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Temperature and Long-Term Breeding Trends in California Birds: Utilizing an Undervalued Historic Database?

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TEMPERATURE AND LONG-TERM BREEDING TRENDS IN CALIFORNIA BIRDS: UTILIZING AN UNDERVALUED HISTORIC DATABASE

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Preface

The California Energy Commission's 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 conducts public interest research, development, and demonstration (RD&D) projects to benefit California.

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.

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Temperature and Long-Term Breeding Trends in California Birds: Utilizing an Undervalued Historic Database is the final report for the *Rapid Global Warming and Breeding in Migratory Birds* project (contract number 500-02-004, work authorization number MR-069) conducted by Stanford University. The information from this project contributes to PIER's Energy-Related Environmental Research Program.

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

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Abstract

Long-term data recorded before regional temperatures were greatly affected by human emissions of greenhouse gases provide an historical baseline with which to compare modern and future trends. Long-term ecological data needed to investigate the influence of temperature on the time of songbird breeding are rare. Significant amounts of data exist in collector descriptions of bird eggs taken in the wild from mid-1800s to mid-1900s. The researchers draw on these data from three museums, and finds that seven of 21 species examined had significant trends in laying date, with some species laying eggs earlier and others later. The largest change was in the Oak Titmouse with an average shift of 20 days later per decade and Phainopepla with the largest earlier shift of 8 days earlier per decade. The associations between the average California temperatures a month or two before laying and times of breeding were strong for six out of the nine resident California songbirds. For migrating species, only two of nine had a strong association between laying date and mean California temperature. These findings provide a baseline to which modern and future phenological shifts may be compared and calibrated. The researcher team offers suggestions for future studies and recommendations for the state of California.

Keywords: global warming, avian, non-traditional data, spring phenology, museum egg collection, historic data, breeding date, directional trend, temperature anomaly, oology, laying date

Executive Summary

Introduction

The globe is warming and California, like most of western North America, has been experiencing changes in the climate over the last 50 years that are more extreme than the global average and much of the rest of the continent (Hayhoe et. al 2004). In particular, winter and spring temperatures have been warmer and spring snow levels have decreased in lower and mid-elevation mountains sites (Luers et al. 2006). These types of changes are predicted to continue in California throughout this century, with the most recent projections anticipating an increase of 3-5.6 degrees C, even under low emissions scenarios (Luers et al. 2006).

One of the most obvious and frequent adaptations seen in plants and animals today is changes in timing of key life history traits(phenology), such as flowering, migration, and breeding. Most phenological studies have focused on the last 20 to 30 years, because easily accessible data are mainly available over this time period. However, understanding how species' phenologies changed before the average global temperatures began to rise rapidly (about mid-1970s) will likely provide insight into the adaptive behavior of these birds. In addition, change in the timing of these events has the potential to radically alter the interactions between species and perhaps even the viability of specific populations of birds. For example, a stable predator-prey interaction would break down if the timing of arrival or emergence of the two species becomes unsynchronized. This in turn could lead to dramatic changes in the population sizes of one and probably both species.

Purpose

Long-term data recorded before regional temperatures were greatly affected by human emissions of greenhouse gases can provide an historical baseline with which to compare current and future trends. This could help increase the understanding of the importance of temperature in the timing of breeding in select songbirds, there by illuminating the species most sensitive to rapid temperature increases. This information, in turn, could be used to help focus future research and monitoring on specific species, a valuable goal given limited resources.

To increase our understanding of how plants and animals will most likely respond to rapid warming projected in the future (IPCC 2007b), researchers need long-term data for both temperature and species. With only short-term data, differentiating between variation or cycles and trends is difficult. The existence of long-term data collected before the mid-1900s is quite rare. In this study the researchers investigated whether or not information taken from collector descriptions of wild-bird eggs over a century beginning in mid-1800s could provide robust information about historical breeding patterns in birds.

Project Objectives

The primary goal of this study was to determine the historical baseline (i.e., before rapid climate change) of breeding phenology for resident and migratory birds in California and whether or not the timing is related to regional temperature. To address this goal, the research team identified two key objectives:

1. Using museum data from eggs, determine species-specific historical timing of breeding phenology in California birds; and,
2. Assess whether the historical timing of breeding in California birds was related to regional temperature or not.

Correlating phenology of breeding with changes in regional temperatures is a way to better understand the effects of climate change on the spring phenology of songbirds. This information has the potential to help decrease uncertainty for resource managers, which could help managers make better predictions about how the breeding biology of songbird might likely response to various scenarios of future climate change.

In this study, the researchers used both museum data from the mid-1800s to mid- 1900s from the University of California at Berkeley's Museum of Vertebrate Zoology, the Smithsonian and the California Academy of Sciences, along with monthly temperature data from 1895 to the mid-1900s for the state of California obtained from The National Climate Data Center.

Project Outcomes

An overarching purpose of this study was to determine if information from egg collections in museums is generally useful for scientific analysis. The great intrigue of these data is, of course, the possible availability of historic data on numerous species beginning as far back as the mid-1800s. These data may not be useful because the data were collected mainly by amateurs without a plan of when or where collecting should occur, and with only a fraction of the eggs held in museums around the country being accessible for computer analyses. The researchers found that the historical data on breeding in birds, while a bit difficult to analyze, do provide useful information about the timing of breeding of select California songbirds. In addition, associations were found between several songbird breeding phenologies and average California monthly temperatures.

Conclusions

The researchers found the egg data to be valuable and of great help providing insights not easily accessible without historical data. Songbirds migrating into California from Mexico or even farther south in general do not exhibit a recognizable association with the average temperatures in California. Several birds that are resident in California, however, do seem to have a strong association between when they breed and what the California temperature is. These residents are being exposed to the temperatures in California throughout their entire reproductive cycle while migrants arrive in California with the beginning of their cycle already begun.

Using historical egg and nest collections that spanned at least 10 years for a given species during the period from 1895 to 1971, the researchers were able to determine that seven out of the 21 species investigated had significant trends in laying date, with some species laying eggs earlier in the year and others laying eggs later. Of the birds examined the greatest change in laying date over time was that of the Oak Titmouse, which was breeding on average 20 days later per decade over 22 years of data. This titmouse did not show a relationship between breeding and any of the temperature variables explored here. The Phainopepla is the species that shows the largest earlier shift in laying date—by a total of -8 days per decade. This species did show a strong relationship with the average California temperature one month before laying the first egg (see below). While beyond the scope of this study, the researchers note that a valuable investigation would be to determine why the titmouse is shifting later and the Phainopepla earlier.

The trigger initiating migration and breeding has been shown in several birds to be a change in day length (e.g. Lack 2008). Several birds, however, are known to use other environmental factors, such as the timing of rains and the change in temperatures (e.g., Wingfield and Farner. 1993). An interesting hypothesis to test would be to determine if the triggers for particular species switch from day length to temperature once a temperature threshold is past. This would help us better anticipate possible shifts that climate change has in store for some birds. The historic data were used to determine which of the California breeding birds showed strong associations between the historic breeding dates and the anomalies in historic state-wide monthly average temperatures. The relationship of temperature anomalies on the time of breeding was strongest in the resident California birds—those that live year round in California. Six out of nine (67%) resident songbirds showed significant correlations with laying date and some aspect of temperature anomalies. The temperature anomalies were not restricted to those occurring during the same month as an egg was collected. In addition to the anomalies for the same month, the researchers used temperature anomalies one month and two months before egg collecting.

The research team finds that, unlike resident species, only two of the nine (22%) migratory species had a strong association between laying date and temperature anomalies in California. The lower number of migrants showing strong associations with temperature anomalies may indicate that either temperature is not a trigger for these migratory birds, maybe the temperatures to which they are sensitive occur in areas outside of the breeding ground, possibly on the wintering ground or perhaps on migration, or another factor, such as availability of prey (Visser et al 2004). If, like the majority of resident species, they were most sensitive to temperatures one or two months before the egg laying begins, then temperatures in the locations where the birds are one or two months before arrival would need to be examined with the species data. Unless there is a consistent relationship between temperatures in the regions south of the breeding site and on the breeding site, which is certainly testable, the authors would not expect the associations between birds and temperatures in their breeding locations to be strong.

Recommendations

As the climate continues to warm dramatically, species around the world are going to suffer and many may go extinct. This problem can be attacked in two different ways: (1) Decreasing the amount of green-house gases, or (2) Managing species to help them adapt to the rapid warming.

Recommendations for Scientists

1. Expand the study presented here on all breeding species in California. The interaction among species can be quite strong and understanding the possible reactions of more species will help managers be proactive rather than reactive.
2. The species found to be associated with temperature need to be monitored.
3. In addition to monitoring bird populations, populations of insects eaten by the birds need to be watched.
4. Facilitate a meeting with curators of egg collection from as many museums as possible to determine a universal format for data entry and retrieval of egg collection documents. Information from the various collections needs to be computerized. This is particularly true for California because it has the largest known collection of eggs in the world: the Western Foundation of Vertebrate Zoology in Camarillo (close to Los Angeles).
5. Refine these results by using regional average temperatures rather than state-wide averages.
6. Based on the findings in this study, models about resident-species reactions to temperatures might be able to be derived. These models could be validated using recent data and used to project possible reactions to future climate disruption.

7. More research is needed to determine if, like resident species, there is a particular time and or temperature that associate strongly with date of first laying. If that can be determined, then, like the resident species, a model could be derived that could predict laying date.

Recommendations for Resource Managers

1. Knowing even a rough window of when the breeding in resident and migrant bird species is strongly associated with ambient temperatures will allow managers to be proactive.
2. Feeding hatchlings is very energy expensive. Once managers know the rough window within which the birds may start laying, then if food resources are not as abundant as needed supplemental food could be readied ahead of time.
3. By knowing from the monitoring project how species populations are changing, a manager could determine a problem earlier than would be possible without the monitoring data. This again could allow proactive rather than reactive interventions.

Benefits to California

As the globe has warmed some species have been adapting to that change by shifting their phenology in the spring, fall or both. Yet, not all species are showing the ability to shift enough to stay abreast with the rapidity of the warming. The inability to shift could be detrimental for a species because it may not be keeping up with the changes of other species. This may not cause a problem, at least for awhile, but if the shifting difference is such that a predator is separated from its prey, then the predator population will drop. By helping resources managers in California to be able to expect that such a mismatch could occur, then anticipatory steps could be taken. For example, providing supplementary food, much like refuge managers provide to waterfowl, could be planned before there is a crisis. More extreme steps may be needed to ensure the survival of many species, but the passage of time and with more research these will become much more evident.

By understanding the changes in species that have occurred and may occur in the future, California resource managers will be better prepared to help facilitate the type of adaptation species will need to endure with rapidly changing climate. One of the primary adaptations in birds is changing the time of breeding. This is particularly true for migrating species, owing to the fact that both migration and breeding are shifting together. Understanding the magnitude of the change and which species are and are not exhibiting changes, state resource managers will be more prepared to facilitate the breeding of species. This includes many endangered species of Neotropical migrants.

The research presented here focuses on birds breeding in California, but similar behaviors, although not exactly the same will be occurring in other animals and even in plants. More research is needed on birds and other species, but the results presented here can hopefully reduce the uncertainty resource managers in California are facing as the globe warms.

1.0 Introduction

1.1. Background and Overview

The globe is warming and California, like most of western North America, has been experiencing changes in the climate over the last 50 years that are more extreme than the global average and much of the rest of the continent (Hayhoe et al. 2004). In particular, winter and spring temperatures have been warmer and spring snow levels have decreased in lower and mid-elevation mountains sites (Luers et al. 2006). These types of changes are predicted to continue in California throughout this century, with the most recent projections anticipating an increase of 3-5.6 degrees C, even under low emissions scenarios (Luers et al. 2006). Even though this may seem as though it is an insignificant amount of warming, species around the globe are already exhibiting major changes on land and in the oceans (Root and Schneider 2002; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006). Indeed, the consistent changes around the globe seen in plants and animals as they respond to changes in regional warming show that the warming temperatures to which they are responding are partly due to natural causes and partially attributable to human greenhouse gas emissions (Root et. al 2005).

In animals and plants, the timing of annually occurring traits (phenology), such as daffodils blooming or frogs laying eggs, has been intensely studied since the mid-1990s. The vast majority of these studies have found pronounced phenological changes over decades that are associated with changes in regional temperatures (IPCC 2001b). The relationship between regional temperatures and phenology provides a means to determine the number of days per decade and per degree of temperature the phenological traits have changed (Parmesan and Yohe 2003; Root et al. 2003). Furthermore, better understanding the responses of species to regional temperature provides us greater scientific confidence from which to predict possible future impacts to species as the globe continues to warm (e.g., Ahola et al. 2004; Visser et al. 2004; MacMynowski and Root 2006).

A consistent pattern of phenological change strongly associated with regional warming is occurring in the vast majority of species in the northern hemisphere (IPCC 2007b, 2001b; Parmesan & Yohe, 2003; Root *et al*., 2003, Root and Schneider 2002). The average number of days changed in North American plants and animals over the last 30 years of the 20th century was roughly 15.5 days, or about 5 days per decade (Root *et al*. 2003). For example, in the Upper Peninsula of Michigan, spring migrants were arriving an average of about 15 days earlier in the spring of 1996 than they had in the spring of 1965. Of the 45 species for which records were sufficiently complete, 19 were arriving earlier, and one species (hermit thrush (*Catharus guttatus*)) was arriving later. The increase in global average temperatures over that time period was around 0.4° C (IPCC 2007a).

In addition to having species arriving earlier to the Upper Peninsula of Michigan, this example also shows that species are not all changing in the same manner. Some species were arriving earlier, but not all species. This differential movement means that current species communities will change in many different ways. Changes in community composition will likely disrupt the current biotic interactions, such as competition and predator-prey interactions, which in turn may influence the population size of species that were being held in check (e.g., population size of prey) by those interactions.

In birds, the time of hatching for many species is synchronized with high abundance of prey. With warming, these two events may be no longer ideally timed, which is leading to a significant drop in population size in some species of birds (Sanz et al 2003). For example, the hatching of two populations of barnacle geese (*Branta leucosis*) occurred after the peak food availability, which resulted in a decline in the survivability of the young (van der Jeugd et al 2009). The population decline in some migratory bird species may be due to the fact that those declining have not been shifting the time earlier when they are leaving their wintering grounds and/or when they are arriving to their breeding grounds. By not shifting, these species are not arriving in time to reproduce when the peak food resources are available to feed their young. This is resulting in a drop in the survivability of the young, which means the population size of these species is dropping (Moller et al 2008). These impacts lead to an increase likelihood of extinction (Sekercioglu et al 2008) for the species influenced by human activity.

1.2. Historical Egg Records

By around 1885 the hobby of oology—the study of eggs—became a common past time, primarily for young boys (Kiff 2005). Indeed, Daniel Carter Beard, co-founder of the Boy Scouts and author of *The American Boys Handy Book* (1893), explained in great detail for the nine-year-old readers of his book, how to collect, empty the contents, and store eggs they collected from wild birds. Although Beard admonished his young readers to only collect eggs for study and to not "…destroy and pillage birds' nests…" the density of many birds dropped significantly after 1885, particularly in areas close to where collectors lived. For example, Ospreys have what has been said to be the most beautiful eggs of all birds, and thus became a prime target for eggers. The population of Ospreys was so badly depleted that in 1916 an egg collector removed the last egg to be laid in the UK until 1956 (http://www.ospreys.org.uk/About%20Scotland.htm).

In North America the Migratory Bird Act (MBA) between the US and Canada made it illegal in 1918 to collect or have in possession nests or eggs of all migratory birds (Ehrlich et al. 1988). The MBA seemed to have slowed down the egg collecting but it certainly did not stop it. Eggers were active until around World War II when collecting wild-bird eggs switched from being viewed by society with pride for helping science and entertaining young boys to being viewed with disdain and harm. Around that same time (1942) the Convention on Nature Protection and Wildlife Preservation was ratified by Congress. This law not only made it illegal to collect eggs and nests, but it was also illegal to be in possession of eggs or nests. Consequently, private collectors were forced to give or sell their collections to museums across the country (Kiff 2005). Now museums curate many hundreds of thousands of eggs with information. That information provides valuable records about birds that lived during a time when data were rarely recorded and maintained (but see Grinnell 1922).

1.3. Project Objectives

Having historic information about species available in natural history museums around the world is invaluable. For example, most of our understanding about the evolutionary pathways (Dumbacher et al 2008) and biogeography (Barker et al 2004) of a large number of the known species on our planet has come from scientists using specimens (e.g., skins or skeletons) preserved and available in the research wings of natural history museums.

The data accompanying eggs in museum collections provide information about breeding phenology in wild birds from the mid-1800s to the mid-1900s. Only a handful of studies have used information from egg collections (e.g., McNair 1987, Anderson and Hickey 1970, Svensson 1978). One possible reason why there are relatively few studies utilizing this resource is that until recently the data had not been converted into digital form. Currently, the vast majority of museums throughout California, the United States, and North America has not yet computerized these valuable data. A goal of this research was to determine if these data were usable in a manner that might help understand historic breeding phenology of California birds. If so, then this may help provide the impetus to have more of the collection computerized. After all, data spanning more than 20 years are rare in ecological studies, and long-term data on the timing of breeding in birds are even rarer (a notable exception is the study on the timing of breeding in the America Tree Swallow [*Tachycineta bicolor*] from 1959 to 1991 throughout North America [Dunn and Winkler1999]).

Using data taken from egg collections, the researchers focused their research around two main objectives:

1. Using museum data from eggs, determine species-specific historical timing of breeding phenology in California birds; and,
2. Assess whether the historical timing of breeding in California birds was related to regional temperature or not.

By focusing research on these two objectives, the findings, which are in the form of correlations, improve our understanding of the effects of climate change on breeding phenology of several Californian songbirds.

Trends from data recorded before regional temperatures were greatly affected by human emissions of greenhouse gases can provide an historical baseline with which the research team can compare recent, current and future trends. In addition, understanding the historical effects of climate on species will increase our understanding about which species are most likely to be sensitive to current and future climate change. This, in turn, can help focus future research and monitoring efforts to most efficiently explore the effects of climatic change on species.

This information can help to decrease uncertainly about various aspects of the current and future management of bird species. By understanding more about what different species are expected to do as the temperature rises, managers may be able to better understand the possible problems before they occur. The phenological shift of some species may not be enough to stay abreast with the rapid pace of the warming. This may result in a problem such as separating a predator from its prey. By helping resources managers in California to be able to expect that such a mismatch could occur, then preventive steps could be taken. For example, providing supplementary food, much like US Fish and Wildlife provide to waterfowl, could be planned before there is a crisis.

2.0 Project Approach

2.1. Data

2.1.1. Museum Egg Collections Data

In order to determine historical timing of egg-laying in California birds and if egg-laying is related to temperature, the researchers used egg-collection data as a proxy for the date of initial egg-laying. The museum egg collections contain eggs for nearly all breeding birds in California. This includes both non-passerine species (e.g., waterfowl, herons, and gulls) and passerines (e.g., sparrows, warblers and wrens). Non-passerines are comprised of many different Orders, but the passerines (songbirds) consist of only one, Passeriformes. Consequently, the species of songbirds show much less variability among species than species from the different Orders of the non-passerines, and the researchers chose to focus only on passerine species.

The data used in this study came from collections of wild bird eggs held in three different museums: the California Academy of Sciences, the Museum of Vertebrate Zoology at UC-Berkeley, and the Smithsonian Museum.

The egg-collection information (i.e., breeding data) ranged from mid-1800s to mid-1900s. These data were sorted by species and subspecies, location, and year. These data contained marine birds, shorebirds, game birds, raptors, and upland birds including passerine birds. The concatenated data for the three museums contained 12,286 records of bird nest and egg collections, representing more than 600 species:

- 4,810 records from the California Academy of Sciences, San Francisco, California
- 1,315 records from the Smithsonian Museum, Washington, D.C.,
- 6,161 records from the Museum of Vertebrate Zoology at UC-Berkeley, California

Around the world the number of sets of eggs (i.e. clutches) laid in a year varies by species, temperature, other weather variables, location and level of predation on the eggs or young. Many birds that breed in California frequently have more than one clutch. The historic egg collectors usually did not indicate which clutch they were removing, and as such museum records do not indicate if the eggs were collected from a first clutch or a subsequent clutch. Most of the 12,286 records were from species that typically have more than one clutch in a year, at least in a portion of their range. Therefore, to be conservative the researchers restricted their analyses to those species known to have a single clutch a majority of years (Ehrlich et al 1988).

To detect historical long-term trends in the date of egg-laying, the data were also restricted so that a species was included if egg records spanned at least 10 years and had at least five records. These restrictions helped to avoid results strongly influenced by short-term fluctuations or outliers in laying date (Torti and Dunn, 2005). The final number of species used was 21 species and 700 records, shown in Table 1.

Table 1 California Bird Species Included in Study

Scientific Name	Common Name	Migratory/Resident	Records
Catharus ustulatus	Swainson's Thrush	Migrant	28
Contopus cooperi	Olive-sided Flycatcher	Migrant	7
Contopus sordidulus	Western Wood-Pewee	Migrant	10
Dendroica petechia	Yellow Warbler	Migrant	8
Geothlypis trichas	Common Yellowthroat	Migrant	42
Myiarchus cinerascens	Ash-throated Flycatcher	Migrant	22
Piranga ludoviciana	Western Tanager	Migrant	16
Wilsonia pusilia	Wilson's Warbler	Migrant	19
Pheucticus melanocephalus	Black-headed Grosbeak	Migrant	18
Carduelis lawrencei	Lawrence's Goldfinch	Nomadic	16
Carduelis psaltria	Lesser Goldfinch	Nomadic	19
Baeolophus inornatus	Oak Titmouse (Plain)	Resident	7
Chamaea fasciata	Wrentit	Resident	26
Corvus brachyrhynchos	American Crow	Resident	7
Cyanocitta stelleri	Steller's Jay	Resident	12
Euphagus cyanocephalus	Brewer's Blackbird	Resident	274
Phainopepla nitens	Phainopepla	Resident	33
Pica nuttalli	yellow-billed magpie	Resident	104
Pipilo maculatus	Spotted Towhee	Resident	17
Poecile rufescens	Chestnut-backed Chickadee	Resident	6
Carpodacus cassinii	Cassin's Finch	Variable	9

During the course of this investigation, the researchers uncovered additional sources of hand written data on the timing of breeding in songbirds, especially for the second half of the 20th century, which could be utilized for future studies. For example, the Cornell Lab of Ornithology at Cornell University houses numerous nest record cards for most North American species (Dunn and Winkler 1999). In addition, museums throughout California and the nation are attempting to get the information accompanying each egg or nest and eggs computerized. If a significant number of museums finish this task, the findings presented here could be expanded, and could include more species, such as those species not having enough samples in the databases to be used in this study.

2.1.1. Climate Data

Monthly mean temperature data were obtained from the National Climate Data Center (NCDC 2008). These climate data represent averages from observational stations throughout the state beginning in 1895. The data are available for individual weather stations or averaged across seven defined climatic zones in California; because the egg records used in this study were averaged across the state to increase sample size, the statewide monthly mean temperature was used. Although higher resolution climate data do exist at NCDC and other repositories (e.g. PRISM), the research team did not deem these data necessary for this study. Precipitation affects aspects of breeding in some birds (Sorenson et al 1998), but the reliability of precipitation data is not as good as temperature data and predictions about future precipitation are less robust at this time (IPCC 2001a). Therefore, the research team opted to focus the investigation here only on effects of temperature.

2.2. Analyses

With the database assembled, the research team performed a set of regression analyses to meet the stated project objectives. Due to the possible influence that many independent variable might simultaneously exert on species, the researchers include multiple linear regressions using data from all species and both temporal and climate factors to enhance power and to investigate robust trends across all species examined. In addition, temporal trends and temperature factors were investigated separately for each species to better understand correlations, which may be individualistic within our species group. Below are details and further rationale underlying calculation and inclusion of each variable.

2.2.1. Considerations of Reproductive Period

The reproductive periods of songbirds are imbedded in their annual lifecycle. This cycle includes pre-nuptial molt and fattening, partial development of gonads, migration to breeding ground, completion of recrudescence of gonads, courtship, nest building, egg-laying, incubation raising and fledging young, post-nuptial molt and fat deposition, and migrating to wintering grounds (Berthold 2001). The annual lifecycle of non-migratory birds includes pre-nuptial molt, gonadal recrudescence, courtship, nest building, egg-laying, incubation raising and fledging young, post-nuptial molt. The timing of temperate seasonal breeders can be triggered by day length, and various environmental cues, such as temperature. The strength of the cues differed both within and among songbird species. Indeed, the timing of vernal testicular recrudescence has been found to vary by two months between two populations of song sparrow. Temperatures, which were believed to be the trigger, varied greatly between the locations of the populations (Perfito et al 2004). Additionally the change in the timing of one stage must influence the timing of many, if not all, other life stages.

As one aim of the present study was to determine the effect of temperature on laying date. Because a change in the timing of a lifecycle stage influences the timing of many, if not most, the researchers considered temperatures across the first few months of the reproductive period and not just the month that egg-laying occurred. The actual breeding period includes activities other than simply laying and incubating eggs. For example, reactivation of the reproductive system of birds begins weeks before breeding activity starts. This is necessary because unlike other vertebrates, at the end of the breeding season the gonads of bird regress in size. In one tropical species, the testes length in the non-breeding season was around 0.1 mm in length and 5mm in the breeding season (Wikelski et al 2000). Here the research team assumed that the pre-nuptial molt and recrudescence period could overlap, certainly in some species. Consequently, the time a pre-nuptial molt takes could range from one to three weeks while the recrudescence can take from two to four weeks. Setting up territories and attracting a mate could be another three to six days. The duration of nest building activity varies by species, but for non-weaving songbirds, the research team assumed that the time for the different species examined here is about four to six days. When the eggs were collected relative to when the first egg was laid is not possible to exactly determine from most of the samples in the collections the research team analyzed. McNair (1987) explained that roughly 85% of the eggs in the museums were collected within a couple of days of the first egg being laid. The remaining 15% could realistically be as late as around half way through the incubation period, because after this time getting the embryo out of the shell without breaking becomes less probable with increased incubation time. Consequently, the worst case scenario is that the dates of collection could be up to 10 days later than the actual beginning of laying for 15% of our records.

Taken together, this suggests that the longest window from gonads reactivating until egg collection could be 54 days (14 days + 28 days + 6 days + 6 days + 0 days = 54 days) and the shortest period would be 18 days (7 days + 14 days + 3 days + 4 days – 10 days = 18 days). If the collection date occurred near the end of a month, then 54 days before that would be two calendar months before the collection date.

2.2.2. Climate Anomalies

The research team calculated regression statistics for the relationship between the laying date and the climate variable for the month of laying and the preceding two months. Climate conditions in these preceding months most likely have the strongest link to conditions experienced immediately before or during breeding, and thus, are likely to be at least as informative and perhaps more so than a single seasonal mean. The temperature data, therefore, needed to be examined for the month the egg specimens were collected and each of the previous two months.

As done in the IPCC (2001a), temperature anomalies were calculated for each month's data, using the difference between recorded temperature and the mean temperature for that month over the time period 1895-1971 (the period for which egg records were available). Using temperature anomaly allowed the researchers to test, for example, if during an April with a positive temperature anomaly (a warmer April than the average April) particular species were laying eggs at earlier dates. Anomalies were calculated for all months; April, May and June are shown here (Figure 1) for consideration of space, as most of the breeding records fall into these months. Anomalies displayed in Figure 1 are calculated with reference to mean temperature from 1895 to 1971.

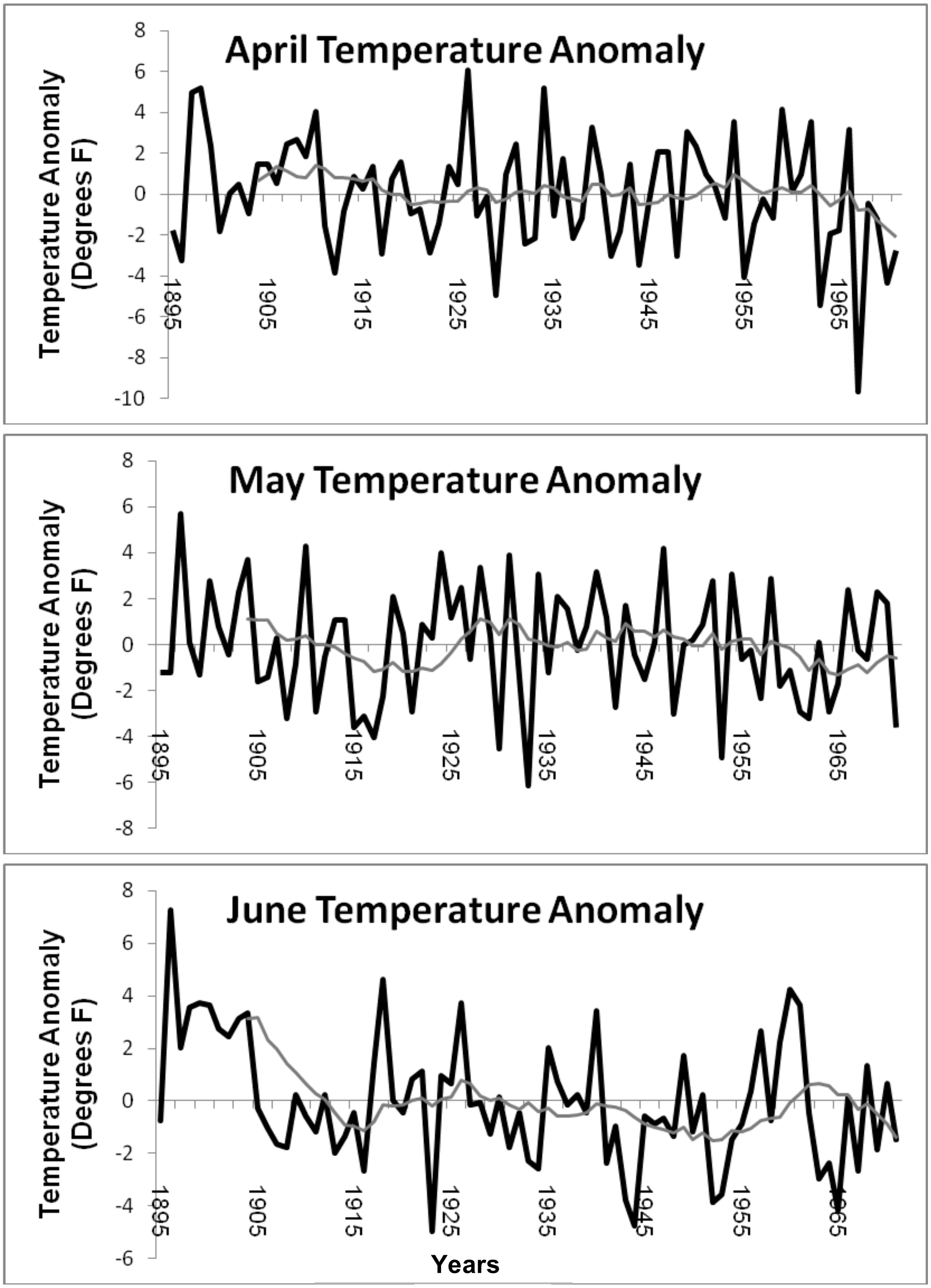

Figure 1. Temperature anomalies (black line) for spring months, and 10 year moving average (grey line). Temperature data are from National Climate Data Center (2008), with anomalies compared to average temperature from 1895 to 1971, the extent of egg collection data used in this study.

2.2.3. Breeding

Multiple linear regressions were used to determine the relationship between laying date and the year an egg was collected, the temperature in that month, the temperature anomaly for that month, the temperature anomaly for the month prior, the temperature anomaly for two months prior, migration type, and the species identity. The research team conducted simple linear regressions between the laying date and years to determine whether a linear shift in timing of breeding had occurred during the historical period.

Additionally, the team used linear regression models to analyze the relationship between laying date and temperature variables separately. All statistics were performed using R 2.5.1 (R Development Core Team 2008).

3.0 Project Outcomes

Songbirds migrating into California from Mexico or even farther south in general do not exhibit a recognizable association with a monthly average temperature in California. Several birds that are resident in California, however, do have a strong association between when they breed and California temperatures. Details of these relationships are given below.

3.1. Historical Timing of Breeding

An overarching goal of this study was to determine if information from egg collections in numerous museums helps the researchers understand the timing of bird breeding from the mid-1800s to the mid-1900s. Indeed, these data have the potential to provide scientists a window through which many aspects of long-term trends in breeding can be analyzed, beginning over 150 years ago. The results of this study show that these data can provide valuable information specifically on the breeding of resident California birds. The researchers found that the data, while challenging to analyze, provide useful information about the breeding phenology of songbirds in California.

3.2. Correlates of Breeding

To determine if the timing of breeding recorded in these historical data were related to temperature, the researchers initially analyzed egg collection data from all species together using multiple linear regression with species as a factor. All factors were significant ($p< 0.001$, Adjusted $R^2 = 0.89$; Table 2) except migration type. The inclusion of species as a significant factor ($p < 0.05$), indicates that species are breeding at different times. Because of this significant effect, the team performed all subsequent analyses separately for each species (Torti and Dunn 2005). Year also appears as a significant factor, suggesting that there is a trend in egg-laying date across all species; however, the partial coefficient is 0.06. There are likely trends toward earlier as well as later laying, and the researchers consider year as a separate factor in subsequent analyses.

Table 2 Multiple Linear Regression of Egg Collection Date and Selected Variables

Factor	Partial Coefficient	P-value
Species	-0.10	0.041
Migrate	0.67	0.205
Year	0.06	0.012
Temp	4.01	< 0.001
Same Month Temperature Anomaly	-3.99	< 0.001
One Month Prior Temperature Anomaly	-0.25	0.060
Two Months Prior Temperature Anomaly	0.40	0.002

To understand the influence of temperature anomalies on species individually, the researchers used multiple linear regression with year, the temperature anomaly from the same month as breeding, the temperature anomaly from one month prior to breeding, and the temperature anomaly from two months prior. Temperature alone was not included as a factor, as it is highly correlated with the Same Month Anomaly (adjusted R^2=0.30, p<0.001). The researchers found that 13 of the 21 species showed significant associations between laying date and one of the explanatory variables, with for nine of the 21 species analyzed showing a significant relationship between breeding date and a temperature anomaly. For five species, this anomaly was in the same month as breeding, for six it was the temperature anomaly one month prior, and for two it was the anomaly two months prior, with some species showing multiple significant relationships (see Table 3). These factors are included in this initial model to explore possible relationships across the entire dataset. The researchers acknowledge that some factors are auto correlated, however most adjusted R^2 of these correlations are less than 0.10, and further analysis of factors separately were conducted to address, in part, these correlations (see below).

Table 3 Multiple Linear Regression of Laying Date and Climate Anomalies and Year for Species Individually.

	Same Month		One Month Prior		Two Months Prior		Year	
Species	**p-value**	**Slope**	**p-value**	**Slope**	**p-value**	**Slope**	**p-value**	**Slope**
Baeolophus inornatus[R]							.079	2.15
Carduelis lawrencei[N]							.076	1.66
Carpodacus cassinii[V]			.084	-6.14				
Catharus ustulatus[M]							.027	0.57
Chamaea fasciata[R]					.045	3.90		
Contopus sordidulus[M]	.038	-3.52					.038	-0.68
Cyanocitta stelleri[R]	.077	2.71	.067	-3.48				
Euphagus cyanocephalus[R]	.006	1.35	.014	-1.25			.002	.264
Geothlypis trichas[M]	.086	2.50						
Phainopepla nitens[R]			.001	-6.99			.021	-.835
Pica nuttalli[R]			.063	-1.01	.002	1.86		
Pipilo maculatus[R]	.032	4.69	.016	-5.0				
Piranga ludoviciana[M]							.018	.57

* There were no significant relationships laying date and explanatory factors for *Carduelis psaltria*[N], *Wilsonia pusilla*[M], *Dendroica petechia*[M] , *Poecile rufescens* [R], *Pheucticus melanocephalus*[M], *Myiarchus cinerascens cinerascens*[M], *Corvus brachyrhynchos*[R], or *Contopus cooperi*[M]. R represents resident species, M are migrant, V are variable, and N are nomadic. Slopes indicate partial coefficients for factor, only those factors with p-value less than 0.10 are shown. Slopes indicate partial coefficients for factor, only those factors with p-value less than 0.10 are shown.

The researchers were interested in trends in the timing of egg laying during the first half of the 20th century, but because of varied patterns in climate over this period (Figure 1), the team do not expect a single linear trend to be likely for egg laying through time. Therefore, the team analyzed the laying dates through time for each species graphically to detect possible trends (Figure 2). There are no consistent patterns through time that appear across all species, with some showing a slight increase in laying date (laying later in the year), others a slight decrease (laying earlier in the year), and other showing no change or curvilinear response.

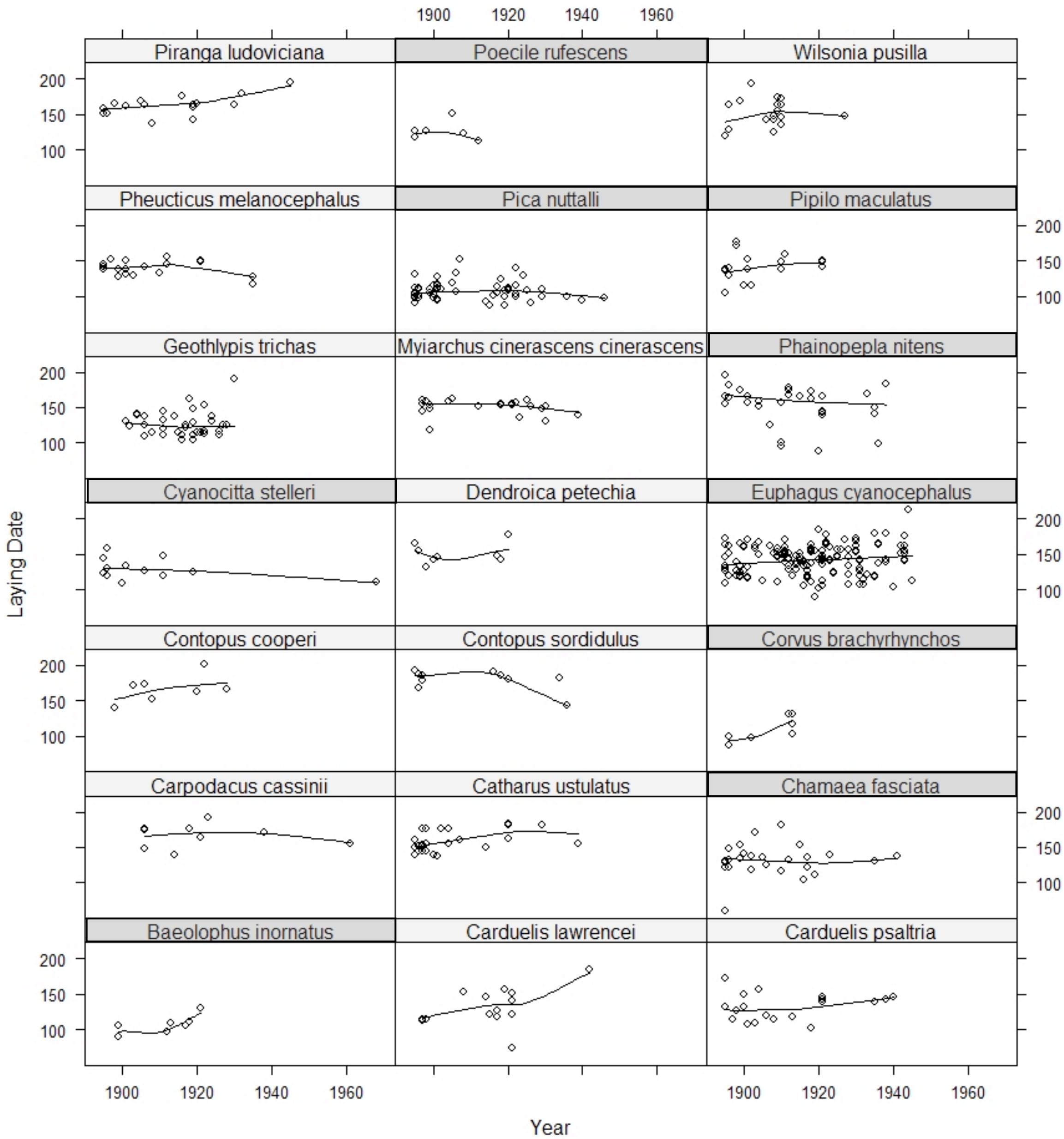

Figure 2 Laying date through time for each species. A LOWESS line is included to indicate possible trends. Dark-grey headers indicate resident species. Laying date is given as Julian day of year (e.g., 100 days is April 8 or 9).

The research team used linear regression to analyze the effect of temperature anomalies on laying date, which is independent of the possible trend in the temperature data resulting from normal progression of seasons in California, and a linear response is possible when comparing data from different calendar months. Overall, the researchers find that seven species showed significant relationships between laying date and temperature anomalies, though with different months and in different directions. Three species (*C. stelleri*, *P. maculatus* and *E. cyanocephalus*) show a significant effect of the temperature anomaly in the same month when considered as the only factor (Figure 3). For these three species with significant trends, all slopes are positive meaning that in years where the egg collection month was warmer than average; the species appear to be laying later. Positive and negative slopes are observed when all species are considered, although not at significant levels.

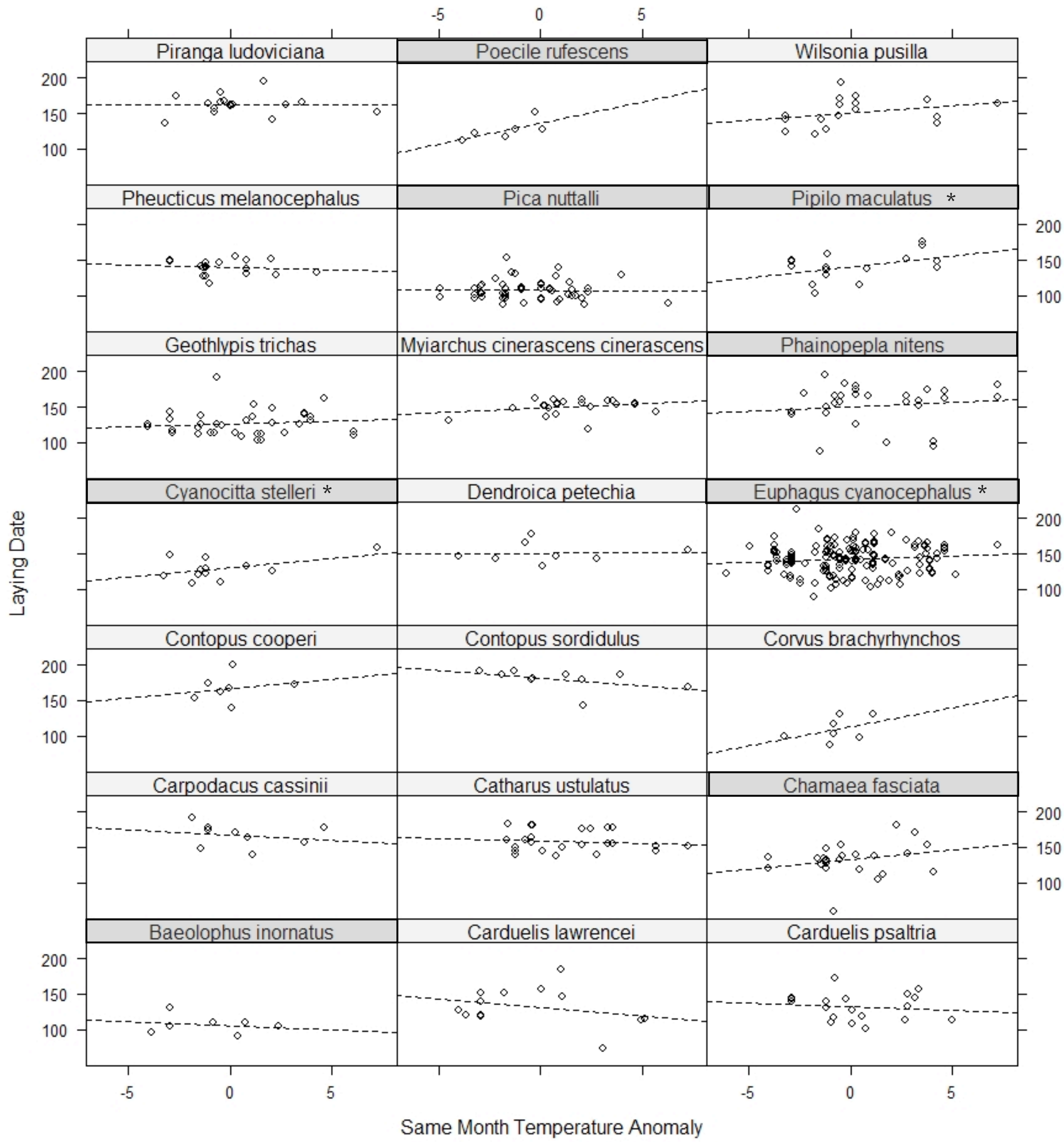

Figure 3. Laying date and temperature anomaly from the month the eggs were laid for each species. Dark-grey headers indicate resident species. Laying date given as Julian day of year. Three resident species show a significant relationship between the egg-laying date and temperature anomaly in the same month as the laying date. There are no significant relationships for migratory species. Dashed lines are linear regression.

When analyzing the relationship between laying date and the temperature anomaly one month prior, the research team find that four species (*C. cassinii, C. stelleri, E.cyanocephalus*, and *P. nitens*) have a significant relationship (Figure 4). For all four of these species the slope of the relationship is negative, indicating that in those years when the month prior to egg collection is warmer than average, the species are laying their eggs earlier. Positive and negative slopes are observed across all species, indicating species breeding both later and earlier, respectively, although not at significant levels.

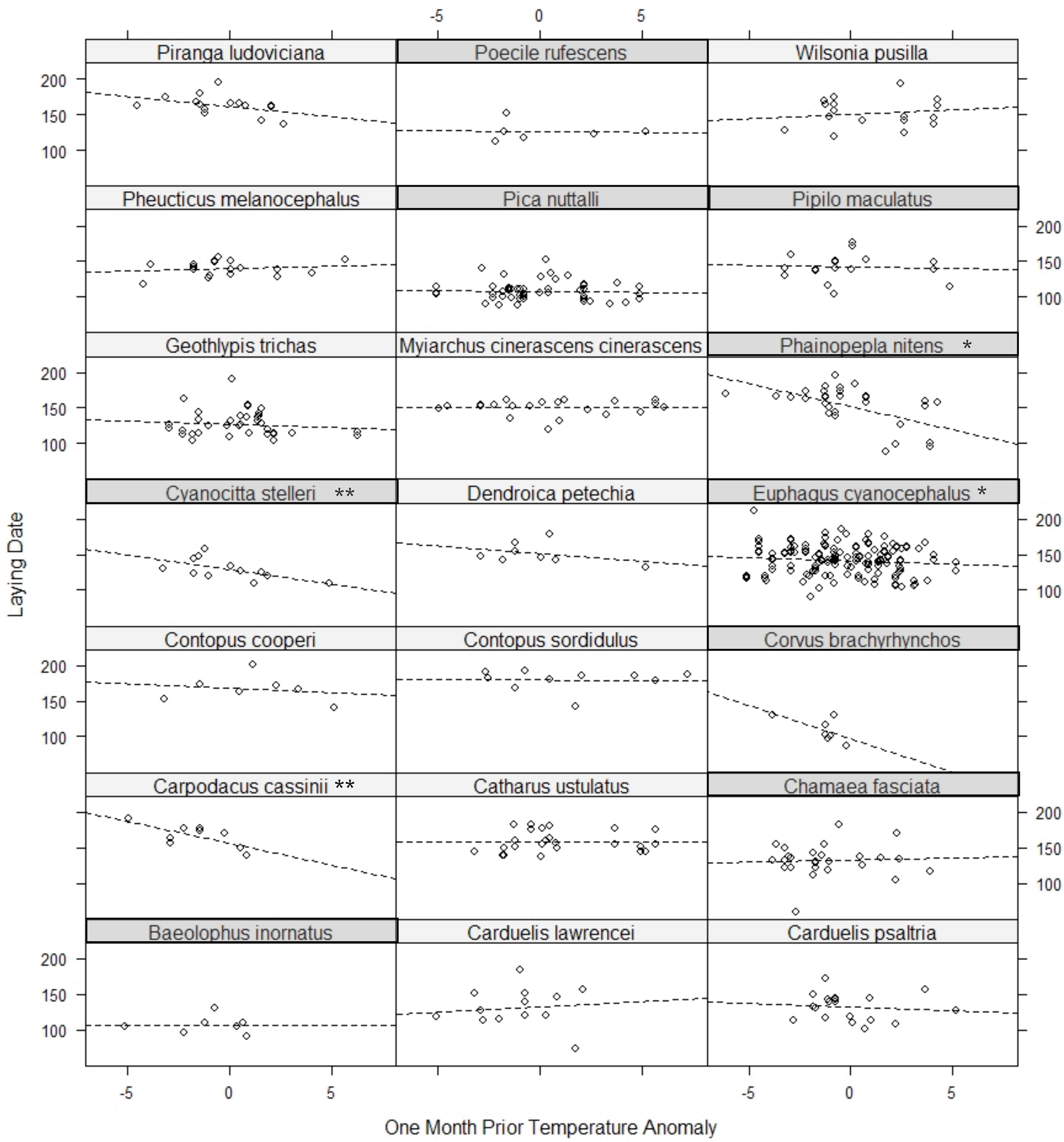

Figure 4 Laying date and temperature anomaly for one month prior to laying for each species. Dark - grey headers indicate resident species. Three resident species and one migratory species show significant relationships between egg-laying date and the temperature anomaly in the month preceding egg laying. Dashed lines are linear regression.

There are four species (*C. fasciata, C. brachyrhynchos*, *P. nitens*, and *P. maculates*) that show significant relationships between the laying date and the temperature anomaly two months prior (figure 5) While the *C. fasciata* and *P. maculatus* have positive slopes, *C. brachyrynchos* and *P. nitens* have negative slopes, again indicating that species respond in a variety of ways.

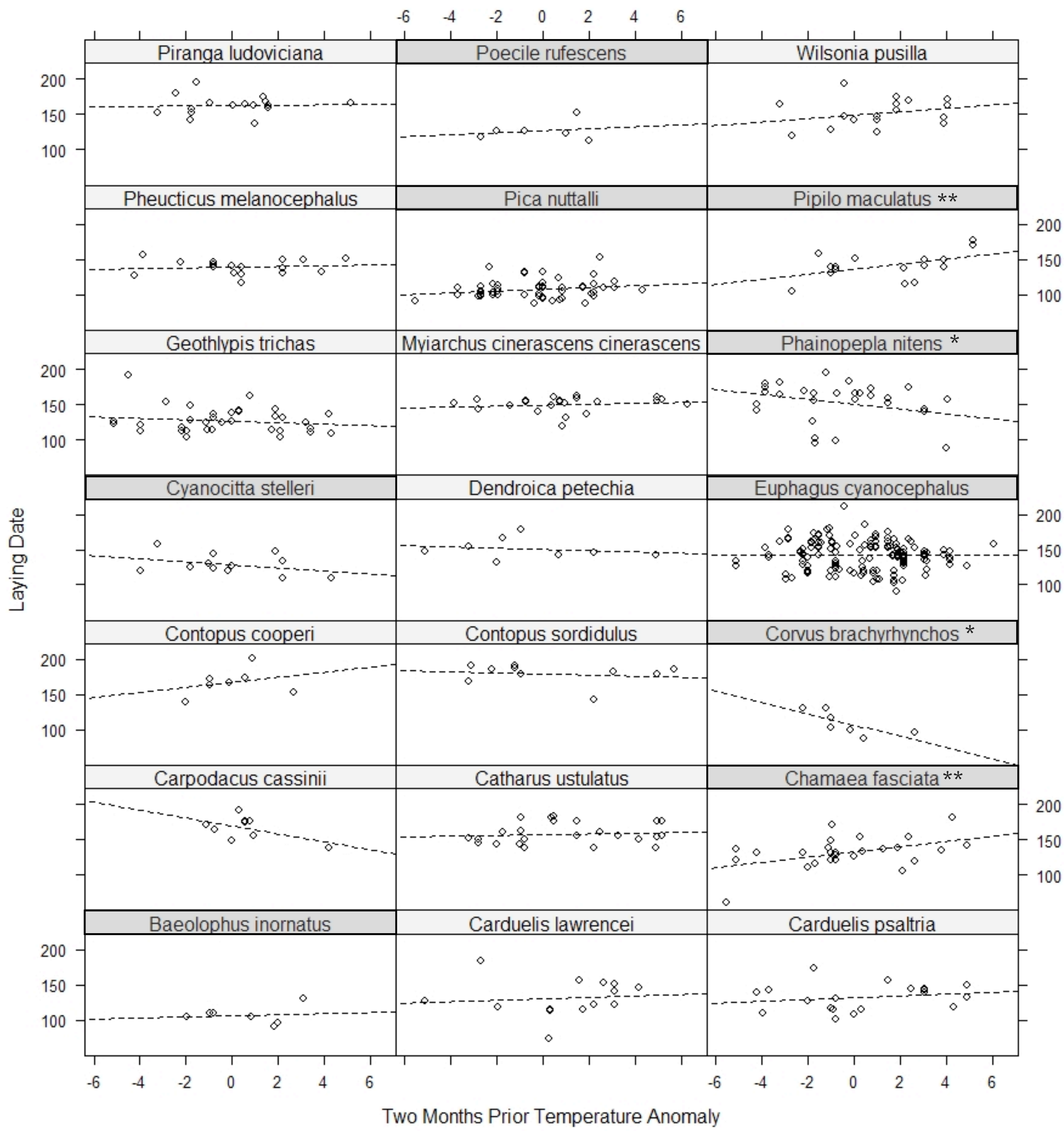

Figure 5 Laying date and temperature anomaly for two months prior to laying for each species. Dark-grey headers indicate resident species. Four resident species show a significant relationship between the date of egg laying and the temperature anomaly from two months prior. No migratory species show a significant relationship. Dashed lines are linear regression.

4.0 Conclusions and Recommendations

4.1. Breeding Trends in Resident and Migratory Birds

Using historical egg and nest collections that spanned at least 10 years for each species during the period from 1895 to 1971, the researchers were able to determine that seven out of the 21 species investigated had significant trends in laying date, with some species laying eggs earlier in the year and others laying eggs later (Table 3). Of the birds examined the greatest change in laying date over time was that of the Oak Titmouse (*B. inornatus*), which was breeding on average 20 days later per decade over 22 years. This titmouse did not show a relationship between breeding and any of the temperature variables explored here. The Phainopepla (*P. nitens*) is the species that shows the largest shift to earlier laying date, with a change of -8 days per decade. While beyond the scope of this study, the researchers note that a valuable investigation would be to determine why the titmouse is shifting later and the Phainopepla earlier.

The historic data were used to determine which of the California breeding birds showed strong associations between breeding dates and the anomalies in historic state-wide monthly average temperatures. The relationship of temperature anomalies on the time of breeding was prevalent in the resident California birds—those that live year round in California. Six out of nine resident songbirds showed significant correlations with laying date and some aspect of temperature anomalies. The temperature anomalies were not restricted to those occurring during the same month as an egg was collected; in addition to the anomalies for the same month, the researchers used temperature anomalies one month and two months before egg collecting.

The research team finds that, unlike resident species, only two of the nine (22%) migratory species had a strong association between laying date and temperature anomalies in California. The lower number of migrants showing strong associations with temperature anomalies may be indicating that temperature is not a trigger for these migratory birds, that the temperatures to which they are sensitive occur in areas outside of the breeding ground (possibly on the wintering ground or perhaps on migration), or that another factor, such as ready availability of prey (Visser et al 2004) affects the timing. If like the majority of resident species, they were most sensitive to temperatures one or two months before the egg laying begins, then temperatures in the locations where the birds are one or two months before arrival would need to be examined with the species data. Unless there is a consistent relationship between temperatures in the regions south of the breeding site and on the breeding site, which is certainly testable, the authors would not expect the associations between birds and temperatures in their breeding locations to be strong.

These results for migratory and resident species suggest that for at least some species regional temperatures may be influencing a period in the breeding cycle other than date of egg laying. Bird-breeding-cycle basics can help to facilitate a better understanding of these findings. Most birds have non-functioning reproductive systems outside of breeding season, which means the gonads recede (Dawson et al 2001); the breeding-season starts when the reproductive system begins to reactivate. The reactivation takes several weeks (Raess and Gwinner 2005), which means that migrating species usually begin their journey with this process started (Gwinner 2003). Upon arrival at the breeding ground the reactivation of the reproductive system is or almost is complete, which allows males to immediately begin finding and defending breeding territory and females inspecting different territories.

One of the purposes of this study is to determine if breeding by California songbirds is related to temperature. As explained above, the answer is yes, yet, the question arises as to what aspect of the breeding cycle is the one that is most sensitive to temperature? Is it the same for all species? Many studies have looked at change in first laying date of birds and many other events during the breeding season and found associations with regional warming (Root et al 2003, Parmesan 2006). Our results highlight how different groups of species, in this case migrants and resident in California, can react in different ways even when nesting in roughly the same location. Many other studies have shown that the first individuals of a migratory species to arrive on their breeding ground are strongly influenced by ambient temperatures on or near the breeding ground (References in Root et al. 2003, 2006). In this study the researchers found that resident species are also strongly influenced by average California temperature anomalies, but in several cases, a month or two before breeding begins. Consequently both migratory and resident species show sensitivity to temperature anomalies. In addition, the trigger initiating migration and breeding has been shown in several birds to be a change in day length (e.g. Lack 2008). An interesting hypothesis to test would be to determine if the triggers for particular species switch from day length to temperature once a temperature threshold is past. This would help us better anticipate possible shifts that climate change has in store for some birds.

Phenological changes such as the ones discussed here are a valuable part of how birds and other animals, for instance frogs (Blaustein et al 2002), adapt to the rapidly changing climate. By shifting the timing of breeding, these bird species are successfully moving temporally with the changing temperatures. The benefit of shifting over time allows certain activities, such as raising young, to occur at roughly the same temperature to which the species has become accustomed over the past hundreds of years while the climate was quite stable. Even so, when different species shift differentially a species could be shifting to stay within a particular isotherm but a species it relies on for food or shelter maybe shifting sooner or later than the original for species, which could cause unfavorable surprises.

Another key conclusion for this study is that these data provide a baseline to which modern and future phenological shifts maybe compared and calibrated. Indeed, it will not only help scientists working specifically on birds, but those working on other organisms could even use these data as a way to hopefully understand the trends seen in species in recent times. Such historic data are not readily available for many other groups of animals, which makes these data even more valuable.

There are several factors that may have the strength of the conclusions presented here. While the research team used the best available data, to generate sufficient sample sizes data were combined for the entire state. This spatial averaging is likely to have masked spatial variation in breeding timing and also likely contributes to variability in laying dates for each species. In addition, California is a complex region with many distinct climatic regions, and the state average temperatures used by the research team limit the research team's ability to analyze possible variation in response across the state. In the future, additional data will be needed to improve investigators ability to detect high-resolution spatial variation over large areas, like California.

4.2. Value of Historic Egg Collections and Future Studies

The historic egg-collection data also provided the researchers information needed to determine which species and how strongly they are influenced by ambient temperatures. Such information could be used to validate changes in current species and project in to the future how these species may respond to warming temperatures. Given the most recent projections of rising temperatures, such information could be priceless. Greater temperature anomalies are predicted in the future (IPCC 2007a), and these species are likely to be sensitive and will have significant responses.

The under-utilized egg and nest data collected from the mid-1800s to mid-1900s are shown in this study to be useful for determining long-term baselines. Indeed, natural history museums are holding valuable information applicable to help disentangle the affects of global changes on the breeding of birds. These data, though, are not necessarily systematic across space or time, which makes detecting climate-related changes or trends a bit difficult. Also, the museum data are not entirely "user friendly," meaning formatting and other actions needed (e.g., combining data from different museums) to ensure the reliability of the data are not at this time straight forward. Nevertheless, these data can certainly provide data that are entirely unavailable otherwise as long pitfalls are avoided, which certainly can be done.

4.3. Recommendations

As the climate continues to warm dramatically, species around the world are going to suffer and many may go extinct. This problem can be attacked in two different ways: (1) Decreasing the amount of green-house gases, or (2) Managing species to help them adapt to the rapid warming. Biologists and resource managers are going to have the task of aiding species. A lot is known about the species needing to be managed, but there are still some studies to be done. The findings of this study will help both biologist and managers to understand how increasing temperatures might be affecting species. Rising temperature is one of the major causes for concern when aiding species to adapt to climate disruption. The tasks facing managers to help facilitate the adaptation of species are numerous and difficult to implement, yet knowing what is required goes a long way toward finding the solutions. Recommendations for scientists first and then resource managers are below.

4.3.1. Recommendations for Scientists

1. The stronger the association between two values, the more reliable the projection into the future can be. The research team recommends that an analysis much like the one presented here be done on as many species breeding in California. Examining all the one-clutch non-passerine species should be fairly similar. Looking at species that are known to lay more than one clutch a year will be a bit more difficult, but certainly possible.
2. The species found to be associated with temperature need to be monitored for at least two reasons: (a) to provide information needed to ensure actions are taken before the species are close to extinction, and (b) to provide more information to be used to understand how temperatures influence species to make a better model of projections into the future.
3. In addition to monitoring bird populations, insect populations need to be watched. The reason for this is that one of the problems with changing phenology is that the food needed by the bird species is often not available at the needed time. This mismatching of timing of predator (birds) and prey (insects) has been recorded as contributing a lot toward the loss of hatchlings, which in turn is causing an overall drop in population size of the bird species.
4. Most museums do not have their wild-bird egg and nest data computerized. This, then, is the perfect time to have meetings with all bird curators and determine a universal format for data entry and retrieval. Once the format is decided, then the information from the various collections needs to be computerized. This is particularly true for California because it has the largest known collection of eggs in the world: the Western Foundation of Vertebrate Zoology in Camarillo (close to Los Angeles). They have around 1,000,000 eggs from ~4,000 bird species (WFVZ 2008). These data need to be made available on the computer before scientists will make use of them.
5. Confirm that breeding in resident birds is closely determined by the temperatures two months before breeding by using more regional climate data and perhaps weekly rather than monthly averages for temperature. This may provide a better understanding of what is determining their time of breeding.
6. The information presented in this study provides a means to derive a model to help determine the laying dates and temperatures for several species. This model could be tested with more current data—say from 1980s to present. When the model(s) are

deemed reliable, then using the models will provide the information about when species could be nesting in the future assuming different warming scenarios.

7. This study indicates that the date of nesting for migrating birds is not strongly associated with temperatures on the breeding ground. More research is needed to determine if, like resident species, there is a particular time and or temperature that associate strongly with date of first laying. If that can be determined, then, like the resident species, a model could be derived that could predict laying date. This model could also be tested with more current data and then used to predict laying date in the future. Having an understanding of the window within which a species is most likely to breed will be valuable to resource managers.

4.3.2. Recommendations for Resource Managers

1. Knowing even a rough window of when resident and migrant bird species are most likely to be breeding will allow managers to be proactive, rather than reactive, when working to manage a species that could be heading toward extinction.
2. Breeding birds feeding hatchlings is energy expensive. Once managers know the rough window within which the birds may start laying, then if food resources are not as abundant as needed supplemental food could be readied ahead of time. Granted, this would be easier for some species than others, but helping at least some will be helpful.
3. By knowing from the monitoring project how species populations are changing, a manager could determine a problem earlier than would be possible without the monitoring data. This could allow proactive rather than reactive interventions.

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