only one climate variable or inconsistent signs for climate variables between locations), and (4) none (no associations). In other words, a species assigned to the highly likely climate association category has an association ($p < 0.10$) of the same sign with temperature (regional or local) at two locations *and* an association ($p < 0.10$) of the same sign with the same climate index (i.e., NAO or ENSO) at two or more data sites.

2.1.5. Migration Pattern

To compare the seasonal passage of the four species in common between the two banding sites, researchers plotted total number of individuals of each species banded a given Julian day for all years of data. They used the non-linear curve-fitting tools of Origin 7.0 (OriginLab, Northampton, Mass. 2002) to fit curves to the plots. Possible peaks were identified using a "peak-picking" algorithm that searched seven-day time units for "peaks" that were at least 25% of the maximum number of individuals on a single day. Peaks that were only from a year or two of unusually high bird records or are not part of a several day trend were disregarded. Finally, the remaining peaks (unimodal to biomdal for each species) were then fit with non-linear curve-fitting tools using a least-squares-fitting algorithm (e.g., Figure 3).

---

[1] See www.cgd.ucar.edu/cas/jhurrell/indices.html.

The same procedure was used to plot the arrival distribution of partial migrant species. After examining three species of migrants at Station 2 (Figure 3) and 11 species of migrants at Station 1 (Figure 4), six species at Station 1 had patterns suitable for further analysis.

2.2. Results

2.2.1. Climate Variables

Researchers evaluated each species' association with the five indices of ENSO (MEI, SOI, NP, transN, N34; see Section 2.1.4). For a given arrival metric, if a species' arrival correlated ($p < 0.10$) with three or more of the indices, it was defined as associated with ENSO at that location. Of all species and all arrival metrics that met this criterion (n=17), only one index —MEI—was consistently associated with *all* of them. NP, SOI, and N34 were associated with 75% or more of the species and metrics in this group. For further analyses, this study used the MEI index as the indicator of ENSO association.

At all COOP stations, the seasonal mean minimum temperature (March, April, and May) is increasing ($p < 0.05$) at 0.65°F–1.40°F (0.36°C–0.78°C) per decade. The seasonal maximum mean temperature is significantly increasing only at Eureka. Monthly mean minimum temperatures for San Francisco, San Jose Airport, and Eureka correlate ($p < 0.05$) with ENSO from February to May and NAO only in May. Independence and Inyokern associate with NAO in March only; in contrast to the Pacific coastal stations, neither location's monthly mean temperature associates with ENSO.

2.2.2. Climate Association

A summary of temperature and climate index associations, for all species, locations, and arrival metrics is provided in Appendix A. Using the criteria specified in the Methods section, five species are highly likely climate associates, eight species are likely associates, four species are possible associates, and three species show no evidence of climate association. The criteria upon which these categories are based are intended to minimize Type I error, that is, incorrectly attributing climate association to species. Given the complexity and high internal variability of migration (i.e., sex and age differential migration, widespread wintering populations) and the noise of observation data over multiple sites (even with the best efforts to filter outliers), it is possible that species' whose migratory initiation or progression are related to climate at some scale are incorrectly categorized (Type II error).

Six species negatively associate with ENSO at least at one location; four of these associate with ENSO at two or more locations. Thirteen species associate with NAO at least at one location and 10 (77%) are negatively correlated. Nine species associate with PDO at least at one location and four associate at multiple locations. The most consistent climate-index associates are: Orange-crowned Warbler (ENSO and NAO at both banding sites), Wilson's Warbler (ENSO at both Station 1 and northern CA region, PDO at both banding sites and northern CA), and Warbling Vireo (ENSO and NAO at both banding sites). For central and northern NAB species, only two species were consistently associated (i.e., same index, $p < 0.10$) between the regions. Most of the other 11 species' arrivals were climate-associated in one region and not the other. For the banding data, three of five species were consistent between locations.

Temperature-species associations are more frequent than climate index associations. Fourteen species negatively associate with local or regional temperature at least at one location. Between

the banding stations, three of five species consistently associate (i.e., same sign, $p<0.10$) with local or regional temperature. For the central and northern California NAB regions, six of 13 species are consistently associated with regional temperature.

2.2.3. Trends in Phenology

Thirteen of the 21 species (62%) exhibit a change ($p<0.10$) in arrival of one or more metrics of migratory passage. Of those, eight are arriving earlier (62%), two are later (15%), and three are uncertain due to different signs at different data sites. Of the 13 species, ten (77%) are classified as likely or highly-like climate associates. The remaining three species are possible climate associates.

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

2.2.4. Effort Analysis

This study's researchers detect no bias toward earlier sightings due to increased reporting for the NAB data. Even though general observer effort might be increasing (i.e., increasing human population), there is no evidence for an increase in reporting of the species in this analysis. For the northern region, there is no change in effort ($p=0.40$) even though the total number of records is lower than the central region. For the central region, effort is constant ($p=0.99$) through 1995 (Figure 2). From 1995–2003, there is a sharp decrease in reports, possibly due to a change in archival patterns or a change in editor. One editor noted more recent emphasis placed upon unusual sightings compared to regular arrivals.

There is no reason to suspect significant bias in the banding data. This study's researchers consistently evaluated the locations and seasons to detect minimum effort from Julian day 45 and consistently through the season until Julian day 160. Minimum effort can be assured for both stations. Data on net hours from 1976–2002 were obtained for Station 2. Spring banding effort declined over the study period at this location, with a sharp drop in 1989 when banding switched from daily to three days per week (pers. comm. Geoff Geupel).

The research team found net hours to be statistically significantly correlated with the total number of birds banded in a season ($r=0.43$, $p=0.03$, outlier year (1997) removed). As a proxy of total effort at Station 1, the team derived the seasonal sum of the total birds banded and conducted a regression analysis. At Station 1, the seasonal total of birds, and therefore the inferred effort, at this site declined from 1988 onwards ($p<0.01$). However, there is a notable range of birds banded per net-hour (4.3–11 birds/100 hours at Station 2). Thus, seasonal totals are indicative, but not completely predictive, of banding effort. This is a caveat in the interpretation of these data. Declining effort would be expected to result in later detection, and hence, trends toward later arrival if banding effort was a significant factor affecting species' apparent phenology. This may explain the trends towards later arrival at Station 2; however, at Station 1, three species are arriving earlier.

Additionally, the research team correlated the first arrival date for each species with the total effort (total birds banded for Station 1 and net hours for Station 2) during the month of the

species' arrival for the entire study period. No species at Station 1 had statistically-significant correlations and four of the six species at Station 2 were also uncorrelated. The two species' at Station 2 with significant correlations were positively associated, i.e. earlier detection of arrival with decreasing banding effort. This counter-intuitive correlation suggests that the association between effort and arrival for these species is spurious.

There is also no reason to suspect consistent significant bias in the individual observer effort data. The sources of the data provided their regular routines of visiting locations or collecting the observations of others (i.e., Santa Clara county). There is the potential for higher variation in the data—both due to individual schedules and the more local reporting—but there is not reason to believe that there is systematic error or unidirectional bias.

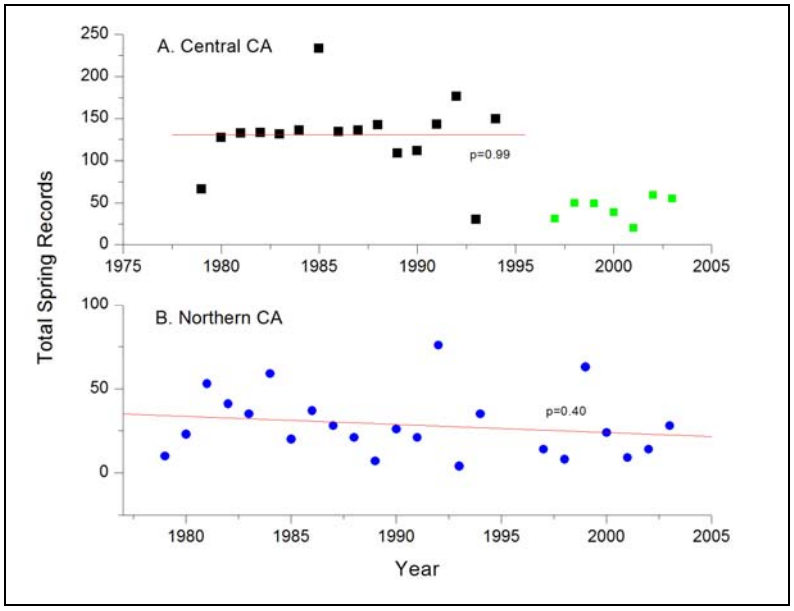

Figure 2. Comparison of Effort in NAB Regions

2.2.5. Migration Patterns between Locations: Complete Migrants

There are notable differences in migration patterns between locations. Most of the species examined are sighted three weeks later in northern California, compared to southern California; the range is 5–45 days between the median dates of first arrival within a species. Only three of 13 species associate with NAO in northern California, compared to eight of 22 species in central California. ENSO associations are comparable.

The banding station results suggest even more remarkable regional differences, both between locations and among species, over a much smaller area. While the median of arrival is similar for all five species in common between the sites, four species' first arrival is approximately a week apart and one species (Pacific Slope Flycatcher) is detected 18 days later at Station 2, compared to Station 1. On Figure 3, the pattern and timing of arrival of the Swainson's Thrush is nearly identical between the sites. In comparison, the Orange-crowned warbler arrives nearly three weeks earlier at Station 2, compared to Station 1. Furthermore, Station 2 captures increase again in the late season, suggesting summer residents, while captures at Station 1 are near zero

by late summer, suggesting only migratory passage. The Wilson's Warbler exhibits a two-peaked distribution at Station 2, with only the second peak in common with Station 1.

For two species, there is an unexpectedly long lag between the median first arrival of the species in the central California region and its median first banding. For the Warbling Vireo, according to the NAB data, the median of first arrival is Julian day 76; in comparison, the median of first banding at Station 1 is Julian day 114, and at Station 2 is Julian day 103, which is 3–4 weeks later. The Wilson's Warbler was similar, with a difference of two weeks between first sighting and first banding. Another two species (Orange-crowned warbler, Swainson's Thrush), however, had quite similar dates of first sighting and first banding.

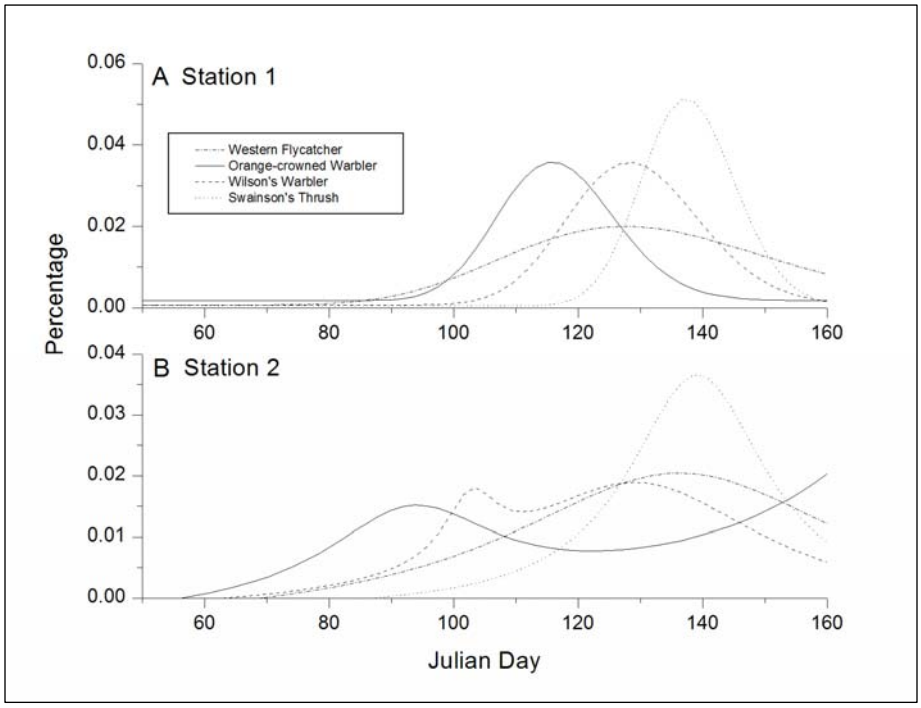

Figure 3. Comparison of four Neotropical migrant species

2.2.6. Migration Patterns between Locations: Partial Migrants

There are remarkable differences in the partial migrant species' passage between Stations 1 and 2. Only three species at Station 2 (Figure 4) had adequate data for further analysis, in contrast to 11 species at Station 1 (Figure 5). None of the species at Station 2 were analyzed for climate associations, since there was no clear peak of arrival during the spring. The Ruby-crowned Kinglet, a winter resident, declined in abundance over the season, as expected. The Song Sparrow, the only species in common between the locations, arrived later at Station 2 and did not peak before the end of the season.

At Station 1, six species that are partial migrants had clear, single peaks within the season suitable for analysis for climate associations: Hermit Thrush, Brown-headed cowbird, Audubon's Warbler, Common Yellowthroat, Lincoln Sparrow, and Oregon Junco. Researchers only computed the median of arrival because the first arrival dates were confounded by

residents of the same species. Only the Common Yellowthroat had a statistically significant trend (earlier).

Compared to the long distance migrants, the climate associations were minimal. The Common Yellowthroat was correlated ($p < 0.10$) with regional anomaly and with local maximum temperature. The Audubon's Warbler was the only other species with a correlation (minimum and maximum local temperature).

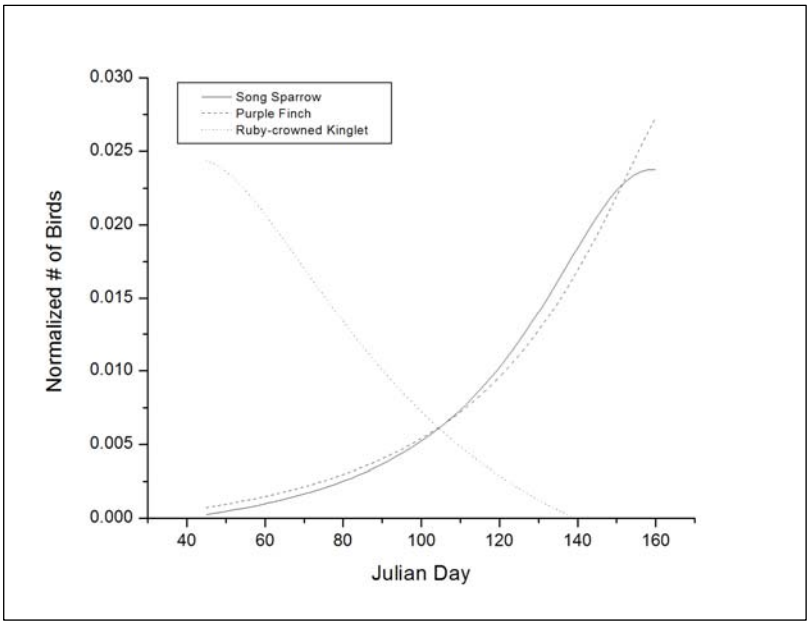

Figure 4. Spring distribution of partial migrants species at Station 2

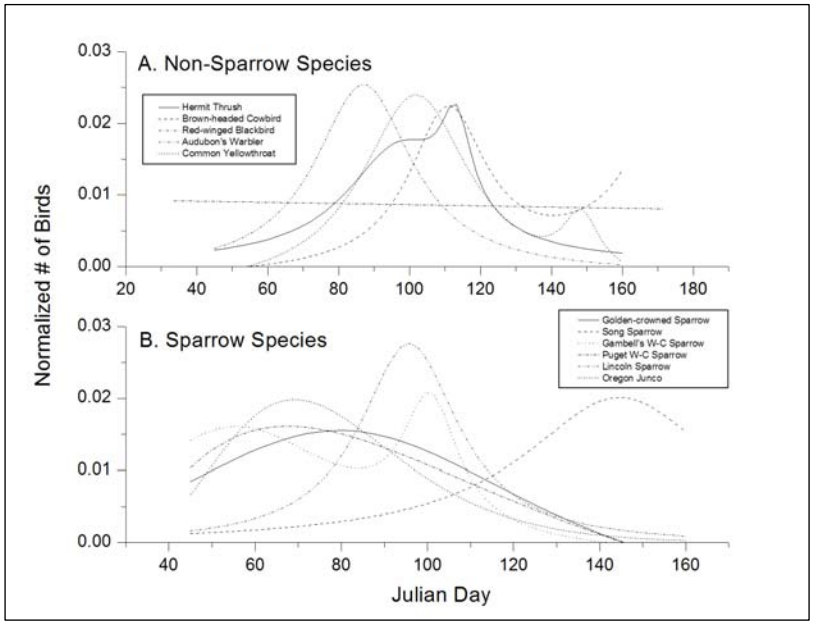

Figure 5. Spring distribution of partial migrant species at Station 1

2.2.7. Metrics of Arrival

Considering only those species categorized as highly likely or likely climate associates, the metric of continuous migration identified a comparable number of trends as the first arrival date. There are only two trends detectible in the median of arrival.. There was no clear difference in the number of arrival-climate associations between the metrics of migratory passage. There were nearly equal numbers of species-location associations with each metric for the climate indices and temperatures.

2.2.8. Comparison with Early Twentieth Century Data

Researchers compared the mean arrival date from Weston (1948) with the mean arrival data from the NAB metric of continuous migration. This was the most conservative analysis possible using the study's data. There were 12 species in common between the central California region and the Weston data. Seven (58%) of those species are arriving earlier ($p < 0.05$). If the first sighting record is used, then 11 (92%) of the species are arriving earlier. Although the authors reiterate the concern about observer bias (more contemporary sightings), these data are still indicative of changes in spring phenology.

2.3. Discussion

The analysis of spring migratory phenology suggests four major conclusions. First, species whose arrival is likely or highly likely associated with climate at multiple scales constitute the majority (77%) of species that are exhibiting trends. In view of weak evidence for the alternative hypotheses to explain the changes, climatic change is the most compelling explanation for these phenological shifts. Second, these species are long distance Neotropical migrants, species hypothesized to have less climate-related influences on their migration (e.g., Hagan et al. 1991; Bradley et al. 1999). Third, there are notable differences within a relatively small region, suggesting the need for multiple data sources and larger-scale research to detect and assess the impacts of climatic change on species. Fourth, in this analysis, there were benefits to public network observer collected data over the banding data in terms of the number (and type) of species sighted and regional consistency. Obviously, the value of a type of data is linked to the purpose of analysis; however, public or individual observer data can have clear value even when banding data is collected in the same region.

This study considered three hypotheses to explain the phenological changes detected in migrant species: (1) an increase in the number of birds (increasing species' population, i.e., Tryjanowski and Sparks 2001), (2) an increase in reporting (increasing observer population), and (3) climate-associated influence on the initiation or progression of migration. This study only found strong evidence for the latter proposition. Much concern has been directed toward overall declining populations of Neotropical migrants (e.g., Terborgh 1989). No references could be found to suggest an increase in Neotropical migrant populations over the past two decades along the Pacific flyway; the most comprehensive study finds widespread declines (Ballard et al. 2003). This study closely examined the issue of reporting bias in the analysis of the data and found no specific reason for concern (see Results). Given the evidence for declining banding/observation effort, as well as species' population declines, this study's calculations of changes in species' arrival are considered to be conservative. Of course, both of these concerns remain a small possibility beyond the ability of our methods to detect or remove.

This study finds compelling evidence that climate-associated species are changing while species' without evidence for the influence of local, regional, or continental climate on their arrival in central or northern California are not shifting their phenology. Multi-scalar and multi-site species data were used to assess each species: the analysis is not dependent upon one location, one data type, or one climatic variable. Furthermore, the species group was not pre-selected in any way to bias the species towards climatic association. The selection of species was solely based on data availability and the desirability of selecting species that are complete migrants.

Thus, this study concludes that climatic change is the most likely explanation for the majority of spring phenological changes in arrival observed among these 22 species of long distance, Neotropical migrants. This study supplements existing research suggesting differential responses between short- and long-distance migrants (Butler 2003; Jenni and Kery 2003; Lemoine and Bohning-Gaese 2003). Butler (2003) finds that short-distance migrants are arriving nearly two weeks earlier in eastern New York, while long-distant migrants arrived only four days earlier on average. Although such a comparison was not possible in this analysis due to confounding of short distance migrants and wintering populations, this study found long-distance migrant species that are arriving 2–3 weeks earlier. Clearly, the results identify multiple species of long-distance migrants that have climate influences on some aspect of their migratory schedule and are exhibiting significant changes in spring migratory phenology.

In addition to suggesting a new methodology for assessing phenological change (i.e., applying the conceptual framework of detection and attribution), the detailed analysis of multiple data sites and types lends insight into migratory phenology over larger scales. The preponderance of studies thus far have examined single-site data to detect climatic influences (e.g., Crick et al. 1997; Winkel and Hudde 1997; Penuelas et al. 2002), though a few recent studies have considered larger scales. If studies are to extend beyond local detection to characterizing changes, and possible impacts, upon species or broad populations, it will be necessary to use larger scales of research and multiple data sites to examine how extensive the changes are and the different factors at play.

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

3.0 Fall Migration

3.1. Introduction

Research on the phenology of fall migration is quite underrepresented compared to studies of spring phenology. This is due to many factors, including fewer stations monitoring fall migration, greater spatial and temporal dispersal of fall migrants (in contrast to following spring "flyways" and movement along riparian corridors), and the more secretive behavior of post-breeding adults making identification and visual counts more difficult. Avoiding several of these issues, the California coastal fall migration system offers a unique opportunity for fall phenological studies.

Throughout coastal California, greater numbers of birds are observed and banded in the fall, compared to spring (Desante 1983). In particular, there are high numbers of hatching-year (HY) birds, compared to adults (after-hatching-year, AHY). Explanations for this phenomenon include wind patterns and the poor development of juvenile navigation systems funneling birds towards the coast (Ralph 1971; Stewart et al. 1974; Ralph 1981). None of these studies have examined the seasonal distribution and timing of arrival for HY and AHY migrants in detail, leaving speculation that adult birds migrate earlier than juveniles.

Furthermore, while fall migration in California has received repeated scrutiny with regard to migrant populations (Pyle et al. 1994; Ballard et al. 2003; Richardson et al. 2003), there has been no detailed analysis of changes in fall phenology at any location and no comparison between locations. Studies consistently find declining populations of a number of species, and one suggests preliminary evidence for changes in arrival (Richardson et al. 2003).

The following analyses offer new insights on both of these questions—the timing of juvenile migration relative to adults and recent phenological changes—using fall phenology data from four locations in central/north California. They examine several categories of migrants, including both short- and long-distance migrants, partial and complete migrants, and for comparison, resident species. As in the preceding analyses of spring migration, these analyses assess (1) trends in arrival, (2) association of arrival with multi-scalar climatic variables, (3) migratory period, and (4) seasonal arrival distribution. Adequate data are available for 16 species of migrants, with long-term term data at 2–4 locations each. Ten species have adequate data on both hatching year and after-hatching-year age classes; the above analyses are conducted for both age classes as well.

3.2. Methods

3.2.1. Data Sources

Fall songbird arrival data for coastal central and northern California was obtained from the U.S. Bird Banding Laboratory. The fall banding season was defined as Julian day 225–335 (mid-August through November). The minimum effort criteria for a banding season were the same as for spring migration. Four banding data locations were selected from multiple possible locations in California. Data at Station 1 was available from 1985-1997, Station 2 from 1969–2000, Station 3 from 1969–2002, and Station 4 from 1983–1999. Stations 1 and 2 are the same as for spring migration. Approximate locations are noted on Figure 6.

Figure 6. Fall locations of banding data

3.2.2. Species Selection

The species selection criteria were the same as for spring. Forty species met these criteria. Of those, there were sixteen migratory species and five resident species with adequate data at two or more locations; analyses were conducted on this subset. Fourteen of the 16 sixteen species had data at three or more locations

For this study, six categories of migratory pattern and residency status in California were created:

1. complete migrant, summer-only resident in central/northern California (CS; all Neotropical migrants)
2. complete migrant, winter-only resident in central/northern California (CW)
3. short-distance partial migrant with winter-only residents in central/northern California (PW)
4. short-distance partial migrant, with year-round populations in central/northern California (SPR)
5. long-distance partial migrant, with year-round populations in central/northern California (LPR)
6. resident, with year-round populations in central/northern California and minimal breeding-only range on the northern Pacific flyway (R)

There are five CS, two CW, one PW, four SPR, and four LPR species (Table 2).

3.2.3. Metrics of Migration

The three metrics of migration are the same as for spring migration. Two measures of the length of migratory passage are also defined. The first is the difference between the absolute first and last days of a species record. The second is the length of continuous migration, calculated by taking the difference between the first and last dates for which there is no greater than a three-day gap between birds banded.

Table 2. Summary of fall species data

Species	Age	Category	St. 1	St. 2	St. 3	St. 4
Fox Sparrow	HY/AHY	PR	X	X		X
Golden-crowned Sparrow	HY/AHY	CW	X	X	X[1]	X
Hermit Thrush	HY/AHY	LPR	X	X	X	X
Lincoln's Sparrow	HY/AHY	SPR	X	X	X	
Myrtle Warbler	HY/AHY	CW	X		X	X
Orange-crowned Warbler	HY/AHY	LPR	X	X	X	
Puget's White-crowned Sparrow	HY/AHY	PW	X	X	X	
Song Sparrow	HY/AHY	SPR	X	X		X
Swainson's Thrush	HY/AHY	CS	X	X	X	X
Yellow Warbler	HY/AHY	CS	X	X	X	X
Audubon's Warbler	-	LPR	X		X	X
Dark-eyed "Oregon" Junco	-	SPR	X	X		X
Ruby-crowned Kinglet	-	PW	X	X	X	X
Western Flycatcher	-	CS	X			X
Warbling Vireo	-	CS	X	X		
Wilson's Warbler	-	CS	X	X		X

[1] For species with age-class data, the underlined stations are data for combined-age only

3.2.4. Climate Association

Researchers calculated the Pearson correlation coefficient between the arrival date (for each migration metric) and climate at the local, regional, and continental scales. Calculations for the local scale used monthly minimum and maximum temperatures recorded at National Weather Service COOP weather station closest to the banding location: San Jose International Airport, California (37°21′N, 121°54′W) for Station 1; Petaluma, California (38°15′W, 122°36′W) for Station 2; San Francisco International Airport (37°37′N, 122°23′W) for Station 3; and Eureka (40°49′N, 124°10′W) for Station 4. The fall analyses used the same regions of mean temperature

anomalies as those used for the analyses of spring migration. Likewise, based upon the analyses of spring migration, the MEI was used as the climate index for ENSO.

As for the spring analyses, for all of the associations, this study examined only the index or monthly mean temperature for the month of arrival and the preceding month in order to minimize spurious associations. Climate conditions in these proximal months have the clearest possible link to conditions experienced immediately before departure from the breeding grounds and/or during migration.

3.2.5. Migration Pattern

To compare the seasonal passage of the different migratory/residency categories of species, researchers plotted total number of individuals of each species banded a given Julian day for all years of data. The analysis used the same procedure used for spring migration.

3.3. Results

3.3.1. Seasonal Migratory Patterns

Seasonal patterns of migratory passage were largely consistent between stations for half of the species. Eight of the 16 species (example, Yellow Warbler, Figure 7A) exhibited strikingly similar patterns between all 3–4 locations of observation, while the other eight species (example, Swainson's Thrush, Figure 7B) were notably different in pattern or timing between two or more stations.

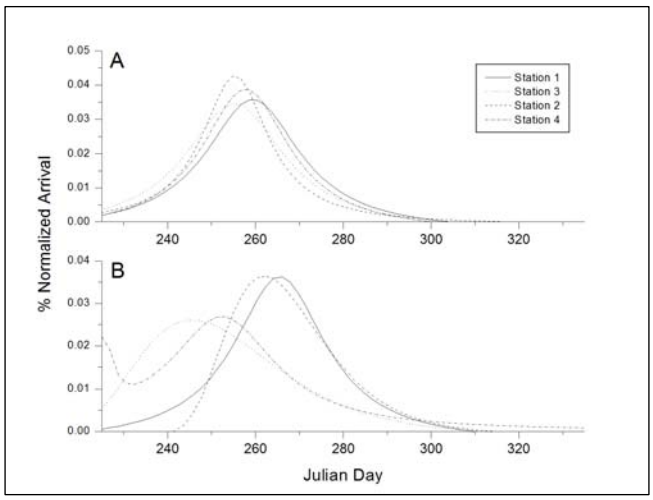

Figure 7. Seasonal distribution at all four stations

The five migratory species categories contrast with the seasonal patterns of resident species. Residents are present throughout the season at Stations 1, 2, and 4 (there were no resident species with adequate data at Station 3). At Stations 1 and 4, there is an overall decline in the number of the birds over the fall, but distributions are flat to shallow peaked. The four species at Station 2 (Figure 8) include two species with multiple broad peaks, suggesting waves of species movement through the area.

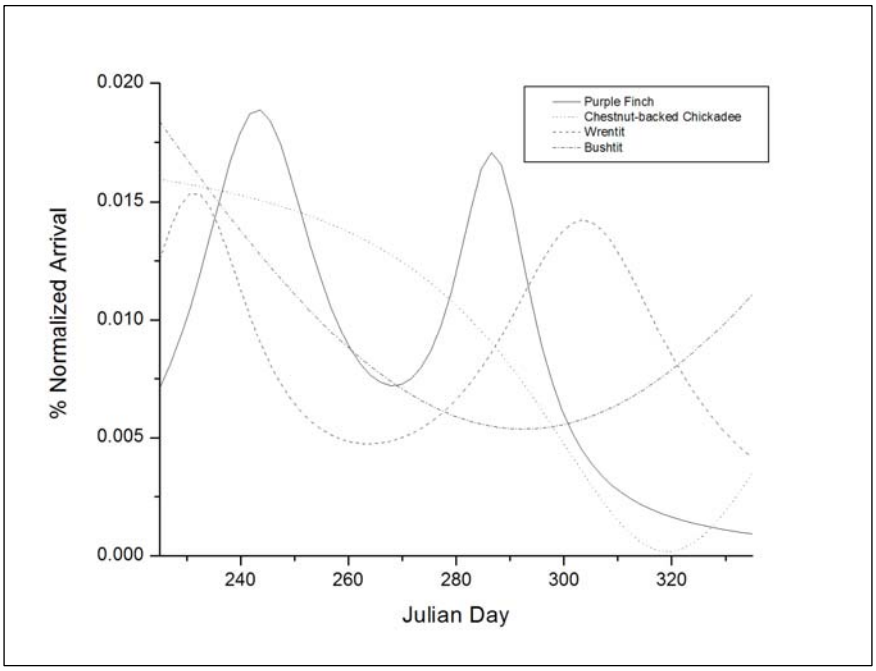

Figure 8. Seasonal distribution of four year-round species at Station 2

Only the complete migrants (both CS and CW) have consistent patterns across all species and all stations. Short and long distance migrants with central/north California year-round populations (SPR and LPR) exhibit heterogeneous seasonal patterns between different species, but the patterns are generally consistent across multiple stations for a single species.

For CS species (n=3), migration begins by mid-August and peaks in mid-late September. All of the species have single-peaked, approximately normal distributions at all stations (Figure 9). Common Yellowthroat is nearly synchronous at all stations. Swainson's Thrush is nearly four weeks earlier at Stations 2 and 4, compared to Stations 1 and 3. Wilson's Warbler peaks very early at Stations 2 and 4—before mid August—in contrast to a late September peak at Station 1.

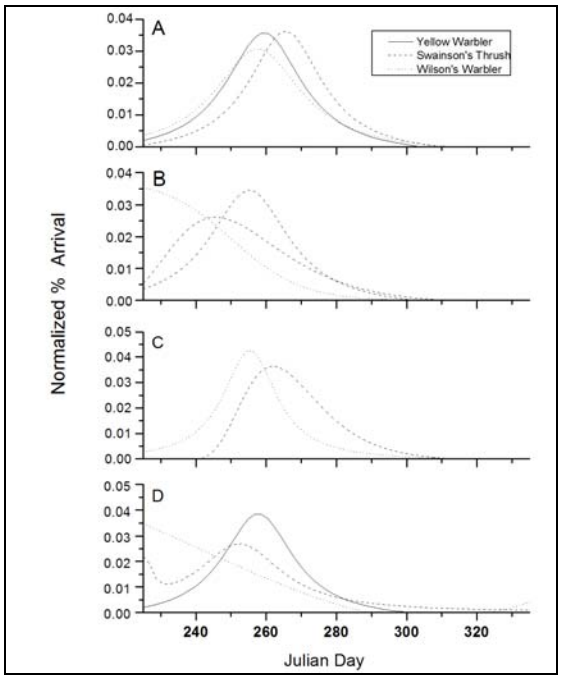

Figure 9. Seasonal distribution of three summer-only species

All CW species (n=3), except Puget's White-crowned Sparrow at Station 1, arrive after late September. There are no early season records; all steeply increase to a peak in mid-late October (Figure 10). The distributions are strongly right-skewed, with a tail extending through November. The distribution of the Golden-crowned Sparrow is the most varied between stations: relatively broad and wide at Station 1 and much narrower at Station 2.

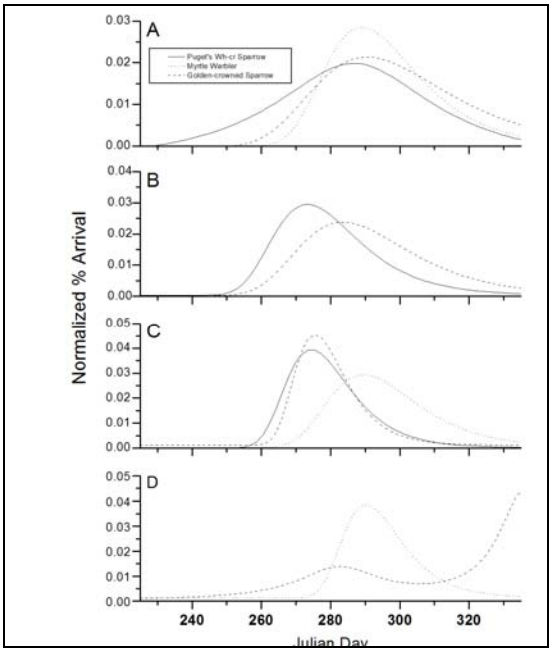

Figure 10. Seasonal distribution of three winter-only species

Both groups of partial migrants (LPR, n=4, Figure 11; SPR, n=4, Figure 12) exhibit varied patterns between species, but general consistency within a species. Hermit Thrush and Audubon's Warbler overlap at all stations, peaking in early October. Orange-crowned Warblers begin arriving in mid August and peak within two weeks of each other at all stations. There are multiple peaks at Station 3. Station 4 has a notable symmetry and concurrence of peaks for all four LPR species. In contrast, SPR species at Station 4 have very dissimilar timing and patterns.

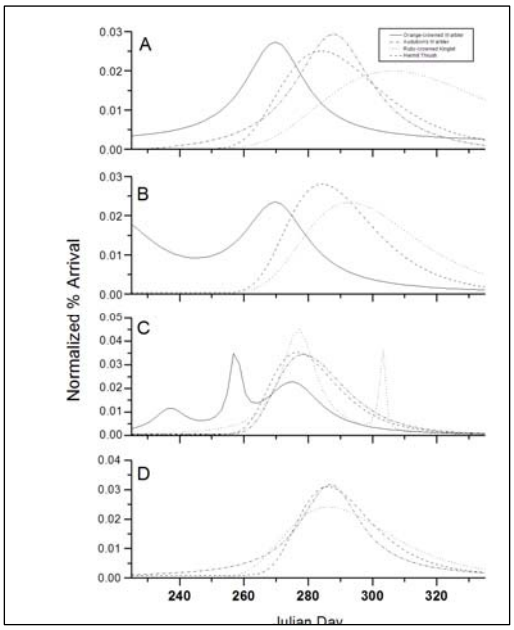

Figure 11. Seasonal distribution of 4 long-distance partial migrant species

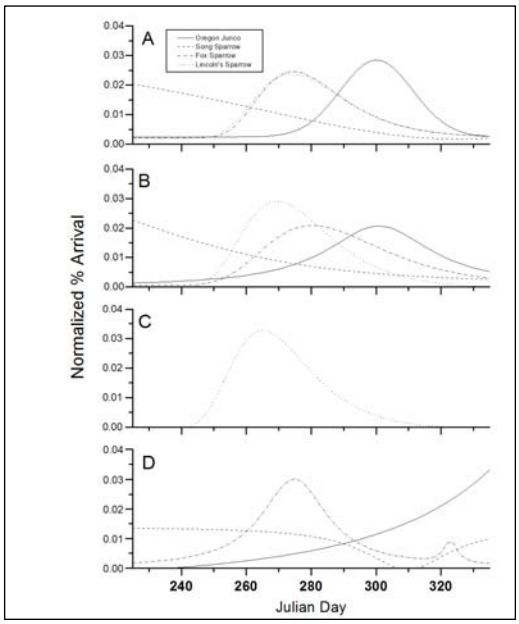

Figure 12. Seasonal distribution of 4 short-distance partial migrant species

Overall, in this analysis, SPR species are more consistent between stations than the LPR species. Lincoln's Sparrow peaks concurrently at four stations (mid-September), Fox Sparrow peaks concurrently at three sites (early October), and Song Sparrow exhibits a consistent, shallow-sloped decline through the season at three stations.

3.3.2. Migratory Patterns of Age Classes

All 11 species with adequate differential age class data exhibited strikingly similar distributions in terms of size and shape. The Swainson's Thrush was an exception; its HY distribution was bimodal while the AHY was single-peaked. For all species, both age classes peak nearly concurrently. Compared to HY patterns, AHY patterns are more narrow and skewed to the right.

Juveniles arrived earlier, but not dramatically so, for most species. Of the 18 species-location pairings, the HY birds were five or more days earlier in nine instances for the median of the absolute first day of banding. For the metric of continuous migration, there were eight instances where HY were five or more days early; for median of arrival, there were nine instances. The HY were not later at any species or location.

3.3.3. Migration Length

For all ages combined, the mean of the total migration length (absolute first to last Julian day of banding) for all species is 7–9 weeks at all four stations. This is comparable for all migratory/residency groups except SPR, which is approximately two weeks longer than the others. The mean of continuous migration for all species is 7–8 weeks at Stations 1 and 2 and 4–5 weeks at Stations 3 and 4.

When age classes are separated, the migratory period of the HY class is, on average, twice as long as the AHY class. For all migratory/residency subgroups, the mean of migration for the HY class is 3–5 weeks longer than the comparable mean for the AHY class. The mean of total migration length is 9–11 weeks for HY birds and 5–8 weeks for AHY birds. Similarly, the mean of continuous migration is 5–9 weeks for HY birds and 2–4 weeks for AHY birds.

3.3.4. Trends in Phenology

When age classes are combined, all sixteen species have a statistically significant trend ($p < 0.10$) in at least one arrival metric (Appendix B). Eleven species are arriving earlier, three are arriving later, and two have mixed directions between locations. Six species demonstrated trends at multiple locations; of those, three species were earlier, one was later, and two had mixed signs. Hermit Thrush (LPR), Lincoln's Sparrow (SPR), and Puget's White-crowned Sparrow (PW) are arriving earlier and Orange-crowned Warbler (LPR) is arriving later. The trends are identified in all metrics of migration: there were 13 instances where the absolute first day of arrival was changing, 11 trends in the day of continuous migration, and 17 instances were the median day of arrival exhibited a trend.

Of the 11 species with adequate age class data, eight species have HY trends and nine species have AHY trends (Appendix C). All HY trends are negative. Of the AHY species, six trends are negative and three trends are positive. As for the combined species, the trends are spread across all three arrival metrics. The species without trends are LPR: Myrtle Warbler and Common

Yellowthroat for HY age class and Myrtle Warbler only for the AHY age class. There is consistency between the age classes. Seven of the eleven species have trends for both the HY and AHY classes; of those, five species are negative (for both age classes).

3.3.5. Climate Variables

The mean monthly minimum and maximum temperatures are increasing ($p < 0.10$) at San Jose and San Francisco airports for July–November during the study period (1969–2002). Mean maximum temperature only is increasing at Eureka for July–October.

For the fall months (September–November), both regional temperature regions strongly correlated with local temperatures at all four stations ($p < 0.10$). In contrast, only the western coastal regional temperature correlated with one station in July and two stations in August. There were no correlations between summer or fall regional temperatures with the indices of ENSO or NAO. Local monthly mean minimum temperatures, however, correlated with MEI from July–October at San Francisco airport (Station 3) and Eureka (Station 4). Local monthly mean maximum temperature correlated with MEI only at Eureka. There were no local associations with NAO.

3.3.6. Climate Associations

All of the complete migrant species (n=7), including both summer-only and winter-only residents, demonstrate multi-site associations with temperature or ENSO/NAO. Overall, however, consistent, multi-scalar climate associations are limited. At least one arrival metric for five species is associated with NAO or ENSO, in the same direction (positive or negative), for two or more locations. Four of the five species are complete migrants. Similarly, only four species' arrival (at least one metric) is associated with temperature at the local or regional scale for two or more locations. Three of these four species are complete Neotropical migrants. Seven species demonstrate inconsistent temperature associations between two or more locations, i.e., positively correlated at one and negatively correlated at another.

When species are broken down into age groups, there are no species with a consistent association with NAO or ENSO at two or more locations. Likewise, there are no consistent associations for either age group with local or regional temperature.

3.4. Discussion

The picture of fall songbird migration through central/northern California is one of variety—both between species and locations—but also shows some notable patterns. First, evidence of fall migratory climatic association is much weaker than previous spring results. Second, there are differences in the length of the migratory period between adult and juvenile migrants, but the peak of migration for both age groups is nearly synchronous. Third, despite widespread evidence of trends in (earlier) arrival across multiple metrics, consistent, multi-site evidence of phenological change is lacking. Fourth, there is similarity in the migratory patterns of species that are complete migrants, but notable differences for other species, both between sites and between species of the same migratory/residency group.

The widespread changes in phenology suggest factors other than the climatic variables and scales examined in this paper are influencing species. There is widespread change—every species had a trend at least at one location—but little consistency between locations. Only the data for the Hermit Thrush and Lincoln's Sparrow strongly suggest that these species are

arriving earlier: there were significant ($p < 0.10$) trends for three locations and multiple arrival metrics for these species. Across all species, the trends were predominantly negative, suggesting more than random, spurious changes. Furthermore, all research to date in the region suggests that populations of songbirds are declining (Pyle et al. 1994; Ballard et al. 2003; Richardson et al. 2003). Thus, one would expect that population-influenced trends would be in a positive direction; that is, there are fewer birds and detection occurs later in the year. Finally, no single banding site recorded a majority of the trends. Since multiple banding sites were used, it is unlikely that unidirectional changes in effort across all four locations account for the widely identified trends in species' arrival.

The climatic correlations do not fully explain the fall phenological changes, though the analyses suggest that complete migrants are more affected by climatic conditions than the partial migrant species. One is left to speculate that large-scale conditions are changing that prompt earlier migration, but are not captured by regional temperature or mesoscale climatic indicators, such as MEI. For instance, it is possible that species are completing their breeding cycle earlier and, thus, departing the breeding grounds earlier, due to advances in western spring (Cayan et al. 2001). Another possibility is unidentified ecological changes that are induced by conditions earlier in the season. Insect emergence might peak earlier or hotter, drier conditions could bring seeds to maturation earlier, prompting birds to begin moving as northern food supplies dwindle. These situations are consistent with other observed changes, but difficult to detect and test on the scale of migrants with broad breeding ranges.

Changes or climatic associations do not appear to differentially affect either age class, which is consistent with the largely synchronous movements of adults and juveniles. While HY birds migrate over a longer period than AHY birds of the same species, the HY individuals arrive earlier (five or more days) for less than half of the species-location pairings (see Results). While there are differences in seasonal migratory distribution between the age classes, the species examined, including at least one species from each migratory/residency grouping, do not evidence dramatic differences. Furthermore, given the larger numbers of juveniles present (Desante 1983), the earlier arrival could be attributed to increased probability of banding, due to a larger regional population.

4.0 Summary and Conclusions

The analyses in the preceding pages highlight the evidence for extensive phenological changes in California migratory phenology—as well as the differences between seasons, between species, between data sites, and between metrics of migration. This study has shown much about the relationship between climate and the timing of arrival, but has also generated many new questions.

These analyses suggest widespread changes in species' phenology in the fall, though with less consistency, and less clearly linked to climatic conditions at the time of migration than for spring migrants. The results of this research do not highlight a particular guild of migrants as more susceptible to climatic change influences upon their phenology. Spring and fall phenology —for complete and partial, short and long distance migrants—appears to respond to annually variable environmental cues to some degree for many species in different residency/migratory categories.

There is evidence that, at least for the Pacific coastal flyway, Neotropical migrants respond to climate variables as strongly as short-distance migrants. However, researchers cannot separate whether this response occurs on the wintering grounds (the initiation of migration) or en-route to California (factors affecting the rate or progression of migration). Three spring species—Black-headed Grosebeak, Wilson's Warbler, and Warbling Vireo—demonstrate the strongest associations with multi-scalar climate, as well as statistically significant trends in arrival at multiple locations. However, the authors are reluctant to downplay the importance of climatic change on phenology for any of the species in this study, since the majority of species' spring phenology indicated association with climate at some scale. Likewise, despite the weaker evidence for climate association, there was evidence of phenological change in many species' fall migratory passage. The authors conclude that there is a high likelihood of differential phenological responses to climatic change between species—which itself is ecologically significant—but that there is no migratory, residency, or life history pattern that predicts which groups of songbird species will be most affected.

The results from central and northern California suggest how different an impression one could have of species' behavior if only one region or one banding location was analyzed. The differences in migration patterns, trends, and climate associations identified at the different sites and scales could be due to differences in data collection, multi-scalar geographical features of the sites, and/or different routes taken by the migrants. Even though the banding stations used in the spring analyses are within 100 km (62 miles) of each other, one is directly on the coast and the other is much farther inland. Likewise, in the fall, there are four data locations from disparate habitats over a small region, owing to the diversity of coastal California topography and climates. At smaller scales, the sites differ in local vegetation as well as surrounding landscape features. These, as well as unidentified wind or cloud patterns, could influence migrants' arrival within an area; however, it is less clear how macro-scale features would strongly influence one species and not another (i.e., the difference in initial arrival dates for the same species at the two stations).

This study's authors agree with Ballard et al. (2003) that assessments of species' change be considered at multiple locations, multiple scales, and using multiple methods. There is both the

opportunity to learn more about a species' biology through comparison and the possibility of greater confidence in results when multiple locations are considered.

Furthermore, from a methodological perspective, it is important to note the differences in trends when one analyzes trends in different arrival metrics. The first sighting of a species is most susceptible to outliers, and particularly for sex-differential migratory species, generally captures the arrival of males. In this sense, while sensitive to changes, first arrival incompletely captures the biology of entire species. The increased variance from outliers might explain why fewer trends were recorded for this metric. A measure of the onset of continuous migration has the advantage of minimizing outliers and indicating the start of the migratory period for the bulk of migrants within a species. For this analysis, it was clearly the most sensitive for trend detection.

The changes in the median of migration contrast between the seasons and illuminate questions about the impact of phenological change on species' abundance. The median of the migratory period clearly captures the midpoint of a species' passage through a region, but is less of an indicator of species' response to changes early in the migratory period, and thus, might explain why no trends were identified in the median of migratory passage during spring. Other studies have found no changes in the median of migration (Marra et al. 2005) compared to studies finding trends in first arrivals (e.g., Bradley et al. 1999; Ledneva et al. 2004).

In contrast, during the fall, statistically significant changes in the median were identified 30% more than changes in first arrival and over 50% more than the beginning of continuous migration. Given the strong evidence for trends in the median of fall migration, it is strongly suggested that the bulk of the population is shifting its phenology and responding to changes over a large scale.

Although climate is clearly associated with the arrival of many Neotropical migrant species, it is unclear how the early spring season changes affect the bulk of the species' populations. While no spring median migration dates are undergoing statistically significant changes, the median of migration associates with climate as frequently as the earlier metrics of migration. This suggests two different interpretations. The first is methodological. Given the limited information on capture effort, the median of spring arrival has too much variance to detect a trend, and thus, the median of spring migration is actually shifting as much as the earlier migratory waves. Thus, phenology is changing throughout the migratory period and affecting the majority of the population.

On the other hand, if the unchanging median spring phenology is accurate, the observed phenological changes disproportionately affect earlier spring migrants, particularly males of the many species of passerines for which males migrate earliest (Stewart *et al.* 2002). This scenario could lead to different selective pressures for early season fitness (Moller 2004), or, conversely, affect such a small proportion of the population that shifting migratory phenology has little potential for changes in breeding success, and thus, abundance of a species (e.g., Wilson and Arcese 2003). Of course, either scenario is dependent upon the concurrent changes in other aspects of ecosystem phenology, such as vegetation and insects, upon which the birds depend for migratory and breeding resources (Both and Visser 2001; Visser and Holleman 2001).

In either case, climate—and therefore climatic change—has a role in some aspects of migratory phenology, but the species' abundance and ecosystem-wide consequences are yet uncertain.

This study's authors hypothesize that changes in spring phenology are more important for population dynamics since factors of territory and early season food abundance can affect reproductive success (Visser and Holleman 2001). Even though it appears that many species are also advancing their fall phenology, it is yet unclear whether these changes are indicative of the season's reproductive success or recruitment. In conclusion, it is critical to develop multiple metrics of phenological change in an analysis so that, if possible, multiple seasonal or population-related aspects of change can be examined. This greater detail on phenology will better inform studies on the ecological impacts of climatic change.

In summary, four general recommendations are offered for future analysis and modeling of phenology under climatic change scenarios:

- Use multiple data sites in order to evaluate change over the scale of a region or species' range
- Develop multiple metrics of phenological change in order capture different aspects of a species' biology
- Create multi-factor assessments of change and association in order to synthesize results from multiple data sites and multiple climatic scales
- Include multiple trophic levels of analysis when possible

Although many modeling efforts emphasize the importance of increased spatial resolution, the results of this study also indicate the importance of increased temporal resolution during the seasons. It is not only the extent of climate-induced changes in phenology that are ecologically significant, but how those changes manifest in particular habitats. Wide-ranging species that uses multiple habitats, as is common for long-distance migrants or montane species that change elevations, are susceptible to changes that occur at different rates, depending upon the locations. For instance, within California, coastal, mountain, and valley habitats will experience different types of phenological changes, based upon factors such as hydrology, proximity to the ocean, elevation, types of vegetation, and others. Populations of the same species, or even an individual of a species, can experience all of these changes across its range.

Furthermore, phenological changes in different parts of a season can have different effects on a species, such as food or water availability, temperature in nesting cavities, or the availability of migratory fuel (e.g., insects). Without understanding the temporal dimension of environmental change, it will be difficult to anticipate rates of change at different trophic levels, which will vary depending upon the suite of species at a given location.

Future modeling efforts are encouraged to consider elements of phenological change at multiple scales, to anticipate the effects on a specific ecological community as well as the larger-scale, diverse changes experienced across a species' range and migratory routes.

5.0 References

Ballard, G., G. Geupel, N. Nur, and Gardali T. (2003) "Long-term declines and decadal patterns in population trends of songbirds in western North America (1979–1999)." *Condor* 105: 737–755.

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

Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. (1999) "Phenological changes reflect climate change in Wisconsin." *Proceedings of the National Academy of Sciences of the United States of America*, 96, 9701–9704.

Butler, C. J. (2003) "The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America." *Ibis* 145, 484–495.

Cayan, D. R., S. A. Kammerdiener, M. D. Dettinger, J. M. Caprio, and D. H. Peterson. (2001) "Changes in the onset of spring in the western United States." *Bulletin of the American Meteorological Society* 82, 399–415.

Crick H., C. Dudley, D. Glue, and D. Thomson. (1997) "UK birds are laying earlier." *Nature* 388, 526.

Desante, D. F. (1983) "Annual variability in the abundance of migrant landbirds on southeast Farallon Island, California." *Auk* 100, 826–852.

Hagan, J. M., T. L. Lloyd-Evans, and J. L. Atwood. (1991) "The relationship between latitude and the timing of spring migration of North American landbirds." *Ornis Scandinavica* 22, 129–136.

IPCC (2001) *Climate Change 2001: The Science of Climate Change.* Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.

Jenni, L., and M. Kery. (2003) "Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants." *Proceedings of the Royal Society of London Series B - Biological Sciences* 270, 1467–1471.

Ledneva A., A. J. Miller-Rushing, R. B. Primack, and C. Imbres. (2004) "Climate change as reflected in a naturalist's diary, Middleborough, Massachusetts." *Wilson Bulletin* 116, 224–231.

Lemoine, N., and K. Bohning-Gaese. (2003) "Potential impact of global climate change on species richness of long-distance migrants." *Conservation Biology* 17, 577–586.

Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. Moore. (2005) "The influence of climate on the timing and rate of spring bird migration." *Oecologia* 142, 307–315.

Moller, A. P. (2004) "Protandry, sexual selection, and climatic change." *Global Change Biology* 10, 2028–2035.

Parmesan, C., and G. Yohe. (2003) "A globally coherent fingerprint of climate change impacts across natural systems." *Nature* 421, 37–42.

Penuelas, J., I. Filella, and P. Comas. (2002) "Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region." *Global Change Biology* 8, 531–544.

Pyle, P., N. Nadav, and D. F. Desante. (1994) "Trends in nocturnal migrant landbird populations at southeast Farallon Island, California, 1968–1992." *Studies in Avian Biology* 15, 58–74.

Ralph, C. (1971) "An age differential of migrants in coastal California." *Condor* 73, 243–246.

Ralph, C. (1981) "Age ratios and their possible use in determining autumn routes of passerine migrants." *Wilson Bulletin* 93, 164–188.

Richardson, T., P. Pyle, R. Burnett, and P. Capitolo. (2003) "The occurrence and seasonal distribution of migratory birds on southeast Farallon Island, 1968–1999." *Western Birds* 34, 58-96.

Root, T. L., D. P. MacMynowski, M. Mastrandrea, and S. H. Schneider. (2005) Human-modified temperatures induce species' changes: joint attribution. *Proceedings of the National Academy of Sciences of the United States of America*, in press.

Root, T. L., J. Price, K. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. (2003) "Fingerprints of global warming on wild animals and plants." *Nature* 421, 57–60.

Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K.-S. Chan, N.G. Yoccoz, and B. Adlandsvik. (2003) Studying climate effects in ecology through the use of climate indices: The North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London Series B - Biological Sciences*, 270, 2087–2096.

Stewart, R., L. Mewaldt, and S. Kaiser. (1974) "Age ratios of coastal and inland fall migrant passerines in central California." *Bird Banding* 45, 46–57.

Stewart, R. L. M., C. M. Francis, and C. Massey. (2002) "Age-related differential timing of spring migration within sexes in passerines." *Wilson Bulletin* 144, 264–271.

Terborgh, J. (1989) Where have all the birds gone? Essays on the conservation and biology of birds that migrate to the American tropics. Princeton University Press: Princeton, New Jersey.

Tryjanowski, P., and T. H. Sparks. (2001) "Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*." *International Journal of Biometeorology* 45, 217–219.

Van Vliet, A. H. J., R. S. de Groot, Y. Bellens, P. Braun, R. Bruegger, E. Bruns, J. Clevers, C. Estreguil, M. Flechsig, F. Jeanneret, M. Maggi, P. Martens, B. Menne, A. Menzel, and T. Sparks. (2003) "The European Phenology Network." *International Journal of Biometeorology* 47, 202–212.

Visser, M. E., and L. J. M. Holleman. (2001) "Warmer springs disrupt the synchrony of oak and winter moth phenology." *Proceedings of the Royal society of London B* 268, 289–294.

Wilson, S., and P. Arcese. (2003) "El Niño drives timing of breeding but not population growth in the song sparrow (*Melospiza melodia*)." *Proceedings of the National Academy of Sciences of the United States of America* 100, 11139–11142.

Weston, H. G. 1948. "Spring arrival of summer residents in the Berkeley area, California." *Condor* 50:81.

Winkel, W., and H. Hudde. (1997) "Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and pied flycatchers (*Ficedula hypoleuca)." Journal of Avian Biology*, 28, 187–190.

Appendix A

Spring Phenology Summary Statistics

APPENDIX A. Spring Phenology Summary Statistics

						Absolute First Arrival			First Continuous Arrival			Median Arrival		
Species	**Type**	**Loc**	**Clim[1]**	**Year1**	**Year2**	**Day**	**days/dec**	**p-val**	**Day**	**days/dec**	**p-val**	**Day**	**days/dec**	**p-val**
Barn Swallow	BBL	stat. 2		1980	2003	54	-8.4	0.00	65	-6.5	0.00			
Barn Swallow	NAB	central	L	1980	2003	76	-23.5	0.00	82.5	-12.3	0.03			
Barn Swallow	NAB	north		1977	2000	108	2.7	0.46	108	2.7	0.46	137	13.6	0.00
Bk-headed Grosbeak	BBL	stat. 1		1979	1994	88	-12.2	0.22	98	-10.9	0.01			
Bk-headed Grosbeak	NAB	central	HL	1980	1992	107	-7.7	0.12	110.5	-9.6	0.03			
Bk-headed Grosbeak	NAB	north		1985	1997	116	-3.8	0.53	124	6.6	0.50	137	2.0	0.68
Bk-thr Gray Warbler	NAB	central	P	1979	1994	89	-10.7	0.37	101.5	-5.0	0.59			
Bk-thrGray Warbler	NAB	north		1979	1994	101	-9.3	0.05	103	-14.6	0.00			
Bl-gray Gnatcatcher	NAB	central	N	1979	2002	65	4.5	0.48	78	2.4	0.45			
Bullock's Oriole	BBL	stat. 1	N	1983	1997	106	11.5	0.09	116	-6.9	0.41	132	15.5	0.07
Cliff Swallow	NAB	central	P	1981	2003	53	1.1	0.62	54	1.5	0.08			
House Wren	NAB	central	P	1982	2003	49	9.2	0.20	71	14.2	0.04			
House Wren	NAB	north		1982	1994	94.5	-13.7	0.42	94.5	-14.9	0.41			
Lazuli Bunting	NAB	central	P	1979	1994	103	-9.7	0.01	111	-7.1	0.05			
MacGillivray's Warbler	NAB	central	P	1979	1994	105	-6.6	0.51	110	-2.8	0.39			
MacGillivray's Warbler	NAB	north		1981	1992	110	7.1	0.16	111	5.6	0.17			
N. Rough-wing Swall.	NAB	central	P	1979	2003	53	-6.0	0.06	61	-6.3	0.02			
Nashville Warbler	NAB	central	L	1979	1994	55	5.5	0.63	109	3.5	0.10			
Nashville Warbler	NAB	north		1980	1994	92.5	8.9	0.70	108.5	3.4	0.87			
Olive-sided Flycatcher	NAB	central	L	1979	2003	103	1.5	0.39	107	0.3	0.81			
Olive-sided Flycatcher	NAB	north		1979	1992	118	5.7	0.41	127	4.7	0.54			
Orange-cr Warbler	BBL	stat. 1		1979	1994	57	3.9	0.64	60	-6.3	0.32			
Orange-cr Warbler	BBL	stat. 2	L	1985	1997	65	-21.9	0.01	87	-14.1	0.14	116	-2.1	0.60
Orange-cr Warbler	NAB	central		1969	2002	74	1.2	0.48	80	1.4	0.36	118	2.8	0.17
Swainson's Thrush	BBL	stat. 1		1979	1992	107	-8.3	0.21	114	-7.5	0.29			
Swainson's Thrush	BBL	stat. 2	HL	1983	1997	115	-6.7	0.23	118	-11.2	0.01	138	-1.4	0.39
Swainson's Thrush	NAB	central		1969	2002	121	-1.5	0.19	125	1.8	0.05	139	-0.3	0.65
Vaux's swift	NAB	central	L	1979	1994	77	-14.7	0.40	113	-4.9	0.04			
Vaux's swift	NAB	north		1980	1994	102	8.7	0.35	106.5	1.2	0.76			
Warbling Vireo	BBL	stat. 1		1979	2003	76	-2.8	0.15	80	-3.1	0.02			
Warbling Vireo	BBL	stat. 2	HL	1981	2003	90	-10.0	0.01	92	-11.9	0.00			
Warbling Vireo	NAB	central		1987	1997	112	-2.3	0.82	124	-0.9	0.95	132	0.9	0.92
Warbling Vireo	NAB	north		1969	2000	101	6.2	0.06	119	6.0	0.02	133	-1.9	0.16
Western Flycatcher	BBL	stat. 1	P	1986	1997	85	-0.4	0.95	93	-1.7	0.83	128	-1.7	0.81
Western Flycatcher	BBL	stat. 2		1969	1997	103	-1.5	0.58	114	-0.4	0.89	132	1.0	0.59
Western Kingbird	NAB	central	L	1979	2003	81	-7.3	0.01	94	-6.7	0.02			
Western Kingbird	NAB	north		1979	2003	105	-0.1	0.98	109	-0.1	0.97			
Western Tanager	NAB	central	P	1979	1994	78	17.3	0.32	107	1.6	0.91			
Western Tanager	NAB	north		1979	1994	106	17.1	0.29	116	21.4	0.22			
W. Wood-Pewee	NAB	central	L	1979	2003	106	0.9	0.64	109	-0.3	0.85			
W. Wood-Pewee	NAB	north		1980	2003	122	-3.8	0.35	127	-4.6	0.29			
Wilson's Warbler	BBL	stat. 1		1979	1994	77	-0.7	0.93	82	-2.3	0.22			
Wilson's Warbler	BBL	stat. 2	HL	1981	1994	97	-1.0	0.84	103	-6.4	0.08			
Wilson's Warbler	NAB	central		1983	1997	90	-17.8	0.01	101	-20.8	0.03	127	2.2	0.37
Wilson's Warbler	NAB	north		1969	2002	91	-2.0	0.25	95	-1.3	0.28	125	2.3	0.15
Yellow Warbler	NAB	central	N	1979	1994	90	3.1	0.84	102	2.3	0.59			

[1] Category of climate association: HL=highly likely, L=likely, P=possible, N=none (see Spring Migration, Results)

Appendix B

Fall Phenology Summary Statistics

APPENDIX B. Fall Phenology Summary Statistics

					Absolute First Arrival			First Continuous Arrival			Median Arrival		
Species	**Group[1]**	**Station**	**Year1**	**Year2**	**Median**	**days/dec**	**p-value**	**Median**	**days/dec**	**p-value**	**Median**	**days/dec**	**p-value**
Audubon's Warbler		St.1	1976	2001	272.5	-12.6	0.00	278	-11.9	0.00	293	-5.8	0.04
Audubon's Warbler	LR	St.3	1968	2002	261	-1.4	0.41	270	-2.0	0.13	283.5	-1.0	0.40
Audubon's Warbler		St.4	1983	1999	261	9.2	0.44	280.5	32.3	0.04	288	11.4	0.00
Fox Sparrow		St.1	1982	2001	255.5	1.0	0.78	256.5	5.2	0.15	285.5	-2.5	0.59
Fox Sparrow	SPR	St.2	1969	2002	255	-0.1	0.90	260.5	-0.3	0.80	287	-2.2	0.06
Fox Sparrow		St.4	1983	1999	255.5	0.0	1.00	257	0.3	0.94	277	-0.9	0.72
Golden-cr Sparrow		St.1	1970	2001	265	-4.3	0.02	266	-7.7	0.00	299	-4.0	0.10
Golden-cr Sparrow	CW	St.2	1969	2002	262	0.8	0.26	263	0.5	0.59	289	-1.4	0.21
Golden-cr Sparrow		St.3	1968	2002	263	-0.2	0.79	266	-1.0	0.25	281.5	-0.7	0.63
Golden-cr Sparrow		St.4	1983	1999	262.5	2.3	0.41	269.5	6.0	0.15	298.5	-13.4	0.17
Hermit Thrush		St.1	1979	2001	262	-17.0	0.00	264	-11.9	0.02	292	-4.9	0.15
Hermit Thrush	LPR	St.2	1969	2002	254.5	-4.8	0.07	264	-0.2	0.78	288.5	1.0	0.20
Hermit Thrush		St.3	1968	2002	269	-3.2	0.05	270.5	-2.1	0.09	277.5	1.1	0.45
Hermit Thrush		St.4	1983	1999	272	-2.4	0.55	276	-7.8	0.16	291	0.1	0.98
Lincoln's Sparrow		St.1	1981	2001	250	3.8	0.34	256	-6.1	0.06	280.5	0.0	1.00
Lincoln's Sparrow	SPR	St.2	1969	2002	257	-2.6	0.02	261.5	-3.8	0.03	273	-0.1	0.96
Lincoln's Sparrow		St.3	1968	2002	255.5	0.4	0.69	257	-2.5	0.09	268	-2.6	0.15
Myrtle Warbler		St.1	1989	2001	269	-1.1	0.82	271	-8.3	0.27	293	4.6	0.64
Myrtle Warbler	CW	St.3	1968	2002	268	-3.6	0.01	274	-4.6	0.01	293	-0.9	0.56
Myrtle Warbler		St.4	1983	1999	275	-0.3	0.88	277	-5.0	0.18	294	-4.5	0.30
Orange-cr Warbler		St.1	1985	2001	236	2.3	0.59	245.5	0.7	0.93	269	3.4	0.30
Orange-cr Warbler	LPR	St.2	1969	2002	228	2.7	0.01	235	6.7	0.04	263	3.9	0.08
Orange-cr Warbler		St.3	1968	2002	235.5	3.9	0.12	253	0.2	0.94	269	5.4	0.05
Oregon Junco		St.1	1970	1995	271	-8.2	0.35	293	-7.5	0.39	304	-7.7	0.06
Oregon Junco	SPR	St.2	1969	2002	229	-1.2	0.52	248	-1.8	0.62	299	1.4	0.42
Oregon Junco		St.4	1983	1999	263	-10.4	0.32	282	2.7	0.52	317	-3.2	0.71
Puget Wh-cr Sparrow		St.1	1970	2001	261	-5.4	0.01	262	-5.4	0.00	289	-3.8	0.11
Puget Wh-cr Sparrow	PW	St.2	1976	2002	260	-2.4	0.13	261	-1.1	0.47	278	-1.8	0.47
Puget Wh-cr Sparrow		St.3	1969	2002	262	-1.0	0.40	264	-3.8	0.00	276	-1.3	0.27
Ruby-crowned Kinglet		St.1	1977	2001	278.5	-9.5	0.01	284	-19.3	0.00	308	-7.6	0.00
Ruby-crowned Kinglet	PW	St.2	1969	2002	264	-1.6	0.19	268	-0.4	0.72	297.5	1.9	0.04
Ruby-crowned Kinglet		St.3	1968	2002	262	-3.2	0.04	268.5	-0.5	0.70	282	-0.5	0.76
Ruby-crowned Kinglet		St.4	1983	1999	267	3.4	0.38	269	6.8	0.14	291	-2.0	0.64
Song Sparrow		St.1	1981	2001	226	0.6	0.27	226	1.0	0.19	252	-2.7	0.52
Song Sparrow	SPR	St.2	1969	2002	226	-0.1	0.73	227	-0.3	0.81	251.5	1.1	0.59
Song Sparrow		St.4	1983	1999	229	-11.9	0.01	230.5	-9.2	0.06	263.5	-5.1	0.29
Swainson's Thrush		St.1	1985	2001	241.5	4.4	0.29	246	5.0	0.27	264.5	-2.9	0.42
Swainson's Thrush	CS	St.2	1969	2002	226	-0.5	0.30	228	-1.3	0.16	252	-1.2	0.20
Swainson's Thrush		St.3	1968	2002	252	1.1	0.25	255	0.6	0.68	266	0.8	0.53
Swainson's Thrush		St.4	1983	1999	226.5	-15.9	0.00	230.5	-15.4	0.00	251.5	-1.5	0.68
Warbling Vireo	CS	St.1	1986	2001	239	10.0	0.06	241	4.6	0.41	255	0.8	0.86
Warbling Vireo		St.2	1969	2002	227	0.3	0.51	230	1.0	0.33	251	-0.3	0.71
Western Flycatcher	CS	St.1	1983	2001	225	0.4	0.24	225	0.4	0.29	251.5	-0.5	0.89
Western Flycatcher		St.4	1985	1998	232	-13.2	0.01	234.5	-4.5	0.68	246	-1.4	0.85
Wilson's Warbler		St.1	1985	2001	231	-1.0	0.68	233.5	-0.5	0.89	257.5	1.4	0.50
Wilson's Warbler	CS	St.2	1969	2002	225	0.2	0.29	225	0.0	0.99	240	-0.3	0.68
Wilson's Warbler		St.4	1987	1999	227	-9.0	0.22				245	1.0	0.89
Yellow Warbler		St.1	1983	2001	236	-8.3	0.08	235	-0.5	0.93	260	-2.1	0.45
Yellow Warbler	CS	St.2	1969	2002	234	-1.2	0.38	240	-0.9	0.51	257	0.0	0.99
Yellow Warbler		St.3	1968	2002	231	0.1	0.92	234	1.7	0.43	255.5	1.9	0.12
Yellow Warbler		St.4	1983	1999	247	-6.5	0.32	252	-3.3	0.44	260	1.5	0.77

[1] Migratory/Residency Group. See Fall Migratation, Methods for abbreviations

Appendix C

Fall Phenology Summary Statistics of Age-Differential Migration

APPENDIX C. Fall Phenology Summary Statistics of Age-Differential Migration

						Absolute First Arrival			First Continuous Arrival			Median Arrival		
Species	**Group[1]**	**Age**	**Station**	**Year1**	**Year2**	**Median**	**days/dec**	**p-value**	**Median**	**days/dec**	**p-value**	**Median**	**days/dec**	**p-value**
Fox Sparrow	PR	AHY	St.1	1983	2001	261	2.6	0.44	266	-1.4	0.76	283	0.5	0.92
Fox Sparrow		HY	St.1	1982	2001	255.5	-5.0	0.28	257.5	2.1	0.54	286	-0.1	0.98
Fox Sparrow		AHY	St.2	1969	2002	263	-0.3	0.84	272	-1.1	0.57	286	-0.5	0.63
Fox Sparrow		HY	St.2	1969	2002	255	-0.1	0.90	261	0.3	0.83	285.5	-2.9	0.03
Fox Sparrow		AHY	St.4	1983	1999	259	-1.0	0.71	261	2.7	0.24	273	8.1	0.03
Fox Sparrow		HY	St.4	1983	1999	258	-0.7	0.84	258.5	-1.0	0.78	277	-0.5	0.85
Golden-cr Sparrow	CW	AHY	St.1	1970	2001	270	-3.1	0.23	274	-2.5	0.48	296	-4.7	0.08
Golden-cr Sparrow		HY	St.1	1970	2001	266	-6.1	0.00	268.5	-10.1	0.00	301	-7.8	0.01
Golden-cr Sparrow		AHY	St.2	1969	2002	264.5	2.7	0.05	270.5	1.9	0.28	282.5	2.3	0.16
Golden-cr Sparrow		HY	St.2	1969	2002	262.5	0.0	0.99	264.5	0.2	0.85	289	-2.6	0.05
Hermit Thrush	LR	AHY	St.1	1985	2001	265	3.9	0.43	268	1.4	0.62	282.5	-2.1	0.54
Hermit Thrush		HY	St.1	1979	2001	263	-6.4	0.04	264.5	-3.6	0.34	292	1.5	0.62
Hermit Thrush		AHY	St.2	1969	2002	274.5	-2.9	0.08	280	-1.7	0.24	290.5	-0.4	0.79
Hermit Thrush		HY	St.2	1969	2002	255	-4.3	0.11	264	-0.3	0.70	288	1.0	0.24
House Finch	R	AHY	St.1	1970	1997	227	-6.9	0.01	229	-2.5	0.18	255.5	-18.9	0.00
House Finch		HY	St.1	1970	2001	225	-1.9	0.06	225	-5.9	0.01	249	-10.0	0.00
Lincoln's Sparrow	PR	AHY	St.1	1983	2001	256	3.5	0.41	262	-3.1	0.21	275	-1.8	0.61
Lincoln's Sparrow		HY	St.1	1982	2001	251	-1.4	0.71	257	-6.4	0.08	280	1.3	0.72
Myrtle Warbler	CW	AHY	St.4	1984	1998	277	-1.4	0.67	279	-5.6	0.24	290	-2.8	0.60
Myrtle Warbler		HY	St.4	1983	1999	275.5	-2.5	0.41	278	-1.1	0.81	294	-5.4	0.17
Orange-cr Warbler	LR	AHY	St.1	1986	1995	252	-10.0	0.51	nd	nd	nd	277	11.4	0.28
Orange-cr Warbler		HY	St.1	1985	2001	237.5	1.8	0.66	245.5	3.3	0.72	269.5	-0.4	0.92
Puget Wh-cr Spar.	PW	AHY	St.1	1970	2001	267	-2.9	0.06	270	-1.9	0.13	285.5	-2.4	0.38
Puget Wh-cr Spar.		HY	St.1	1970	2001	261	-4.0	0.02	262	-4.1	0.01	290	-4.5	0.05
Puget Wh-cr Spar.		AHY	St.2	1976	2002	268.5	0.6	0.73	nd	nd	nd	277	2.8	0.24
Puget Wh-cr Spar.		HY	St.2	1976	2002	260	-2.4	0.13	261	-0.4	0.83	278.5	-2.4	0.37
Song Sparrow	PR	AHY	St.1	1981	1997	231	-2.8	0.59	nd	nd	nd	261.5	-4.8	0.52
Song Sparrow		HY	St.1	1981	2001	226	0.7	0.29	226	1.1	0.13	248	-0.9	0.81
Song Sparrow		AHY	St.4	1983	1998	245	0.5	0.94	nd	nd	nd	275	-4.0	0.41
Song Sparrow		HY	St.4	1983	1999	231	-12.6	0.00	231	-13.6	0.01	261	-5.2	0.32
Swainson's Thrush	CS	AHY	St.1	1986	2001	243.5	8.0	0.06	249.5	4.1	0.31	264	-5.6	0.17
Swainson's Thrush		HY	St.1	1985	2001	245	-1.4	0.75	249	-2.2	0.61	265	-1.7	0.73
Swainson's Thrush		AHY	St.4	1984	1997	238	-8.3	0.26	nd	nd	nd	256	13.6	0.00
Swainson's Thrush		HY	St.4	1983	1999	226.5	-16.0	0.00	230	-17.7	0.00	250	-1.5	0.68
Yellow Warbler	CS	AHY	St.1	1986	2001	237	0.3	0.95	242	1.6	0.70	255	-3.3	0.37
Yellow Warbler		HY	St.1	1985	2001	236	0.5	0.91	236	0.0	1.00	259.5	-1.0	0.74

[1] Migratory/Residency Group. See Fall Migratation, Methods for abbreviations