

EFFECTS OF CLIMATE CHANGE ON MIGRATION AND BREEDING
PHENOLOGY IN THE SAN FRANCISCO COMMON YELLOWTHROAT

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ABSTRACT

Scientists believe that one consequence of recent climate change is the reduction of the long-term viability of many natural populations. The nature and scope of climate change effects on living organisms, however, are still poorly understood and, for this reason, scientists are focusing their research in these areas. One area of particular interest is how climate change is influencing species' phenology (seasonal timing of events). One group for which seasonal behaviors are of particular importance is migratory birds. These animals may be especially impacted by climate change, because their survival and breeding success depends on their ability to engage in specific behaviors, often with other species, over specific spatial and temporal gradients. My study involves an examination of this issue in the local population of Common Yellowthroats (COYE) in the San Francisco (SF) Bay Area, CA, which are a California Species of Special Concern (SSC). Using a long-term data set, I explored whether SF COYE have exhibited shifts in the timing of breeding and migration over the last several decades and, if so, whether these shifts are correlated with temporal changes in local temperature and precipitation levels. The results of this study suggest that spring temperature likely influences SF COYE migratory behavior, but that other factors may have a stronger effect on temporal patterns of SF COYE phenology. The value of my study is multifaceted: first, it involves an exploration of factors that may be limiting population sizes of a western North American SSC passerine; second, it involves an analysis of multiple life history traits which are potentially affected by climate in a single avian species; and third, it employs the use of multidecadal data, allowing for an examination of long-term phenomena in nature.

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STATEMENT OF THESIS

For this study, I examined information from a 25-year data set, collected and maintained by staff of the San Francisco Bay Bird Observatory. I used these data to determine if correlations exist between certain variables related to climate change and measures of breeding and migration phenology in the San Francisco Common Yellowthroat, a California Species of Special Concern (CDFW, 2016).

BACKGROUND

In the face of environmental change, there are three main mechanisms that would allow for a natural population to maintain long-term viability: 1) migration to a new, more suitable environment; 2) expression of phenotypic plasticity in one or more morphological characters within at least some individuals; or 3) adaptation through an evolutionary shift in one or more morphological characters. In some cases, however, environmental change occurs so quickly that natural populations are unable to respond fast enough and, as a consequence, suffer declines in the form of range restrictions, reduced size, or even local or global extinction. This can and does happen naturally, as exemplified by the K-T mass extinction, which occurred 66 million years ago at the end of the Cretaceous period. This event culminated with the elimination of non-avian dinosaurs along with 50% of all other organisms. Preponderance of evidence suggests that earth is currently undergoing a sixth mass extinction (Barnosky et al., 2011). Scientists believe that the current wave of species decline is unlike past extinction events, however, in that human actions are to blame (Dirzo and Raven, 2003). These actions are causing environmental changes at an unprecedented rate (Pimm et al., 2014), resulting in the current loss of biodiversity.

Climate change, characterized, in part, by increasing global temperatures, is one example of a human-influenced environmental change that has been linked to detrimental impacts on natural populations (Buse et al., 1999, Hill et al., 1999; Pearce-Higgins et al., 2005; Veteli et al., 2005; Antoniazzi et al., 2011). In the past century, the global temperature of the earth has risen 0.8°C (NRC, 2010), and with the continued burning of

fossil fuels, temperatures on earth are predicted to continue to increase 1.1 - 6.4°C by the end of the 21st century (NRC, 2010; IPCC, 2014). As a consequence, features of weather events such as onset, duration, and intensity will continue to change, in turn affecting variables such as daily local temperatures, timing of seasons, and patterns of precipitation.

These potential changes in climate are a critical issue for living organisms which exhibit behaviors, such as flowering, breeding, hibernating, and migration, that are tightly linked to seasonally changing factors like daylight, temperature, or precipitation. This connection between the biology of a living organism and seasonality is referred to as phenology. Like any other heritable character, phenology is subject to evolutionary change through natural selection, allowing a population to become phenologically adapted over many generations to a particular environment. Examples of this include the temperature-induced emergence from winter sleep of bears in North America (Pigeon et al., 2016) and the onset of migration of wildebeest in Africa stimulated by the increase in salinity and decrease of water levels of watering holes during the dry season (Pennycuick, 1975).

Species that have coevolved and have formed tight ecological relationships with other species are particularly vulnerable to climate change due to the potential for seasonal interspecies interactions to occur out of synchronization. This is especially true when key phenological characteristics of the affected partner species are triggered by different stimuli. This can ultimately lead to the development of temporally or spatially mismatched activities between the coevolved populations. For example, a gradual

increase in day length, a factor independent of climate change, stimulates many insectivorous bird species to migrate to breeding grounds, whereas the timing of insect emergence at the breeding grounds is typically related to climatic factors, such as temperature. The effects of such phenological mismatches may be exacerbated if acting synergistically with other factors influenced by climate change, such as population explosions of pest species (Veteli et al., 2005) and parasites (Antoniazzi et al., 2011) or the degradation or loss of suitable habitat (Hill et al., 1999). It is because of this long-term potential for disruption in ecological interactions and the broader implications this might have for healthy community function that more researchers are beginning to examine the status of species phenology in the context of climate change.

Although some general trends have been observed regarding the effect of climate change on the phenology of certain groups of plants and animals, species differ in the degree to which climate change influences their phenological behaviors. Depending on the species, seasonal activities can be triggered by several stimuli, often in combination, including photoperiod, climate, and endogenous programming (Carey, 2009; Fusani et al., 2009). The degree to which a specific stimulus triggers a phenological response may be affected by latitude, migration distance, or other factors specific to a species' ecology (Carey, 2009). For example, latitude can influence the degree to which photoperiod or climate triggers phenological responses. Since latitudes near the equator do not have a strong change in photoperiod or climate throughout the year, some species in this area have a stronger reliance on triggers other than changes day length or climate or exhibit continuous breeding (Carey, 2009).

Avian Migration and Climate Change

Migratory birds are considered particularly vulnerable to climate change-influenced phenological mismatches, because they rely on environmental cues and interact with natural populations in multiple regions. The environmental cues which different migratory species use to determine when to begin and end certain behaviors or physiological processes may be directly or indirectly related to climatic variables and, thus, potentially affected by climate change. Studies have documented recent effects of climate change on migrating avian populations, including temporal shifts in the onset of migration (Mills, 2005; Kobori et al., 2012; Jahn et al., 2013), changes in length of stays at stopover points (Mills, 2005; Barton, 2012), shifts in arrival time at destination points (Sparks, 1999; Butler, 2003; Kobori et al., 2012), and changes in migratory distances traveled (Visser et al., 2009; Heath et al., 2012). Further complicating matters is the fact that climate change-influenced modifications may not be consistent between or even within a species. For example, in Chicago, the timing of arrival of passerine birds was more strongly correlated with anomalies in monthly mean temperature in males than in females in many species (MacMynowski and Root, 2007).

Long-Distance Versus Short-Distance Migrants

Empirical evidence suggests that the distance generally traveled by migrating bird species can influence the degree with which climate change affects their populations, with long-distance migrants (LDMs) and short-distance migrants (SDMs) showing different responses to climate change. For example, multiple studies have found that

LDMs advance arrival time by more days than SDMs (Butler, 2003; Hulbert and Liang, 2012; but see Mills, 2005). Migration in LDMs is more likely to be triggered by photoperiod than in SDMs, because photoperiod remains constant year to year. However, during the migration journey, factors such as climate may cause species to adjust arrival to breeding grounds. Additionally, LDMs and SDMs are initiated to migrate by different climate localities or scales. LDMs have been found to use climatic cues at their wintering grounds to time arrival to breeding grounds (Cotton, 2003) or large scale climate patterns, such as the North Atlantic Oscillation (NAO) (MacMynowski and Root, 2007). MacMynowski and Root (2007) found that SDMs, in contrast, were more likely to initiate migration based on temperature near breeding grounds. These studies suggest that because the starting and ending points for SDMs are geographically closer, these regions may have more similar climates, making assessment of cues at one point directly applicable to the other.

Migration Phenology and Species Interactions

While migratory birds are spending time at or traveling between breeding and wintering grounds, they come into contact with other species over various spatial and temporal gradients. These species may provide food for, compete for resources with, or form symbiotic relationships with migratory birds. It is often the case that migrating species' survival and reproductive success depend on their ability to match the timing of specific behaviors (e.g., initiation of migration) to that of other species (e.g., prey species). Thus, one potentially devastating effect of climate change, which could lead to

detrimental short-term or long-term population level consequences, is the alteration of life histories and/or behaviors in those species with which migrating bird populations normally interact.

This issue was demonstrated in a study on Sparrowhawks (*Accipiter nisus*), a predatory bird in Finland, and several long-distance migrating passerine species (Lehikoinen et al., 2010). Sparrowhawks demonstrated increased migration duration between 1979 and 2007 (Lehikoinen et al., 2010). This ultimately resulted in an increase in the overlap in migration activity between the passerine species, which typically serve as prey for the Sparrowhawks (Lehikoinen, 2011). Although this shift likely resulted in increased foraging opportunities for the Sparrowhawks, the shift also caused increased predation pressure on the migrating songbirds during what is already a demanding and risky time period for them.

Avian Breeding and Climate Change

Breeding is one of the major motivations for migration in birds. Thus, factors affecting aspects of migration, including timing of arrival to breeding grounds, duration of stay, and length of overall breeding season, have the potential to influence the time frame during which breeding activity occurs in some bird species (Buse et al., 1999; Pearce-Higgins et al., 2005; Riou et al., 2011) and may indirectly affect the circumstances surrounding breeding activity (e.g., Currie et al., 2000; Neilson and Møller, 2006; Janiszewski et al., 2014).

Climate change can cause subtle changes in the specific time frame during which breeding and related activities occur. As with migration phenology, changes in breeding timing can ultimately cause population-level changes, and these changes are typically caused by shifts in life history factors such as reproductive output (Buse et al., 1999; Pearce-Higgins et al., 2005; Riou et al., 2011; Drever et al., 2012).

Misalignment of Migration Phenology and Breeding Success

Climate change can significantly affect migration timing, and consequently can influence arrival timing to breeding grounds. Birds arriving to breeding grounds later than normal are at risk of being outcompeted for high quality breeding habitat (nest sites with more food and/or fewer predators). In several migratory bird species, such as the Northern Wheatear (*Oenanthe oenanthe*) on Bardsey Island in Wales, males arrive to breeding grounds before females and establish territories (Currie et al., 2000). In 1991-1993, 5-26% of Northern Wheatear males did not find a mate for breeding (Currie et al., 2000). The researchers found that Wheatear males which arrived early were more likely to find a breeding partner, have higher quality territories, and exhibit increased breeding success.

The effects of climate change on the duration of the breeding season (which can influence reproductive output) in birds have been examined in a number of studies. For example, European Turtle Doves (*Streptopelia turtur*) are LDMs that breed on the southeast coast of England which have exhibited population declines in recent years (Brown and Aebischer, 2003). In 2000, the doves arrived at their breeding grounds at

approximately the same time of year as they did in 1963 (Brown and Aebischer, 2003). It was discovered, however, that they left their coastal breeding grounds an average of 8.1 days earlier (i.e., mean departure date) in 2000 compared to 1963. Thus, the doves' stay at their breeding grounds was an average of 12.2 days shorter (Brown and Aebischer, 2003) in 2000.

Climatic factors other than temperature may have influenced the length of the Turtle Dove breeding season. This is supported by the fact that neither dove arrival nor departure dates were significantly correlated with temperature (Brown and Aebischer, 2003). Brown and Aebischer (2003) suggested that a mismatch between the timing of their breeding and peak availability of food resources resulted in lower food supplies and might have influenced the birds to stop breeding earlier. Ultimately the decline in the dove population was correlated with, and subsequently attributed to the shortening of the breeding season (Brown and Aebischer, 2003).

It is worth noting that many birds with altered migration phenology in relation to climate do not have significantly changed breeding duration. Some birds can alter migration speed (Ahola, 2004), possibly to "correct" for changes in migration timing, so that they arrive at breeding grounds when conditions are optimal. Likewise, Cotton (2003), found that the breeding season had not largely changed for 20 species of migratory birds even though migration phenology had been influenced by climate. Both the arrival date and departure date advanced at similar rates for the majority of the species, meaning that there was not a change in the total duration of breeding timing. However, Cotton (2003) averaged data from all 20 species and out of the 20 birds the

Lesser Whitethroat (*Sylvia curruca*) and European Turtle Dove had the greatest reduction in breeding season duration when analyzed individually.

Phenology Mismatches between Chick Rearing and Prey Availability

One mechanism by which long-term climate change could negatively impact breeding success would be via incongruity between timing of chick rearing and prey availability. Some researchers have used models to further explore this issue. Using existing data sets and predicted climate scenarios for 2077-2099, Pearce-Higgins et al. (2005) modeled past and future Golden Plover (*Pluvialis apricaria*) hatch dates and timing of emergence of tupulids, which serve as prey for Golden Plovers. Models revealed that Golden Plovers exhibited an earlier average lay date and therefore hatch dates, with warmer temperatures and increased levels of rainfall (Pearce-Higgins et al., 2005). Modeling future scenarios in comparison to 1960-1990 30 year means, Pearce-Higgins et al. (2005) predicted Golden Plovers will advance mean lay date by 18 days between 2070-2099 while the timing of emergence of tupulids was predicted to advance by only 12 days during the same time period. This would result in misalignment of six-days between plover hatch date and tupulid emergence. Using separate data, Pearce-Higgins et al. (2005) predicted that these differences in chick hatching and prey emergence will negatively affect future plover breeding success by 11%.

Climate change induced temperature shifts may also affect the ecology of potential prey (Buse et al., 1999; Riou et al., 2011). In a multi-phase study, Buse et al. (1999) found that Great and Blue Tits (*Parus major* and *Parus caeruleus*) have a lay date

associated with winter moth emergence. Unfortunately, this current evolutionary alignment between predator and prey may not result in corresponding temperature shift-induced phenological change. It was demonstrated that winter moth pupae developed more quickly with warmer temperatures (Buse et al., 1999). This meant that prey development sped up, and Tits may not track this change in prey quality. In fact, further study demonstrated that Tit chicks whose hatching was artificially delayed by seven days exhibited a reduction in mass, body size, and fledging success. These negative physical consequences for chicks, including mortality, suggested to the researchers that this prey species may be at its peak weight and abundance when chicks first hatch with fewer and smaller pupae available to chicks when they are learning to forage on their own.

Effects of Climate Change on Habitat Quality

Shifts in climatic factors over time can diminish the ability of habitats to support breeding avian species with the mechanisms by which this can occur varying. For example, growing conditions may favor invasive species of plants over native ones. Wolkovich et al. (2013) suggested that invasive plant species in North America may be better able to adapt to climate change because exotic species better adjusted flowering time with shifts in climate compared to native plant species. This would be expected to negatively impact breeding opportunities and success in birds, among other species, since, in general, native plants are more likely to support quality nesting habitat and food sources for parents and chicks during the breeding season (Catling, 2005).

The effects of climate change on vegetation may disrupt current patterns of nesting success in other ways. For example, Borgmann et al. (2013) monitored Dusky Flycatcher (*Empidonax oberholseri*) nests in northern California in 2006-2008 and found that the risk of nest predation was lowest in birds that started breeding earlier in dense foliage. Although the authors of this study did not specifically relate their findings to climate factors, bird and plant species are likely to change phenology as the climate changes such that birds may not be nesting when plants are in an optimal condition for concealing nests from predators.

Climate change-influenced effects on nesting success may also include range expansion or more frequent breeding of various pathogens and parasites (Harvell et al., 2002). As a consequence, the potential exists for at least some bird species to be raising their young in environments with increased threat from harmful microorganisms. This can be devastating to breeding success as Watson (2013) found that exposure to parasites negatively affected clutch size, hatching success, and number of young produced in a meta-analysis of 31 avian species. Moreover, other studies have shown that parasite intensity in nestlings can increase with warmer temperatures and more rainfall, and cause higher nestling mortality (e.g., Antoniazzi et al., 2010).

CURRENT PROJECT

Although a number of studies have examined the effect of climate change-related issues on avian biology, there remains much to explore. My project represents an effort to further contribute to this body of knowledge through the examination of the local effects of global climate change on the life history and phenology of a locally migratory bird found within the SF Bay Area.

For my thesis research, I used information from an existing long-term data set compiled by staff at SFBBO to investigate the relationship between climate change variables and migration and breeding phenology in the SF COYE. I chose the SF COYE as my focal species for several reasons. First and most importantly, it is a Species of Special Concern in the SF Bay Area (CDFW, 2016) prioritizing the need for researchers and conservationists to acquire a more thorough understanding of the factors affecting its population status. Secondly, the SF COYE is a locally migratory species, breeding in the natural area surrounding the banding station controlled by SFBBO in the spring and migrating away from the station in the fall (communication with SFBBO staff). As described above, migratory species are especially vulnerable to the effects of climate change for a variety of reasons. Thus, focusing on a species like this increases the intellectual value of this kind of study. Finally, upon reviewing the SFBBO data set, I found that there was an extensive amount of information available for this species, which makes conducting a study of this kind feasible and likely to yield worthwhile results.

COYE are small warblers found throughout North America which are nocturnal migrants. Different subspecies of COYE have varying migration strategies (short-

distance, long-distance and resident) in different regions (Guzy and Ritchison, 1999). In migratory populations, male COYE arrive first to breeding grounds and establish territories. COYE typically breed monogamously, but females will sometimes mate with more than one male (Guzy and Ritchison, 1999). COYE have one or two broods each year, with between one and six eggs laid per brood, and females incubate the eggs for 12 days (Guzy and Ritchison, 1999). The young born are altricial and leave the nest approximately eight days after hatching (Guzy and Ritchison, 1999).

There are 13 subspecies of COYE, three of which are found in California (Guzy and Ritchison, 1999). As a species, COYE are slowly declining, but some populations have recently experienced more dramatic declines (Foster, 1977b; Guzy and Ritchison, 1999). The focal species for my study, the SF COYE, has experienced severe population declines since its geographic range was originally described in 1944 (Guzy and Ritchison, 1999; Gardali and Evans, 2008). Studies suggest that loss and degradation of habitat are the greatest threats to the SF COYE (Foster, 1977b; Guzy and Ritchison, 1999; Gardali and Evans, 2008).

An additional potential threat to the long-term viability of the SF COYE populations is global climate change (Gardali et al., 2012); however, the extent to which this may be an issue is unknown. Data yielded by previous studies on other subspecies of COYE show that COYE phenology has been historically affected by climatic variables (Mills, 2005; MacMynowski and Root, 2007; Hurlbert and Liang, 2012). For example, MacMynowski and Root (2007) show that median spring migration in Chicago COYE was significantly affected by local temperature anomalies and, similarly, first arrival and

first continuous migration (three days in a row) were significantly correlated with the NAO index (it is worth noting that they did not, however, find a correlation between COYE fall migration and climate). Murphy-Klasset et al. (2005) and Hurlbert and Liang (2012) revealed similar trends with COYE spring migration in Manitoba, Canada and eastern North America, respectively.

Mills (2005) also included COYE in a temporal analysis of passerine migration using banding data in Ontario, Canada, but could not correlate migration patterns observed with climate variables. The data used encompassed the spring and autumn migration of SDMs and LDMs. Although there was a population of locally breeding COYE, the migrating COYE were considered to be LDMs passing through the area. COYE significantly advanced first arrival date during the study period (1975-2000), although this method is often criticized for only detecting timing of male migration and for biasing results based on population size. Mills (2005) also used median migration date in place of first arrival date; nevertheless, the trend showed COYE arriving earlier during spring migration and exhibiting significantly advanced autumn migration (3.7 days per decade). In this region, male and female COYE did not significantly differ in timing of autumn or spring migration (Mills, 2005).

Because COYE subspecies have differing ecology and migration patterns (Guzy and Ritchison, 1999), and there is variation in regional climate, the results yielded in the above-mentioned studies do not necessarily predict SF COYE response to the effects of climate change. For example, although studies exist of COYE migration phenology, these studies usually focus on populations of COYE that are LDMs. SF COYE are considered

residents in the San Francisco Bay Area (Grinnell and Miller, 1944) but act as seasonal local migrants which winter in salt marshes and breed around brackish and freshwater areas (Grinnell and Miller, 1944; Foster, 1977a). There are two historical accounts of SF COYE observed further south along the California coast, suggesting that there could be a small subset of the population that behave as longer-distance migrants (Grinell, and Miller, 1944). Given their relatively restricted range and migratory behavior, SF COYE are considered SDMs for the purpose of this study.

Additionally, SF COYE are predicted to be negatively affected by climate change because of resulting habitat changes associated with a changing climate (Gardali et al., 2012; Thorne et al., 2012; Veloz et al., 2013). These other climate related threats in combination with potential phenological mismatches may exacerbate the difficulty of SF COYE coping with climate change.

Given that phenology of other subspecies of COYE have been affected by climatic factors and that the potential consequences of this in combination with predicted changes in SF COYE habitat, it is worth exploring the response of breeding and migration phenology of SF COYE to the increasing effects of climate change. Thus, the questions of if and how climate change might be affecting SF COYE phenology are of value for understanding comprehensive effects of climate change on the SF COYE.

Hypothesis

The current study is designed around three main questions: 1) Have there been temporal trends in temperature or precipitation at the study site during the study period?

2) Is spring migration phenology of the SF COYE changing in relation to temporal or climate variables? 3) Is breeding phenology of the SF COYE changing in relation to temporal or climate variables?

I hypothesized that there have been detectable changes in local climate patterns, aligned with expected global climate change-influenced environmental shifts, and that the changes are affecting breeding and migration phenology of SF COYE in the SF Bay Area. It is common for SDM passerine birds to initiate these behaviors earlier over time, (e.g., Mills, 2005) and earlier arrivals can directly relate to warmer spring temperatures (e.g., MacMynowski and Root, 2007). In the current study, I predicted that the data would show that SF COYE migrate earlier in spring and breed sooner now than in the recent past. I also predicted that climate patterns in spring months would best explain these changes in these birds' migration and breeding timing since spring occurs immediately prior to and during migration to breeding grounds and immediately prior to breeding.

A multifaceted approach was used to address these questions. My first two objectives were to determine if data compiled in the long-term SFBBO data set revealed evidence of a temporal shift of SF COYE migration phenology and/or breeding phenology in the SF Bay Area. Secondly, using data from PRISM Climate Group (Oregon State University), I determined whether there have been changes in climate variables over time that are aligned with expected outcomes of climate change. Finally, I examined elements of SF COYE phenology in the context of the climate data to determine if there is a correlation between any trends observed in each of two data sets. If

this were to bear out, it would provide support for the idea that global climate change is influencing shifts in key climate variables in the region which is, in turn, affecting aspects of SF COYE phenology.

METHODS

As mentioned above, my study involves an analysis of previously collected data that are compiled within a 25-year, multi-species database maintained by personnel affiliated with SFBBO. Although the banding station has been in operation for 30 years and there were some data for all 30 years, I only analyzed available data involving SF COYE collected at this field station during the time period in which data were collected consistently and frequently (1989-2013). The COYE data that were analyzed included variables representing time to breeding and migration phenology. I also used climate data over this period collected by the PRISM Climate Group at Oregon State University.

Locale of Avian Data Collection

The migration and breeding phenology data were originally collected during the period of 1982-2013 at Coyote Creek Field Station (CCFS) located at 37°28'N, 122°03'W in Milpitas, CA. This site is a riparian restoration site and mist nets were set up in different vegetation habitats. Since it is a restoration site, the vegetation in this area has been undergoing human-assisted change over the course of the past 30 years (Jaramillo et al., 2003). Although annual capture rate of SF COYE increased at CCFS during 1987-1996, the changes in habitat were not expected to have largely affected SF COYE migration or breeding timing. Any changes in existing plant communities could have affected breeding success over time as suggested by the findings of Borgmann et al. (2013) described above; however, this issue was not examined in the current study.

Birds were trapped using mist nets, a commonly used research technique (mist nets are thin and difficult to see at a distance and birds are trapped when they fly into the net). Mist nets were 1.83m (6ft) or 3.66m (12ft) long. In 1987 36 mist nets were established and an additional 12 mistnets were instituted in 1995. Starting in 1989, birds were trapped three days per week (less frequently in 1982-1988). The nets were opened 30 minutes before sunrise and checked at least every 30 minutes for the next five hours, weather permitting. After being extracted from the net, each bird was banded with a unique coded ring on their leg so that individuals could be distinguished from one another. Using the Pyle Guide (guide for aging and sexing birds while in the hand), birds were aged and sexed based on time of year and morphology such as plumage and skull pneumatization. Additional morphological data collected include fat content, weight, molt, wing length, brood patch size, and size of cloacal protuberance. Birds were then released low to the ground and no further data were collected from them unless/until they were trapped in the net again on a different day. Recaptured birds were designated as individuals that already had a band on their leg from previously being trapped and processed.

Although it is uncommon for other subspecies of COYE to spend much time in the vicinity of the study site (Grinnell and Miller, 1944; Foster, 1977a), there is potential for some accounts of other COYE subspecies to be present in the data set, such as other COYE subspecies passing through the region during migration. Birds captured were not identified to the level of subspecies. Therefore, all COYE captured during this time period are included in the data set and are presumed SF COYE in this study.

Initial Filters on Avian Data

Before analyzing the relationship between climatic, migration, and breeding variables, I created plots of SF COYE abundance, prevalence of SF COYE breeding characteristics, and net hours (sum of the number of hours each person spent at the banding station while nets were open) at CCFS by month for each year during the study period. I examined SF COYE abundance at CCFS to confirm that SF COYE arrival to this locale occurred during the same time period they have historically been documented migrating in spring (Mills, 2005) and to confirm that the migration period (March –June) used in other related studies (e.g., MacMynowski and Root, 2007; Hurlbert and Liang 2012) applied to the SF COYE. Examining net hours revealed that the nets were not in operation during a portion of the years 1998 (February and December), 1999 (January–May) and 2002 (February and March). February and December do not overlap with spring migration or breeding timing; thus, 1998, which only lacked sufficient net hours during these months, was left in all of my analysis of SF COYE phenology. However, the time periods January–May and February–March overlap with both SF COYE spring migration and the onset of the breeding season. Therefore, the years 1999 and 2002, which lack sufficient net hours during these time periods, are not included in any of my analyses involving SF COYE phenology.

After these initial filters, and prior to statistical analysis, additional filters were placed on the data in this order: 1) the removal of all hatch-year (juvenile) birds and 2) the removal of all occurrences of an individual apart from the first capture (only the first record of each bird was kept). Birds that were known to have died since initially being

captured (mortality records) were kept in the data set. Data in this form were used for all analyses of total SF COYE adults. In my sex-specific analyses (only females or only males), all birds of unknown sex were also not used. For this reason, in some years, the statistical count of total SF COYE adults, which includes adults of unknown gender, may be greater than the sum of the statistical counts of SF COYE females and males when considered individually.

Since male and female COYE often differ in migration phenology (e.g., MacMynowski and Root, 2007), and male and female SF COYE have differing ecology (e.g., Kelly and Wood, 1996), male and female SF COYE may be affected differently by climate. Therefore, I used measures of migration and breeding timing that allow for separate analyses of male and female migrating timing and breeding phenology.

Avian Data: Timing of Migration

The timing of migration was determined by the median time individual SF COYE were first observed at CCFS during spring migration (March 1-June 30), a variable here called the median arrival date (MAD). SF COYE typically start to arrive to CCFS in mid-March (Figure 1). Because some SF COYE individuals were at CCFS outside of the spring migration and breeding periods, only birds observed during the time period of spring arrival were included in my analysis of SF COYE migration phenology. Spring migration data were compiled for SF COYE total adults, females, and males. The MADs of females and males to CCFS were analyzed separately since males arrive to breeding grounds before females (Figure 1).

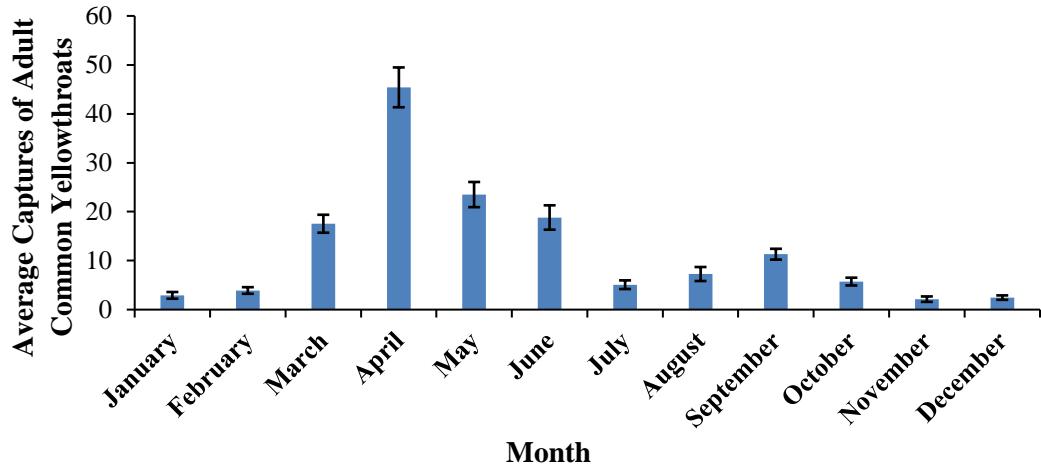


Figure 1. Average monthly captures of adult San Francisco Common Yellowthroats at Coyote Creek Field Station 1989-2013. The years 1998, 1999, and 2002 are not included as they include months in which no data were collected. Error bars are standard error.

Avian Data: Timing of Breeding

The timing of female breeding was determined using two measures, the first appearance of and the median time of year individual SF COYE females showed physical characteristics indicating the birds were in breeding condition at the time of capture. Leading up to the time before laying eggs, female SF COYE lose feathers from their breast and this area becomes highly vascularized to aid in keeping the eggs and chicks warm during development. Since the presence of this anatomical feature, known as the brood patch, reveals whether a female bird is in breeding condition, it was used as an indicator of breeding timing in SF COYE females. The size of the brood patch (scaled 0-5) indicates how far along a female bird is in the nesting process. For example, the presence of a full brood patch is an indication the female bird is likely actively sitting on

a nest. A smaller brood patch indicates the female will soon or has recently stopped raising chicks.

Like with SF COYE females, the timing of male breeding was also determined using the same two measures, but with different physical feature observed that indicate breeding condition. At the onset of the breeding season, a male bird's cloaca swells for easier transfer of semen to the females. This externally visible feature, referred to as the cloacal protuberance, reveals whether a male bird is in breeding condition (scaled 0-3). For this reason, this feature was used as an indicator of breeding timing in male SF COYE. The presence of a large protuberance is an indication the male bird is actively attempting to breed. A small protuberance indicates the male will soon or has recently stopped attempting to breed.

Since brood patches and cloacal protuberances only occur during the breeding season in SF COYE (Figure 2), the data were not filtered to a date range within each year. Because of the low number of accounts of breeding adults during some years of the study period, all birds with a brood patch (recorded as ≥ 1 on the 0-5 scale) or cloacal protuberance (recorded as ≥ 1 on the 0-3 scale), regardless of size, were used in this analysis.

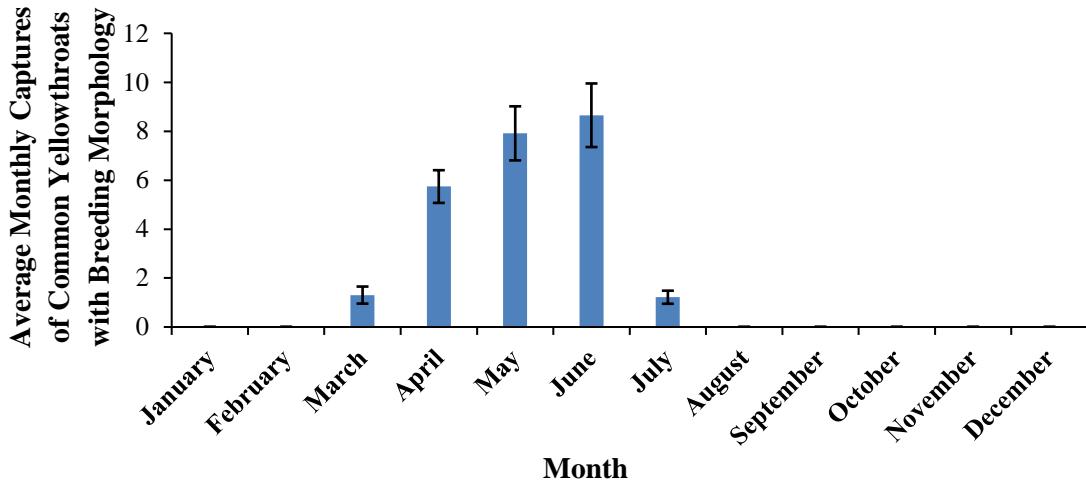


Figure 2. Average monthly captures of San Francisco Common Yellowthroats with breeding morphology (brood patch or cloacal protuberance) at Coyote Creek Field Station 1989-2013. The years 1999 and 2002 are not included as they include months during the breeding season in which no data were collected. Error bars are standard error.

Climate Data

The avian data used in this study were analyzed in the context of existing climate data. The climate data I used were originally collected by PRISM Climate Group personnel. PRISM Climate Group uses a variety of sources and modeling techniques to obtain quality climate data covering the United States. PRISM climate data have been used before in similar studies (e.g., Hurlbert and Liang, 2012) and were used for this study because data are available in 2° latitude – long blocks. This allowed for climate data within a relatively small area (4 km block) encompassing the study site to be used for analysis.

The climate variables I used for my analysis were seasonal mean daily temperature and seasonal mean daily precipitation. These variables were chosen because they have been shown to affect multitrophic interactions including phenology of insects

(Jamieson et al., 2012), the main food source for COYE (Guzy and Ritchison, 1999).

Daily values of mean temperature and mean precipitation were gathered from the PRISM data explorer (<http://prism.oregonstate.edu/explorer/>), and were then averaged across seasons in each year. The spring season was defined using the spring period employed by Hurlbert and Liang 2012, (February-April). Therefore, the remaining seasons used in this study are defined as: summer (June-August), autumn (September-October), and winter (November-January). SF COYE variables were correlated with climate data recorded for the preceding autumn and winter (e.g., 1988 autumn and winter climate variables were correlated with SF COYE 1989 spring migration and breeding timing). SF COYE variables were correlated with the climate data recorded for the spring and summer of the same year (e.g., 1989 spring and summer climate variables were correlated with SF COYE 1989 spring migration and breeding timing).

Statistical Analysis

As I analyzed the climate and SF COYE phenology data, I looked for trends within and between my variables to determine whether: a) seasonal climatic patterns have changed significantly during the period of 1989-2013; b) SF COYE spring migration and/or breeding phenology have changed significantly during the period of 1989-2013; and c) there is a significant correlation between identified patterns in the climate and SF COYE data being considered. Results were considered significant at the threshold of $P < 0.05$ and were considered to trend toward significance at the threshold of $P \leq 0.10$.

I used linear regression to look for temporal trends in local seasonal temperature

and precipitation in the vicinity of CCFS. To test validity of the modeled PRISM climate data at the study site, I correlated PRISM spring temperature with known spring temperature in the immediate area surrounding the Mineta San José International Airport (see Appendix A). This airport was chosen because it best predicted temperature at the study site in an informal analysis that compared local airport temperatures to temperatures at CCFS (SFBBO, unpublished data).

For my analysis of predictors of change in SF COYE phenology, I used linear regression to compare measures of SF COYE migration timing and breeding phenology against year and to look for temporal trends during the study period. Linear regression was also used to look for seasonal predictors of climate change (e.g., temperature and precipitation) on SF COYE breeding and migration timing. There was the potential for correlations between sample sizes and the study time period to confound my results regarding climate-related effects on SF COYE phenology. Therefore, I also used linear regression to compare the number of SF COYE individuals recorded migrating through the area in spring and number of SF COYE individuals recorded breeding at the site against year.

RESULTS

Seasonal average daily temperature and precipitation varied only slightly during autumn 1988 - summer 2013 (Table 1). During this time period, the greatest seasonal spreads (maximum minus minimum account observed) in temperature and precipitation occurred in spring, with a difference of approximately 3.5 °C and 3.8 mm between years. Winter precipitation also had a relatively large spread during the study period (3.1 mm) compared with what was recorded for summer and autumn precipitation (Table 1). Precipitation in autumn and summer was low overall, averaging approximately 0.2 mm in both seasons.

Table 1. Summary of descriptive statistics of climate variables during autumn 1988 - summer 2013. Temperature is in degrees Celsius and precipitation is in millimeters.

Variable	Mean	Range	Standard Error
Autumn Temperature	19.61	18.82-20.68	0.100
Winter Temperature	11.22	10.01-12.87	0.163
Spring Temperature	13.18	11.40-14.86	0.168
Summer Temperature	18.96	17.30-20.44	0.174
Autumn Precipitation	0.232	0.00-0.80	0.482
Winter Precipitation	1.803	0.51-3.61	1.694
Spring Precipitation	1.761	0.13-3.92	1.758
Summer Precipitation	0.202	0.00-0.61	0.410

Although there was inter-annual seasonal variation, there was no strong linear correlation between any of the examined seasonal climate variables and year ($R^2 \leq 0.10$, $P \geq 0.14$; Table 2). Moreover, although not significant, all climate variables except winter temperature and autumn precipitation were negatively correlated with year (Table 2).

Table 2. Seasonal temperature and precipitation linearly regressed with year during 1989-2013. No results shown are statistically significant.

Climate Variable	Coefficient	R ²	p-value
Autumn Temperature	-0.01	0.02	0.46
Winter Temperature	0.02	0.02	0.49
Spring Temperature	-1.99	0.05	0.27
Summer Temperature	-0.00	0.00	0.87
Autumn Precipitation	0.03	0.01	0.67
Winter Precipitation	-0.09	0.01	0.73
Spring Precipitation	-0.16	0.02	0.53
Summer Precipitation	-0.08	0.09	0.14

Temporal Variability in the SF COYE

The average MAD for all SF COYE during the study period was April 23.

Average male MAD was four days earlier than average female MAD (Table 3).

Table 3. Descriptive summary of median arrival date (MAD) of San Francisco Common Yellowthroats to Coyote Creek Field Station during 1989-2013 (1999 and 2002 excluded).

Variable	Mean	Range	Standard Error
Total MAD	April 23	April 5-May22	2.70 days
Female MAD	April 26	April 10-May 28	2.43 days
Male MAD	April 22	April 3-May 22	2.96 days

The number of individual SF COYE at CCFS in spring did not significantly changed during 1989-2013 ($R^2 = 0.03$, $P = 0.41$, Figure 3), although yearly sample sizes did range widely during the study period (see Table 4, Range values). Females represented some of the smallest sample sizes across the sampling period, averaging 21 birds per year during spring.

All measures of SF COYE migration timing were significantly explained by year, with MAD for all adult SF COYE as well as males and females separately increasing

over the years of the study period ($R^2 \geq 0.47$, $P = 0.00$, Table 5, Figure 4). Year explained a similar proportion of the variation (47-51%) in total, female, and male SF COYE MAD.

Table 4. Descriptive summary of number of San Francisco Common Yellowthroats (SF COYE) at Coyote Creek Field Station during spring migration during 1989-2013 (1999 and 2002 excluded).

Variable	Mean	Range	Standard Error
Total SF COYE	63	30-95	3.88
Female SF COYE	21	7-39	1.75
Male SF COYE	41	18-62	2.61

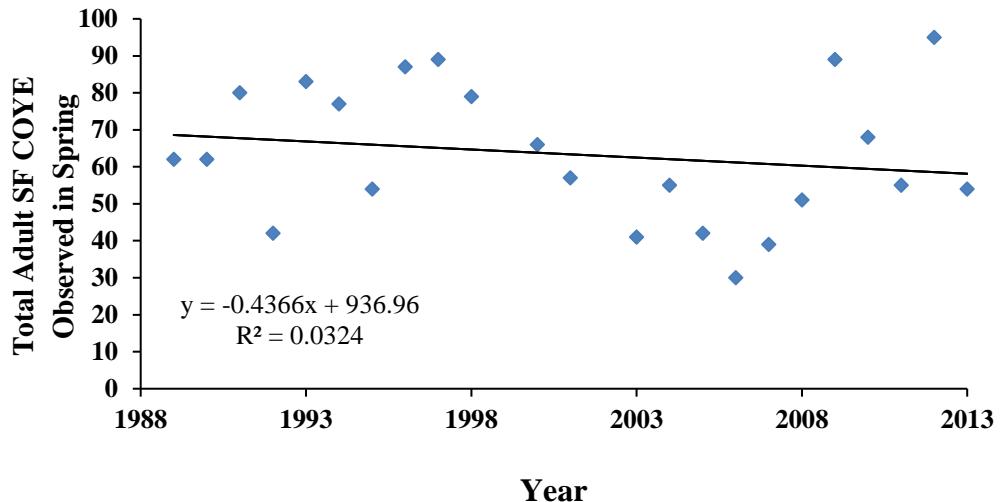


Figure 3. Total number of adult San Francisco Common Yellowthroats observed at Coyote Creek Field Station during spring linearly regressed with year.

Table 5. Median arrival date (MAD) of total, female, and male San Francisco Common Yellowthroats (SF COYE) linearly regressed with year during 1989-2013 (1999 and 2002 excluded). Significant relationships are bolded and indicated with an asterisk (*).

Variable	Slope Coefficient	R ²	p-value
*Total SF COYE MAD	1.19	0.50	0.00
*Female SF COYE MAD	1.04	0.47	0.00
*Male SF COYE MAD	1.32	0.51	0.00

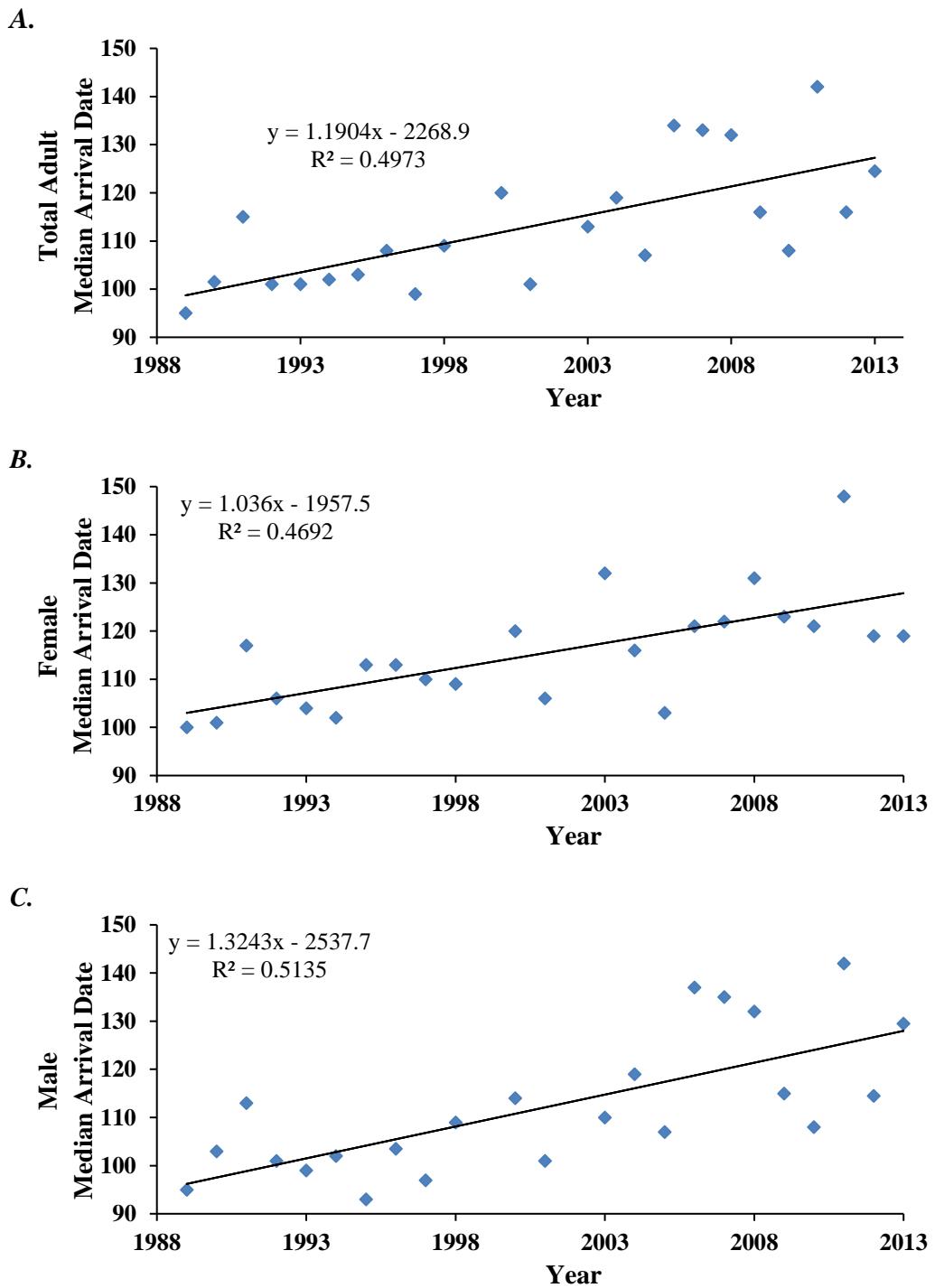


Figure 4. San Francisco Common Yellowthroat median arrival date (ordinal day) linearly regressed with year (A. Total Adults, B. Females, C. Males).

Table 6. Total San Francisco Common Yellowthroat median arrival date (1989-2013) linearly regressed with seasonal climate variables (1999 and 2002 excluded). Relationships showing a trend toward significance are bolded.

Variable	Slope Coefficient	R ²	p-value
Autumn Temperature	-7.66	0.09	0.15
Winter Temperature	2.48	0.02	0.48
Spring Temperature	-5.76	0.12	0.10
Summer Temperature	-2.66	0.03	0.44
Autumn Precipitation	-1.43	0.08	0.21
Winter Precipitation	-0.22	0.02	0.49
Spring Precipitation	0.01	0.00	0.98
Summer Precipitation	-1.30	0.04	0.33

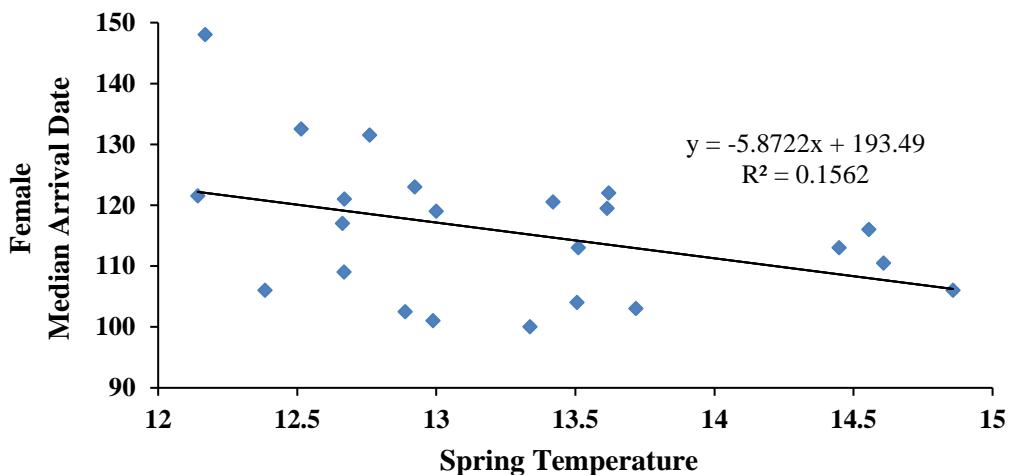


Figure 5. Female San Francisco Common Yellowthroat median arrival date (ordinal day) during 1989-2013 (1999 and 2002 excluded) linearly regressed with spring temperature (degrees Celsius).

Out of the climate variables included in the analysis, female and male MAD were best explained by spring temperature, with which they negatively correlated. The correlation between spring temperature and female MAD approached significance ($R^2 = 0.16$, $P = 0.06$; Table 7, Figure 5), with female SF COYE appearing to arrive 5.87 days earlier with each degree Celsius increase. The relationship between spring temperature and male MAD trended toward earlier arrival with warmer spring temperatures, but was

not statistically significant ($R^2 = 0.13$, $P = 0.10$, Table 8), with male SF COYE appearing to arrive 6.43 days earlier with each degree Celsius increase.

Table 7. Female San Francisco Common Yellowthroat median arrival date linearly regressed with seasonal climate variables. Relationships showing a trend toward significance are bolded.

Variable	Slope Coefficient	R^2	p-value
Autumn Temperature	-3.40	0.02	0.49
Winter Temperature	3.82	0.07	0.22
Spring Temperature	-5.87	0.16	0.06
Summer Temperature	-3.03	0.05	0.33
Autumn Precipitation	-1.25	0.07	0.22
Winter Precipitation	-0.02	0.00	0.93
Spring Precipitation	-0.07	0.00	0.81
Summer Precipitation	-0.93	0.03	0.44

Table 8. Male San Francisco Common Yellowthroat median arrival date linearly regressed with seasonal climate variables. Relationships showing a trend toward significance are bolded.

Variable	Slope Coefficient	R^2	p-value
Autumn Temperature	-9.40	0.12	0.11
Winter Temperature	2.27	0.02	0.55
Spring Temperature	-6.43	0.13	0.10
Summer Temperature	-2.46	0.02	0.52
Autumn Precipitation	-1.13	0.04	0.37
Winter Precipitation	-0.33	0.04	0.34
Spring Precipitation	-0.06	0.00	0.86
Summer Precipitation	-1.78	0.07	0.22

Analysis of Inter-Annual Breeding Phenology

The total number of SF COYE with breeding morphology (either a brood patch or a cloacal protuberance) significantly increased during the study period ($R^2 = 0.64$, $P = 0.00$, Figure 6). Sample sizes for brood patch, however, were very low overall (Table 9), with instances of especially low sample sizes (1-3 individual females with a brood patch) occurring in 1992, 1993, 1994, 1997, 1998, and 2007.

Table 9. Descriptive statistics for number of San Francisco Common Yellowthroat individuals at Coyote Creek Field Station each year that had either a brood patch or a cloacal protuberance greater than zero during 1989-2013 (1999 and 2002 excluded).

Variable	Mean	Range	Standard Error
Brood Patch	7.5	1-20	1.15
Cloacal Protuberance	17.3	5-41	1.93

The timing of SF COYE with breeding characteristics varied widely during the study period. Most notably, the difference between the earliest and latest annual median cloacal protuberance during 1989-2013 was 76 days (Table 10). The earliest annual first brood patch and cloacal protuberance recorded both occurred in March, and the earliest annual median brood patch and median cloacal protuberance occurred in April.

Table 10. Descriptive statistics for timing of brood patches and cloacal protuberances of San Francisco Common Yellowthroats during 1989-2013 (1999 and 2002 excluded).

Variable	Mean Date	Range	Standard Error
Median Brood Patch	May 26	April 21-June 17	3.26 days
First Brood Patch	April 25	March 27-May 23	3.23 days
Median Cloacal Protuberance	May 15	April 3-June 18	4.20 days
First Cloacal Protuberance	March 30	March 10-April 22	2.02 days

Median brood patch and median cloacal protuberance exhibited a significant positive correlation with year (Table 11). Year explained 19% of the variation in median cloacal protuberance ($P = 0.04$). These significant relationships show SF COYE advancing date of median breeding morphology by more than one day each year (Correlation coefficients = 1.15-1.35, Table 11).

Table 11. Median and first appearance date of brood patch (BP) and cloacal protuberance (CP) linearly regressed with year during 1989-2013 (1999 and 2002 excluded). Significant relationships are bolded and indicated with an asterisk (*).

Variable	Slope Coefficient	R ²	p-value
*Median BP	1.35	0.44	0.00
First BP	0.07	0.00	0.87
*Median CP	1.15	0.19	0.04
First CP	-0.05	0.00	0.85

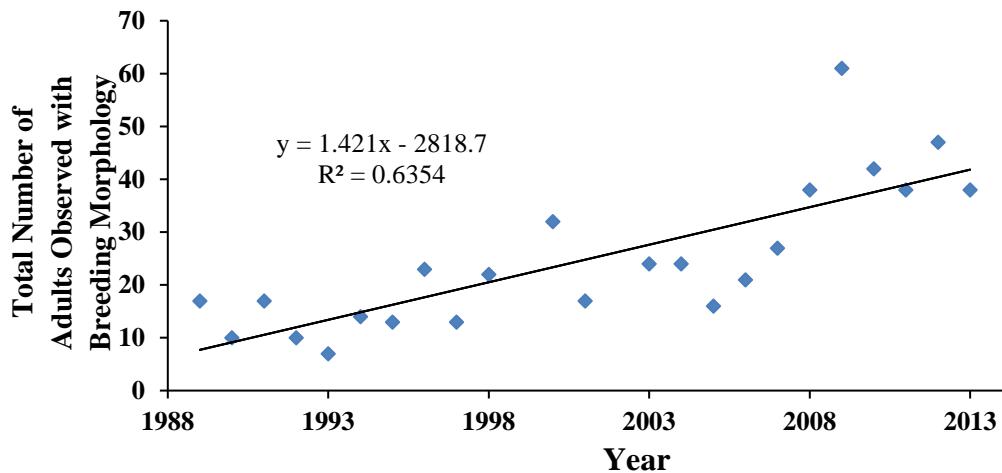


Figure 6. Total number of San Francisco Common Yellowthroats observed with breeding morphology (either a brood patch or a cloacal protuberance) linearly regressed with year.

Analysis of the Relationship between Climate and Breeding Phenology

There were no significant correlations between any of the climate variables and measures of breeding timing (Tables 12, 13, 14 and 15); however, first cloacal protuberance trended toward a significant negative correlation against winter precipitation ($R^2 = 0.14$, $P = 0.08$, Table 15, Figure 7).

Table 12. Median date of all observed brood patches (1989-2013) linearly regressed with seasonal climate variables (1999 and 2002 excluded).

Variable	Slope Coefficient	R ²	p-value
Autumn Temperature	-0.75	0.00	0.91
Winter Temperature	5.59	0.12	0.11
Spring Temperature	-1.21	0.00	0.78
Summer Temperature	1.91	0.01	0.65
Autumn Precipitation	-0.31	0.00	0.82
Winter Precipitation	-0.09	0.00	0.81
Spring Precipitation	0.17	0.01	0.65
Summer Precipitation	-1.33	0.01	0.41

Table 13. Date of first brood patch (1989-2013) linearly regressed with seasonal climate variables (1999 and 2002 excluded).

Variable	Slope Coefficient	R ²	p-value
Autumn Temperature	5.33	0.03	0.42
Winter Temperature	-4.41	0.05	0.29
Spring Temperature	3.98	0.04	0.36
Summer Temperature	-1.63	0.01	0.69
Autumn Precipitation	-1.16	0.03	0.40
Winter Precipitation	-0.07	0.00	0.85
Spring Precipitation	0.40	0.05	0.29
Summer Precipitation	-1.61	0.05	0.32

Table 14. Median date of all observed cloacal protuberances (1989-2013) linearly regressed with seasonal climate variables (1999 and 2002 excluded).

Variable	Slope Coefficient	R ²	p-value
Autumn Temperature	-4.38	0.01	0.61
Winter Temperature	-0.09	0.00	0.99
Spring Temperature	0.57	0.00	0.92
Summer Temperature	-0.12	0.00	0.98
Autumn Precipitation	0.13	0.00	0.94
Winter Precipitation	0.11	0.00	0.83
Spring Precipitation	0.66	0.09	0.17
Summer Precipitation	-0.60	0.00	0.77

Table 15. Date of first cloacal protuberance (1989-2013) linearly regressed with seasonal climate variables (1999 and 2002 excluded).

Variable	Slope Coefficient	R ²	p-value
Autumn Temperature	-0.58	0.00	0.89
Winter Temperature	-3.60	0.09	0.16
Spring Temperature	-1.01	0.01	0.71
Summer Temperature	0.61	0.00	0.81
Autumn Precipitation	-0.34	0.01	0.70
Winter Precipitation	-0.41	0.14	0.08
Spring Precipitation	0.17	0.02	0.49
Summer Precipitation	-0.58	0.02	0.57

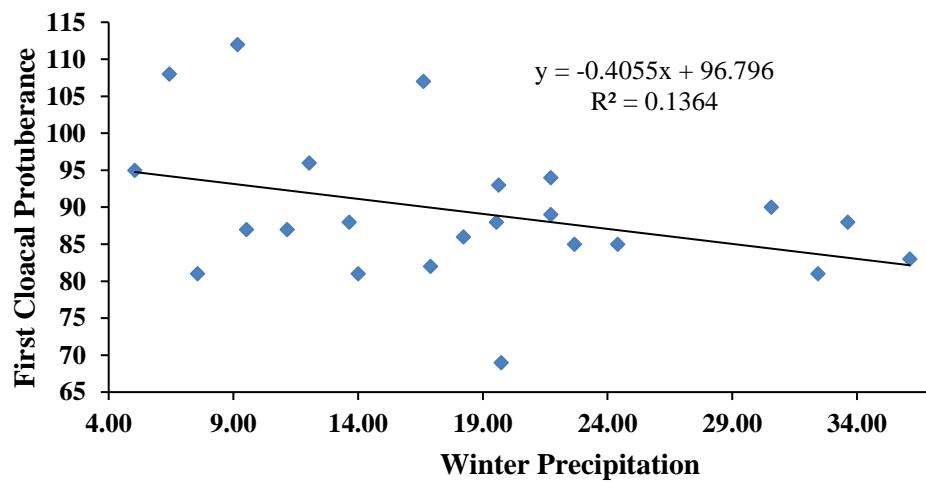


Figure 7. First appearance date of cloacal protuberance (ordinal day) linearly regressed with winter precipitation (hundredths of cm).

DISCUSSION

Temperature and Precipitation Effects on SF COYE Phenology

Unlike the long-term regional trend demonstrating an increase in temperature in the Bay Area during 1950-2000 (Ekstrom and Moser, 2012; IPCC, 2014), temperature at CCFS did not exhibit a positive correlation with year. This may be explained by the close proximity of CCFS to the San Francisco Bay. Water has a high heat capacity and requires a significant amount of energy to heat up and cool down. As a consequence, coastal areas like the SF Bay have milder climates. This effect may continue as time progresses since future climate scenarios projected to 2070-2099 for the Bay Area predict that coastal areas will have milder seasons compared to inland areas (Ekstrom and Moser, 2012). Similar to historical Bay Area precipitation, precipitation at CCFS did not show a clear pattern (Ekstrom and Moser, 2012). Because some variability existed in local temperature and precipitation, it was still possible to assess the effect of local climate on SF COYE phenology.

The results of my study suggest that there was no significant effect of seasonal temperature on SF COYE time of arrival to the CCFS breeding site, although there was a trend toward significance in the linear relationship between spring temperature and female and male arrival dates. This trend, however insignificant, indicates that between 1989 and 2013, female and male SF COYE were arriving over five days earlier with each increase in degree Celsius with females typically arriving to the breeding grounds four days after males.

These findings support my original hypothesis that SF COYE phenology would be most strongly influenced by spring climate since this is the season during which SF COYE are initiating migration to breeding grounds, and may therefore most accurately represent habitat conditions at breeding grounds. The observed trends are also consistent with existing studies involving analyses of COYE migration timing to breeding grounds. MacMynowski and Root (2007) found that median arrival date of COYE to breeding grounds near Chicago was significantly influenced by recent local temperature anomalies. Hulbert and Liang (2012) also found an influence of climate on migratory COYE: spring temperature significantly negatively correlated with average arrival date of COYE to breeding grounds at several sites in eastern North America. Additionally, slower migrants were more likely to be influenced by climate factors, and COYE were among the two slowest migrants out of 18 species included in the investigation (Hulbert and Liang, 2012).

In my study, I found that seasonal precipitation did not appear to affect SF COYE migration or breeding timing. Instead, there was only a trend toward significance in the relationship between the first cloacal protuberance recorded and winter precipitation, with the first cloacal protuberance appearing to occur 0.41 days earlier per millimeter increase in winter precipitation.

While not a finding in my study, it has been demonstrated that precipitation can affect migration and breeding timing. Beaumont et al. (2015) showed this to be the case in some endangered Australian bird species. Despite this and other examples, there is a relative dearth of published studies involving the effect of precipitation on songbird

phenology compared to those highlighting the effect of temperature on the same. This may be due to a bias for publishing “positive results” or findings that reveal the presence of effects rather than the lack of them. If this is the case, then there are likely many more unpublished studies with findings consistent with those of my study, in which no significant effect of precipitation on SF COYE breeding or migration timing was found.

Although unexpected, given the lack of published studies on the topic, it is possible that the first annual appearance of cloacal protuberance in male SF COYES was actually influenced by winter precipitation, but was not found to have a significant effect here because of other influencing factors. For example, seasonal precipitation did not vary widely during the study period and was low overall, such that it is possible that the variations in precipitation were too subtle for SF COYE to have exhibited detectable phenological responses. Additionally, the first occurrence of a phenological trait can be affected by population-level changes, such as changes in population size or distribution, one of which or both appears to have occurred in SF COYE at CCFS during the study period (indicated by the number of COYE breeding significantly increasing during the study period).

The potential for precipitation to affect SF COYE phenology is noteworthy, because precipitation has been documented as influencing measures of songbird breeding success in studies focusing on a single species in North America (e.g., Skagen and Yackel Adams, 2012) and breeding duration (e.g., Jankowiak et al., 2014). In these studies, increased seasonal precipitation led to either greater breeding success or a longer breeding season. For example, Skagen and Yackel Adams (2012) found that Lark

Bunting (*Calamospiza melanocory*) clutch size, nest survival, and productivity significantly increased with spring precipitation. In my study, breeding success and breeding season length were not analyzed, and consideration of the relationship of these traits remains an opportunity for future research on potential effects of precipitation on SF COYE life history traits. Additionally, given the trend toward significance between winter precipitation and first occurrence of cloacal protuberance found in my study, further analysis of precipitation effects on SF COYE breeding phenology may also be worth future consideration.

Finally, it is worth noting that, in my study, sample sizes of individual SF COYE at CCFS present annually during spring migration or in breeding condition varied between years. The small yet variable nature of the male and female sample sizes, particularly in earlier years of the study period, may mean the data set is not robust enough to capture a significant relationship where one could otherwise exist.

Temporal Effect on SF COYE Phenology

Additional key findings in this study are that there have been significant shifts in SF COYE phenology and demographics at CCFS between 1989 and 2013. Specifically, there has been an increase in the number of SF COYE breeding at CCFS and shifts toward later male and female arrival dates and breeding onset over time. Jaramillo et al. (2003), using this same data set over a shorter period of time, also found that the number of SF COYE with a substantial (>2) brood patch and cloacal protuberance increased during 1987-1997. Results from a concurrent breeding bird

census (1988-1997) indicated that the number of SF COYE estimated to be at the site during the breeding season was not significantly increasing. The results of this study notwithstanding, the banding data set (which uses brood patch and cloacal protuberance as a measures of breeding bird abundance) is likely a more reliable method of determining the number of breeding birds each year since the census depends on observers counting singing males or inconspicuous females, in which individual SF COYE may be double counted or missed during data collection.

Although the results of my study indicate that there has been an increase in the number of SF COYE breeding at CCFS, the number of adult SF COYE individuals at CCFS during spring migration has not significantly changed. This may initially appear to be in contrast with the results of Jaramillo et al. (2003), which found that annual capture rate of SF COYE, and number of SF COYE estimated during point counts, both point toward an increase in SF COYE presence at CCFS over time. The CCFS capture rate reported by Jaramillo et al. (2003) may include recaptured adults and juveniles which were not included in my analysis. It is also conceivable that the total number of SF COYE present during the spring has not significantly changed, as my results suggest, but rather the number of SF COYE that can be found at CCFS on an annual basis has changed. This would be possible under multiple scenarios, such as the number of SF COYE wintering at CCFS has increased, breeding output has increased over time with an increasing number of juveniles present at CCFS at the end of the year, or other populations of SF COYE that historically were not present at CCFS in large numbers during spring migration have increased their use of CCFS as a migration stopover site.

Since local seasonal climate and the number of SF COYE at CCFS during spring has not significantly changed over time, the cause for the observed shift in SF COYE migration and breeding timing remains unclear. One probable factor is the temporal shift in habitat quality that has been occurring at CCFS. CCFS is a restoration site that was reestablished during the period between 1987-1993. It steadily matured and increased in habitat complexity and plant diversity during 1986-1996 (Jaramillo et al., 2003), and has likely continued to increase in habitat quality since that time period. This, in turn, may have facilitated an increase in insect abundance and/or quality that would have greatly benefitted SF COYE which, along with several other small songbirds, are “foliage gleaners,” that gather insects from vegetation surfaces. In support of this idea, CCFS annual capture rates of birds that fall into this category of avian foragers increased as a whole between 1987-1997 (Jaramillo et al., 2003). Moreover, Jaramillo et al. (2003) cite improvement in habitat quality as the reason for increases in annual abundance of birds and breeding diversity at this locale during this period.

Further support for this idea is that in the later years of my study, more SF COYE have been electing to breed at CCFS, which likely reflects a shift in their breeding range. It appears that historically, most SF COYE passing through CCFS in spring would continue on, searching for higher quality breeding grounds beyond CCFS. As the restoration site has matured, however, an increasing number of SF COYE may have chosen to stay at CCFS and breed there. Preliminary examination of SF COYE capture rates throughout the year support this notion, with an increased number of adult SF COYE captures appearing to occur later in summer over time (Appendix A, Figure 2).

In addition to CCFS increasing in habitat quality, changes in nearby habitats may have influenced SF COYE distribution in the region during this time period. While the SF Bay Area has become more urbanized overall (Cox, 2014), targeted environmental efforts have occurred, including efforts in recent years to restore salt marsh habitats (Williams and Faber, 2001). These nearby habitat alterations may also have an impact on the timing of SF COYE seasonal presence at CCFS.

Habitat changes could have caused the shift towards later arrival and breeding timing of SF COYE at CCFS in various ways. First, restoration around San Francisco Bay could have increased the value of wintering grounds to SF COYE, such that the birds remained around the bay for a longer period of time before migrating to CCFS to breed. Second, the birds may have shifted to staying at wintering grounds which are further away, increasing the time it takes for them to get to CCFS in spring. Third, changes in habitat function at CCFS could have shifted such that the best time to arrive at breeding grounds and raise chicks is later in the year. Fourth, SF COYE may have extended the duration of their breeding season, shifting the median breeding timing to a later date. Given the right conditions, COYE are known to raise two broods of chicks in a single breeding season (Guzy and Ritchison, 1999). Since habitat quality has likely improved at CCFS, it is possible that more SF COYE have chosen to raise a second clutch over time. The increase in the number of second clutches would increase the length of the breeding season. Further analysis of SF COYE wintering grounds, breeding conditions and breeding duration may help clarify the degree to which each of these possible scenarios has had an effect on SF COYE arrival time and breeding timing at CCFS.

CONCLUSION

Significance of Climate Change Effects on SF COYE Phenology

Although there were no significant temporal climate trends found in my study, spring temperature and winter precipitation were the climate variables found most likely to affect SF COYE phenology. Despite not meeting the threshold of significance, SF COYE arrival date to CCFS is likely in part influenced by spring temperature given the consistency of this finding with previous studies, small sample size constraints, and near significant results despite confounding changes in distribution of SF COYE at CCFS. As for the effect of precipitation, without further available evidence, the insignificant effect of this climate factor on SF COYE phenology appears to accurately represent the lack of a relationship between precipitation and SF COYE behavior.

While I did not identify a temporal relationship with the climate variables analyzed, climate in the San Francisco Bay Area region is predicted to change in the future. Under intermediate climate change predictions (extending to the 2080 to 2099 period), all of North America is expected to increase in average annual temperature (Cayan, 2008; Ekstrom and Moser, 2012). California is expected to increase in annual temperature by 1.5°C - 4.5°C between 2000 and 2100 depending on the climate change scenario (Cayan, 2008) with the Bay Area projected to increase by an additional 2°C - 6°C by the year 2050 (Ekstrom and Moser, 2012). Northern California is not projected to largely change in precipitation, but parts of southern California are projected to decrease in precipitation by 5-18% (Ekstrom and Moser, 2012). In these areas of southern

California, spring precipitation is expected to decrease the most with winter precipitation remaining stable (Ekstrom and Moser, 2012). Since precipitation in northern California is not projected to largely change in the near future, potential changes in precipitation in the Bay Area may also be small.

There are likely to be ecological consequences resulting from either the effects or the non-effects of climate change on SF COYE phenology. SF COYE may be in part shielded from climate change effects because of the wintering and breeding grounds' close vicinity to the San Francisco Bay, which is expected to continue to have milder climates in the near future (Ekstrom and Moser, 2012). Negative effects are likely to arise if SF COYE are not able to time migration and breeding with optimal nesting habitat conditions (e.g., spring plant growth) and food sources (insect abundance). Both temperature and precipitation play key roles in spring plant growth and spring and summer insect abundance. Because temperature is more variable in this region and is more likely to considerably change under current climate change scenarios, it is especially important for SF COYE to be able to time phenology with temperature. Given the possibility that SF COYE can adjust arrival to breeding grounds using spring temperature, they may be able to mitigate some of the potential negative effects of climate change on their population.

The effect of precipitation on SF COYE phenology, however small in this region, may impact SF COYE breeding success. Although it is not expected, the potential influence of precipitation on the onset of breeding could not be confirmed in this study.

Thus, whether precipitation could cause a mismatch in SF COYE breeding timing with other factors (such as lower predation risk or food abundance) remains unknown.

Other factors causing temporal shift in SF COYE Phenology

The temporal shifts in SF COYE arrival and breeding timing in combination with the increased number of SF COYE breeding at CCFS each year were the most significant results found in this study and were unrelated to climate variables. This shift in population breeding range coincides with and, thus, may ultimately be explained by changes in quality of local habitat, especially by an increase in breeding habitat value to SF COYE at CCFS. This concept is supported by the previously documented increases in vegetation structure and complexity, presence of other foliage-gleaning birds, and annual capture rates of SF COYE at CCFS (Jaramillo et al., 2003).

Suggestions for Further Study

This research along with few other studies (mostly conducted as Master's theses or as a part of larger multi-species studies conducted by Point Reyes Bird Observatory) have contributed significantly to an understanding of the ecology of the SF COYE. The current study would have benefited from larger sample sizes and having a reference site that was not undergoing restoration during the study period. Had both of these elements been available in this study, it is possible that a significant trend between SF COYE arrival to breeding grounds and spring temperature would have been revealed and/or

whether winter precipitation affected the presence of the first cloacal protuberance would have been more definitively demonstrated.

While analyzing my data, several other questions arose that would be worthy of further examination to assess the potential influence of climate change on SF COYE. Additional studies in areas where specific breeding or wintering grounds have not undergone habitat change may give further insight to the ability of SF COYE to adapt to climate change. SF COYE breeding duration and breeding success are variables not analyzed in this study, but are additional life history traits that can be influenced by climate and are worth further study. An investigation in the effect of climate change on insects in the Bay Area would allow for an assessment of the potential for the occurrence of mismatches between SF COYE breeding and insect abundance. Finally, large scale climate phenomena, such as the NAO, may have affected SF COYE phenology. Other climate variables not used in this study may be investigated in relation to SF COYE phenology to determine if a relationship exists.

Broader Significance

The short and long term consequences of global climate change is of growing concern for biologists and conservationists worldwide. My thesis research aligns with current efforts to more deeply examine the potential effects this phenomenon may have on natural populations. Specifically, I sought to determine whether a link exists between abiotic factors commonly associated with climate change and the migration and breeding phenology of the SF COYE exists. This is especially important because the SF COYE

has experienced a dramatic decrease in range (Foster 1977a), and the potential impacts of climate change on key activities relating to population viability have not been previously examined in this species. Overall, relatively few of the climate change studies focused on western North American birds focus on this topic. The existing studies of climate change and birds in this region often either do not focus on phenology (e.g., Veloz et al., 2013) or involve larger bird species (e.g., Drever et al., 2012; Heath et al., 2012). This thesis contributes towards filling this gap in information, since the effects of climate change are not expected to be geographically uniform and effect species differently.

Beyond the focus on a western species already facing a declining range, I examined if and how long term changes in climate are linked to multiple life history and phenological traits in a single species which is important for understanding comprehensive effects of climate change on a species. Although there have been numerous studies focusing on either avian migration or breeding phenology, relatively few have examined both traits together (although see Lehikoinen et al., 2010, Burger et al., 2012). Ultimately, studies like mine contribute toward a broader understanding of how climate change broadly affects a single species which, in turn, reduces the possibility that, conservation efforts will be misdirected. For example, some current habitat restoration projects may not sufficiently mitigate the negative consequences of climate change on a population if they allow for climate-caused mismatches between food availability and chick rearing, or if all interacting species lack the mobility to reach climate-shifted habitat locations.

One additional element of value associated with my study is that it employed the use of a long-term data set. Long-term data sets are valuable to ecological research in that they offer researchers an opportunity to examine questions over broad spatial and temporal frameworks. Moreover, long-term data sets are critical for studying slower, episodic or rarer ecological phenomena such as the effects of climate change on migration and phenology. In addition, longer term data sets allow for retrospective analysis that some authors believe is the best way to learn about ecological phenomena in nature (e.g., Franklin, 1988). Shorter studies with extrapolative modeling (e.g., Pearce-Higgins et al., 2005) and controlled experiments (e.g., Buse et al., 1999) are also used to make inferences about past and future phenology patterns, but there are limitations to the conclusions that can be drawn from this kind of analysis. Thus, my study highlights the value of using a long-term data set to answer questions about ecological processes and phenomena.

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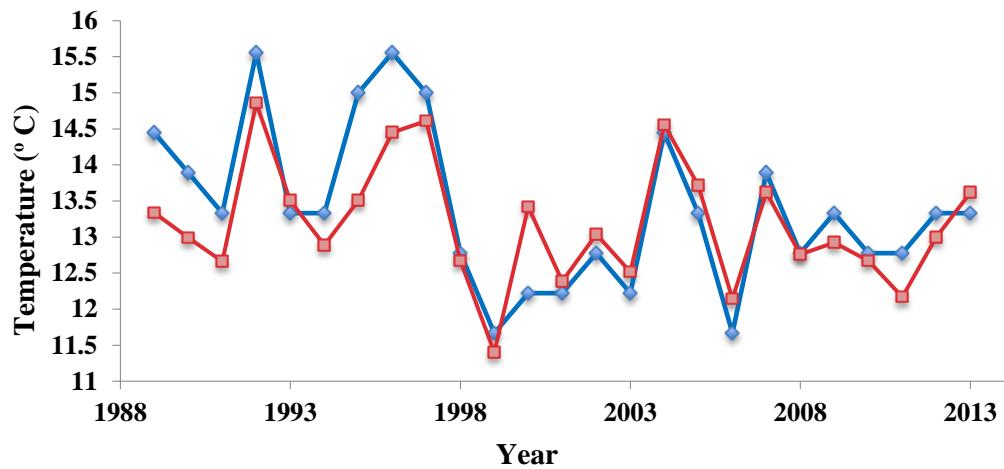
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APPENDIX A: SUPPLEMENTAL ANALYSIS

Temporal Climate Data

Displaying yearly spring temperatures at the San Jose Airport and the modeled temperatures at CCFS (PRISM) on the same graph shows similar trends between the two data sources (see Appendix A, Figure 1). Historical weather data at San Jose airport were not available for every day of the period under consideration. Consequently, mean temperatures at San Jose airport during spring (February 1 - April 30) were correlated with daily mean temperatures reported from PRISM during the same time period.



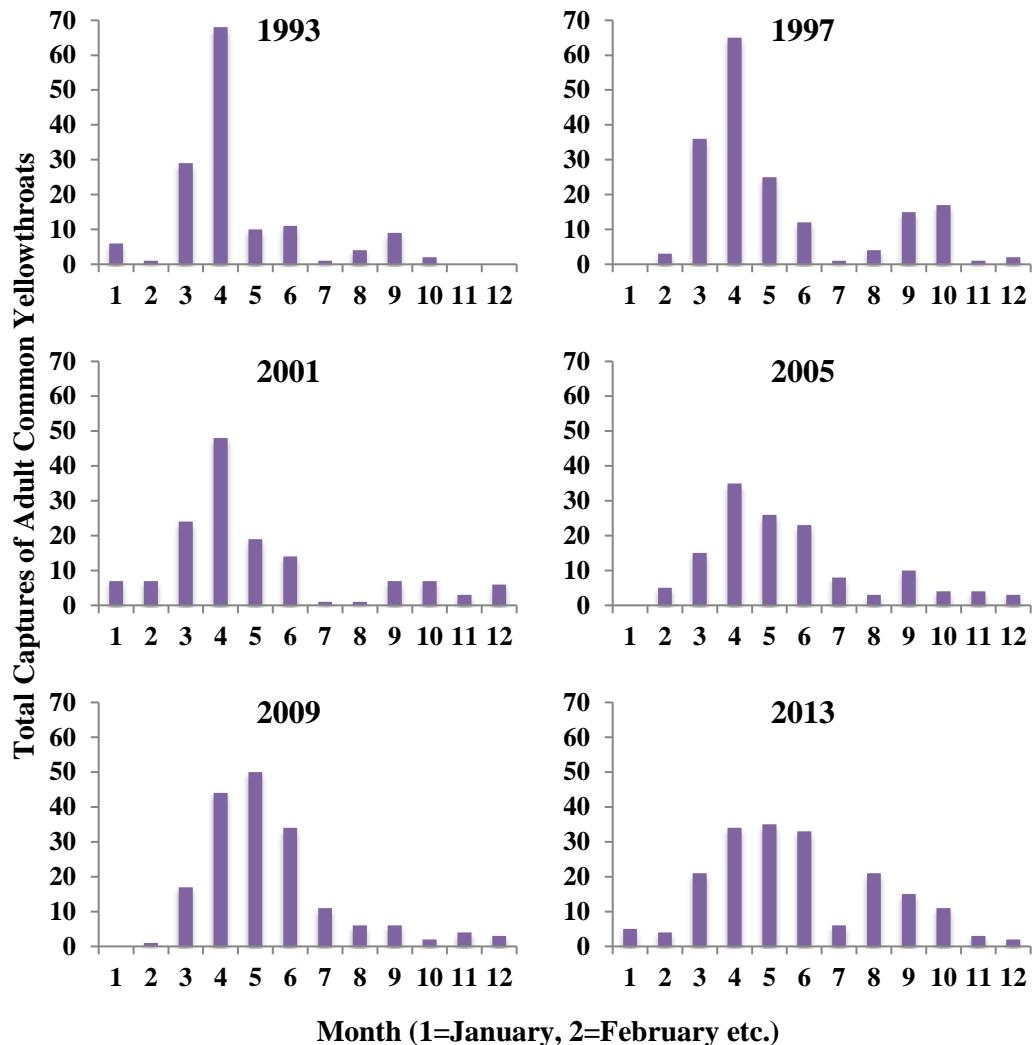
Appendix A Figure 1. Mean spring temperature in degrees Celsius at San Jose airport (blue data; wunderground.com) and modeled average mean daily spring temperature at Coyote Creek Field Station (red data; PRISM) in 1989-2013.

Moreover, an analysis using linear regression indicates that the temperature values are strongly correlated ($R^2 = 0.72$, $P < 0.001$, Appendix A Figure 1). Given the different locations of the stations and incidences of days with missing values at San Jose

Airport, the similar trend in spring temperature indicates that PRISM weather data are a valid proxy for the weather at CCFS.

Other Temporal San Francisco Common Yellowthroat Data

Additional data exploration revealed that there may be other temporal trends on San Francisco Common Yellowthroat (SF COYE) presence at CCFS that was not in the scope of this study. For example, there is visible variation in the amount of time SF COYE spend at CCFS each year (Appendix A Figure 2). It is currently unclear what the exact nature of this variation is, but graphical representation of capture rates at the station may offer a clue as to possible patterns that should be analyzed in a future study. When interpreting Appendix A Figure 2, it is important to note that these figures represent capture rate and not necessarily abundance of COYE in any given month since the same bird could be captured multiple times. At least three possibilities could explain the observed pattern in Appendix A Figure 2: 1) SF COYE have increased the amount of time spent at CCFS by exhibiting a later departure date, 2) SF COYE are arriving and leaving later, indicating a shift in the timing of the breeding season, or 3) SF COYE have not shifted in the time frame of their breeding but have spread out their activity over a longer period of time such that capture rates follow a bell curve rather than a large peak. A combination of the above hypotheses could be true, and may indicate a shift or lengthening of the breeding season.



Appendix A Figure 2. Monthly occurrences of total adult Common Yellowthroats at Coyote Creek Field Station every five years during the study period starting with 1993. The data are not filtered for unique individuals so that presence of individuals is displayed throughout the year.