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Changes in Spring Arrival Times: Climate change and the phenology of spring bird migration

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Changes in spring arrival times: climate change and the phenology of spring bird migration.

A LITERATURE REVIEW AND DATA MODELING THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

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ABSTRACT

Climate change and weather affect the phenology of bird migration; however, specific climatological factors associated with these observed effects have only recently been described. The relationship between local, regional, and global climate patterns and avian migration are increasingly important to understand due to the widespread, and potentially negative, implications (such as reduced fecundity) of rapid human induced climate change on bird populations. Migratory birds are under selective pressure to arrive at breeding areas at the optimal time to set up nesting territories and exploit seasonally abundant food resources, and because climate change has the potential to occur more rapidly than species can adapt their migratory behavior, negative impacts to populations may occur as a result of climate change. Human-induced climate change is a driving factor in changing migration phenology, but the effects may be confounded by endogenous controls and changing conditions along migratory routes. However, despite strong endogenous controls, long-distance migratory birds can alter the timing and rate of migration in response to a changing climate. In this thesis I explore the relationship between spring migration phenology and climate.

The literature review addresses the relationships between a changing climate and corresponding changes in avian migration phenology. I summarize the current state of understanding of how anthropogenic climate change is impacting spring migration. The literature documents a clear change in spring migrant arrival dates over time. To more thoroughly explore these relationships I present the results of a quantitative data modeling exercise that models the variation in migration phenology of birds in Maine. I used publicly available and crowd sourced data to assess how climate change may be related to the advance in spring arrival dates of migratory birds in Maine. A model selection approach was used to develop a predictive model of spring migrant arrival dates. I demonstrate that, as documented in the literature, many passerine species in Maine are arriving increasingly earlier in the spring, as documented in the literature for other regions. Migration strategy, foraging behavior, and pressure from exogenous and endogenous controls affect migration phenology, but I demonstrate that anthropogenic climate change has caused an advancement of median spring arrival times in Maine.

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INTRODUCTION

Phenology is the study of the timing of biological events over the course of a year (Bradley et al. 1999). Phenology may include study of the cycle of leaf production in deciduous trees, the timing of salmon migration, the variation in when lilacs bloom each spring, and bird migration, as well as any other similar annual process or behaviors that occur in other taxa. The effects of climate change on global avian migration phenology are well established in the literature, birds are arriving earlier to spring breeding grounds than they did just a decade ago (Usui et al. 2017). The different spatial and temporal scales at which avian migration phenology changes contribute to our understanding of the underlying mechanisms by which climate change affects migration. Few researchers have evaluated phenological changes in migratory populations breeding the U.S.A. state of Maine.

Each year in spring, and again in fall, millions of birds migrate long-distances from the tropics and sub-tropics to temperate, sub-arctic, and arctic regions. Migratory birds are exhibit reoccurring behavior annually, and as such, they are suitable indicators of the effects of rapid human induced climate change (Studds and Marra 2011). Birds compete for mates, territories, and resources at breeding grounds in the spring, and thus the timing of arrival can ultimately impact reproductive success (Richardson 1978, Knudsen et al. 2011). Weather patterns and climate contribute to the timing (i.e., phenology) of annual migrations, as well as conditions once birds arrive at breeding grounds (Knudsen et al. 2011). In this review I explore how spring migration phenology is changing at multiple spatio-temporal scales. These scales include local short duration (small-scale) conditions such as temperature, as well as regional and longer duration (intermediate-scale) phenomena such as atmospheric pressure differentials. Finally, I discuss how global climate change (large-scale) and corresponding changes in phenology on certain bird species in Maine, U.S.A.

At the local level and over short periods of time (i.e., weeks or months) small-scale and short duration weather systems (e.g., how much rain falls in a given month) may influence spring migration phenology (Studds and Marra 2011). At an intermediate-scales and time periods (one or two years) migrant arrival patterns may be driven by regional climate trends, such as fluctuations in regional temperature patterns and changes in hemispheric pressure differentials (Hüppop and Hüppop 2003). Ultimately, global large-scale temperature and climate trends, such as human induced warming over the course of decades, have been shown to affect migration patterns (Bradley et al. 1999) (Figure 1).

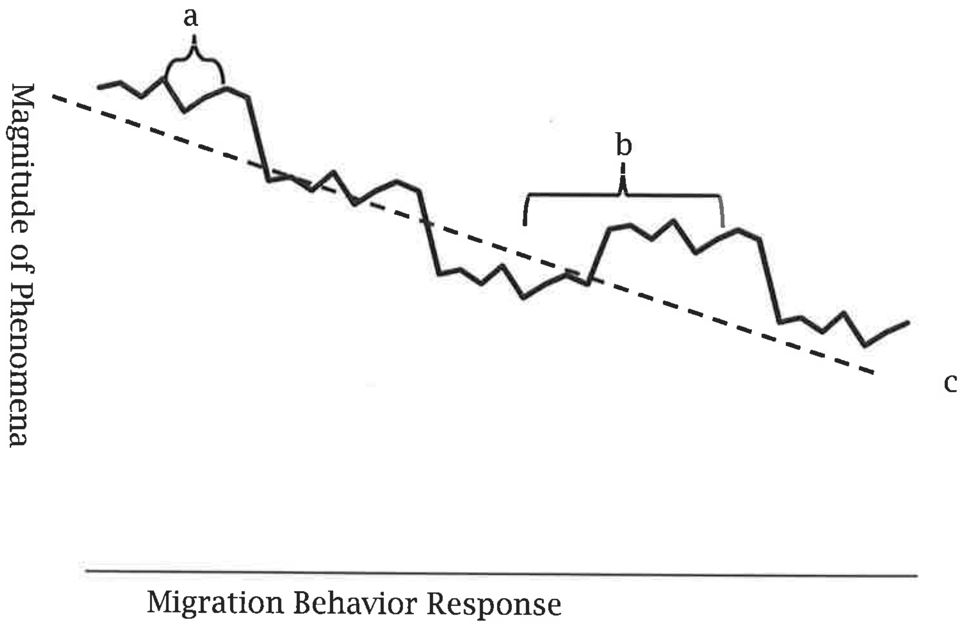

Figure 1. Conceptual model of factors driving migration on three scales, small (a), intermediate (b), and large (c, dashed line). Some factors fluctuate over a short duration (a) for example annually, whereas other factors fluctuate over multiple years (b). Long duration factors are evident only over a larger period of time (c).

Migration and arrival timing are largely a function of environmental conditions but are also driven by endogenous controls and experience (i.e., the maturity of the migrant). Therefore, comprehensive analyses of phenological responses to multiscale spatio-temporal trends often consider phylogeny, biotic (i.e., food resource availability), and abiotic (i.e., climate and weather conditions) factors. Even with these and other confounding factors, climate has been identified as the most significant factor contributing to annual and inter-annual variation in spring migration (Knudsen et al. 2011).

To determine at what spatial and temporal scales climate change is affecting avian migration phenology I explore how climatic and weather factors drive spring migration behavior at small, intermediate, and large scales, as documented in the literature (Table 1). In Chapter 2, I present the results of the quantitative data exploration and modeling of spring migrant arrival phenology in Maine, U.S.A. In Chapter 3, I discuss implications of the themes presented in the Chapter 1 literature review and my own data exploration from Chapter 2.

CHAPTER 1. LITERATURE REVIEW

I searched JStor and Google Scholar for the terms "avian migration phenology" and "climate change" and reviewed literature from 1950 - 2017. I chose to focus on studies that evaluated migration phenology at different spatio-temporal scales to determine at which scales climate change is affecting migration timing.

Table 1. Summary of literature review findings by author and spatio-temporal scale.

Citation	Spatio-Temporal Scale	Summary of Findings
Studds and Marra 2011	Small Scale	Changes in precipitation influenced abundance of insect food resources which changed migration departure dates of American redstart.
William et al. 1977	Small Scale	Wind direction and speed affected the flight speed and duration of migrant flight in the Caribbean
Ernie et al. 2002	Small Scale	Migration rate (birds/km/hour) was correlated with variation in other local small-scale weather conditions including temperature, atmospheric pressure, cloud cover, and wind speed and direction
Kemp et al. 2010	Small Scale	Used radar to demonstrate a significant increase in the rate of migration in the Netherlands during the passage of weather fronts in spring and fall

Wilson 2007	Intermediate	Demonstrated a clear relationship between NAO and the behavior of some passerine migrant species in Maine due to the fluctuation of NAO.
Marra et al. 2005	Intermediate	Showed that NAO explained a significant amount of variation in migration behavior for multiple species.
Cotton 2003	Intermediate	Proposed that changes to migration phenology are a result of variation in seasonal duration at wintering grounds and not NAO or ENSO at breeding grounds.
Hüppop and Hüppop 2003	Intermediate	The relationship between earlier arrival dates and higher NAO values was statistically significant in 21 species.
MacMynowski and Root 2007	Intermediate	Seventy-three percent of the long-distance migrant species' spring migrations were correlated with NAO.
Bradley et al. 1999	Large	Demonstrated a significant change in arrival date across a 61 year study period, 6 avian species (37.5%) arrived earlier, and overall 19 (35%) of the phenophases evaluated showed statistically significant increases in "earliness".
Ward et al. 2016	Large	Birds arrived at breeding grounds an average of 0.12 days earlier per year across the 50 year study period. Overall, all 16 species had significantly earlier first arrival dates.
Miller-Rushing et al. 2008	Large	Of 32 species studied, 8 species had mean arrival dates significantly earlier across the 33 year study, which was directly attributed to effects of climate change
Usui et al. 2017	Large	Showed that birds advanced spring migration by 2.1 days per decade using 73 studies of migration phenology from 1749 – 2014 across 5 continents and 413 species.

1.1 Migration

For the purposes of this review, I restricted my literature to that covering the northern hemisphere. Similar phenomena occur in the Southern Hemisphere, but the majority of accessible literature is from North America and Europe (Usui et al. 2017).

I define migration as the seasonal movement of birds from wintering areas to breeding grounds each year (Alerstam and Christie 1993). Individuals arrive in the Northern latitudes of the east and west hemisphere each spring in time to mate, raise young, and consume seasonally abundant food resources before migrating back to wintering grounds in more southerly latitudes in fall. For example, approximately 80% of avian species that breed in northern North America spend winter in sub-tropical and tropical latitudes of North America, the Caribbean, Central America and South America (Richardson 1978). This bias in the literature may be a result of fewer studies conducted in the Southern Hemisphere or a language bias with fewer studies published in English from this region.

Spring migration (i.e., northbound movements) occurs from early April to late May, but the precise timing varies by latitude and species (Morris et al. 1994, Berthold 2001, Morris et al. 2003, Mills et al. 2011). Fall migration is less compressed, beginning in mid-August and continuing through October or later, and thus autumnal migration phenology can be more difficult to accurately quantify than spring phenology (Morris et al. 1994). Although autumnal migration may consist of a larger number of birds than spring migration (presumably due to recruitment from young of the year), spring migration is characterized by a greater number of migrants arriving during compressed time periods (Stevenson 1957). The relatively short duration of spring migration may arise from birds striving to arrive at breeding grounds before intraspecific and interspecific competitors do (Bruderer 1997, Karlsson et al. 2012). Observations of the phenology of spring migration are more likely to be representative of the breeding population as a whole, than are samples of fall migration, which for many species is more diffuse. Therefore, spring migration phenology trends should serve as a better model for the effect of climate change on migratory behavior.

1.2 Weather and Climate Indices

Weather (i.e., which is the condition of the atmosphere at a given time, and climate, (i.e., which is trends in atmospheric conditions over longer periods of time) are particularly strong drivers of migration, and high quality data on weather conditions at different spatio-temporal scales are needed to measure the relationship between weather and migration phenology (Gordo 2007). Fortunately, high quality empirical weather data are readily available from long-term weather stations and automated sensing equipment. Weather stations can monitor real time temperature, wind speed, wind direction, and barometric pressure at frequent intervals, generating a robust historical record of weather and climate conditions. These observations are then used individually to describe local small-scale trends, in combination with regional data sets to characterize intermediate regional weather phenomena, or included in large meta-analyses to describe global climate conditions.

The effects of weather on migration, especially from data recorded over long periods of time, may be summarized in multiple ways. For example, studies that are conducted for only a single migration season may use temperature data recorded within the study area daily or hourly. For longer duration studies, researchers often use regional datasets that are expected to be representative of the study area and that can be summarized by month or year. For example, Hüppop and Hüppop (2003) used mean temperature recorded during the spring migration period, and Ward et al. (2016) used daily minimum and maximum air temperatures to calculate a mean daily temperature and then averaged these values across a 50 year study period. These different temperature data summaries are used to assess migration phenology responses to temperature variation.

1.3 Migration Data Collection

Different metrics generated by the different methods of observing avian migration provide variables that are useful for building models of migration phenology when incorporating local, regional, and global scale weather predictor variables. Unlike weather conditions, observations of migratory birds are more challenging to record. Birds are highly mobile, small relative to human observers, and can be difficult to track (Tasker et al. 1984). Therefore, researchers have developed different techniques to document migratory behavior of birds.

Generally, three categories of migratory bird observations provide data on spring migration phenology. Observations of birds departing wintering grounds provide a temporal starting point for a migration event. Observations of birds starting migration, often called "departure observations", may be confounded by different individuals departing at different times, but they are useful in providing a timespan of when a population's migration begins. Then there are observations made during migration, *en route* to breeding areas. These *en route* observations may include observations of birds in flight or arriving and departing to and from stopover areas. Finally, there are observations of birds arriving at their final breeding area for the season. These "arrival observations" may be more accurate than departure or *en route* observations, because birds, males in particular, exhibit obvious changes in behavior upon arrival when they begin to establish a breeding territory, and are easier to observe (Alerstam and Christie 1993).

Different techniques have been developed to generate avian migration data, including traditional visual observations as well as technologically aided techniques. Traditionally, observers used binoculars or other optics to enhance detection probabilities (e.g., Tasker et al. 1984). These observations generate basic information about species identities, arrival times, and other behaviors (e.g., foraging activity). These traditional direct observations are the most common method for sampling migration behavior, but other methods of sampling migration generate different types of data. Recently, citizen science initiatives such as eBird have given all observers the ability to record and share their observations, making them useful and readily available for scientific studies (Wood et al. 2011).

Direct methods of sampling avian migration, such as capturing and banding birds, provide additional metrics about migrants, including sex and physical condition (Gustafson et al. 1997). Recently, technological advances including radar, acoustics, thermal imaging, and GPS technology have been employed to sample behavior of migratory birds (Haselmayer and Quinn 2000, Nohara et al. 2007, Bridge et al. 2011). Each method provides a different type of information on migrants and migratory behavior. For example, radar systems allow scientists to study the number of migrants using a given air space and the relative height and flight speed of birds, but it provides no information about which species are being tracked (Nohara et al. 2007). Acoustic monitoring can provide data on the species composition of migrants, but it is limited by the distance at which a microphone can record individuals and may be biased by infrequent vocalizations during flight (Haselmayer and Quinn 2000). Thermal imaging, along with radar and acoustics, can be useful for observing nocturnal migration patterns, but it has a limited detection range and provides only relative information about size and body type insufficient for species recognition. Nano-tags and GPS tracking technology are precise methods for tracking and recording observations of migratory birds, but they are often limited by the number of individuals that can be realistically outfitted with tags and trackers, thus limiting sample size (Schwarz et al. 1993, Diemer et al. 2014, Brown and Taylor 2015).

In order to model avian migration patterns, we need data describing observed patterns. Common metrics of migratory bird behavior include date of arrival at known migratory stopover locations and breeding grounds, observations of birds during migration along migratory thoroughfares, and date of departure from wintering grounds (Hüppop and Hüppop 2003, Studds and Marra 2011). These dates can be generated by direct observation of birds or by any other methods previously described. Arrival dates (i.e., the first date birds arrive at summer breeding areas) and other observations are often described using summary statistics such as first arrival date, mean arrival date, and median arrival date. First arrival dates are often used for studies of migration phenology, but they are heavily biased by population demographics, especially across years (Usui et al. 2017). For example, in a year with a particularly large number of new recruits to a given population there may be an adherently higher number of earlier or later arrivals, which would skew a mean arrival date earlier. Conversely, few observations of individuals early, or late, might similarly bias a mean arrival date. Other metrics are less biased by demographics, such as mean arrival date. By using the average date of arrival of each individual in a given population to a specific area during the breeding period in spring, small population sizes or observation period are less likely to influence observations. Similarly, median arrival date or first arrival dates can be used to describe migration phenology. For example, the median arrival date for all American redstarts in Maine from 1994 - 2005 was estimated to be May 15 (± 6 days) (Wilson 2007).

To understand how climate change is impacting migration, researchers have used migration metrics in statistical models to develop models of migration; however, there are differences in the relative amount of bias in the different types of independent variable metrics used. For example, in Usui et al.'s (2017) meta-analysis of 73 migration phenology studies, the researchers noted that studies using first arrival dates were more subject to bias than those using mean or median arrival dates (the researchers did not differentiate between studies with mean and median arrival dates). Bias in first arrival date variable was attributed to data collection methods that may have resulted in an incomplete sampling of a portion of the migration period or in fluctuations in the size of the sample population. These errors resulted in a prediction fewer migrants arriving in a given year, which may have affected detection probabilities (Usui et al. 2017).

The following sections describes the different scales of weather and climate change mechanisms. I have categorized these independent factors and the corresponding variation in migration phenology into; small, intermediate, and large temporal and spatial scales.

1.4 Small-Scale Trends and Responses

1.4.1 Small-Scale Weather Trends

Wind, temperature, precipitation, and food resources may drive migration patterns over short periods of time (i.e., hours and days) and across relatively small geographical areas (i.e., a few hectares to a few hundred hectares) (Erni et al. 2001, Studds and Marr 2011). These small-scale trends in localized weather conditions influence migration phenology, probable impacts include departures from wintering areas and shifts in duration of migration period (Gordo 2007).

Wind, temperature, and precipitation are generally functions of the interactions of different air masses in the atmosphere, the relationship between high and low atmospheric pressures, and the variable amount of moisture that different air masses can hold. The changing dynamics of cool and warm air manifest as differences in atmospheric pressure, and the movement of air within and across different pressure gradients causes increased wind speeds and may result in precipitation or storms (Figure 2). High-pressure systems are generally dry and unlikely to result in precipitation, whereas low pressure systems often produce rain. A low-pressure system is an area of low atmospheric pressure typically accompanied by strong winds, temperatures fluctuations, and precipitation (Bagg et al. 1950). Passage of these low pressure systems is often followed by the arrival of a high pressure system, with few clouds, little to no precipitation, and light winds aloft, but passage of the front is destabilizing and may lead to short duration storm conditions (Figure 2). These short duration, relatively localized atmospheric phenomenon directly affect migratory behavior and indirectly influence migrants due to secondary the impacts on changes in food resource availability.

1.4.2 Small-Scale Weather Trends and Corresponding Changes in Phenology

Researchers have evaluated how small-scale weather trends such as localized precipitation, wind, and temperature patterns may affect migratory bird behavior. A multiyear study of American redstarts (*Setophaga ruticilla*), an insectivorous neotropical wood-warbler, was conducted to evaluate local weather conditions on migration from wintering areas in two forest types in Jamaica (Studds and Marra 2011). The author documented short term weather impact on migration departure dates and on availability of food resources in wintering areas. For every 50 mm annual reduction in March rainfall, there was an equivalent 3-day advance in departure of male birds in second-growth scrub across the six year study period (Studds and Marra 2011). The magnitude of the effect of rainfall on migration departure differed depending on the American redstart's wintering habitat (mangrove or scrub) and whether the individuals were male or female.

Studds and Marra (2011) used a linear mixed model, including rainfall and sex, to demonstrate a change in spring departure dates of 74 American redstarts from Jamaican wintering areas including birds from black mangrove forest and second-growth scrub. Of interest is the consistently earlier departure dates of males, presumably these earlier departures gain the migrant some sort of competitive advantage on breeding territories (Studds and Marra 2011 Figure 2).

To further investigate the relationship among rainfall and departure dates, Studds and Marra (2011) sampled arthropod biomass in late spring. Arthropod biomass varied in relation to the quantity of rainfall in March, with biomass greatest when rainfall was highest. The researchers included arthropod biomass as a variable in a linear mixed model of departure dates and precipitation and they concluded that, on average, American redstarts of mangrove forests delayed departure by 1-day for every 9.2 mg reduction in arthropod biomass (Studds and Marra 2011). This effect was even more pronounced in the scrub habitat population, resulting in a 1-day departure delay for a 3.5 mg reduction in arthropod biomass. These findings are a clear example of how small-scale weather trends occurring over a short time period drive migration phenology, but they do not demonstrate causation.

In addition to precipitation, researchers also investigated how localized wind speeds and directions potentially affect migration phenology. Observations of wind speed and direction in light of bird migration patterns include early work by William et al. (1977) and more recent studies by Kemp et al. (2010). Williams et al. (1977) collected data that have served as a benchmark for future studies of localized weather conditions and migration. They used marine radar to observe a relationship between migrant departure time and localized effects of low pressure fronts and associated wind directions and speeds. Wind direction and speed affected the flight speed and duration of migrant flight in the Caribbean. Migrants were more likely to depart ahead of, or after, passage of a low-pressure front than when a front was stationary over an area (Willams et al. 1977). The authors concluded that passage of low-pressure systems potentially trigger migration departure by providing favorable wind speeds and vectors that would facilitate migratory flight. Rate and altitude of migration across the Caribbean and western Atlantic Ocean was associated with variability in these localized weather systems. Although the researchers presented no clear statistical evidence for weather impacts on migration rate and altitude, their use of radar technology was a ground-breaking approach to migration research at the time. Although their study lacked rigorous statistical analysis, their methods set the stage for other the use of radar by other ornithologists.

Erni et al. (2002) identified a clear relationship between migratory behavior and localized weather conditions in Germany, using a modern avian radar system to observe migration rates under different wind and rain conditions (Erni et al. 2002). Conical scanning pencil beam tracking radar produced a concentrated radar beam capable of high resolution returns that sampled nocturnal avian migration in Germany. They found that a significant negative correlation between migration intensity and rain duration; greater rain duration was correlated with reduced migration intensity. Migration rate (birds/km/hour) was correlated with variation in other local small-scale weather conditions including temperature, atmospheric pressure, cloud cover, and wind speed and direction (Erni et al. 2002).

In 2010 Kemp et al., used radar to demonstrate a significant increase in the rate of migration in the Netherlands during the passage of weather fronts in spring and fall. Migration occurred 16.9 % faster than fall migration through the same area due to localized effects of wind speed and direction (Kemp et al. 2010). Migration speed is the speed of individual migrants, and migration rate is the magnitude of individuals moving through a given area.

1.5 Intermediate-Scale Trends and Responses

Small-scale weather conditions vary over a short time period (e.g., days or months) and act on discrete geographic areas such as an island or ecoregion. Intermediate-scale weather trends occur over a year or multiple years and across a larger spatial area. Studies demonstrate that small-scale, short duration localized weather conditions are correlated with migration phenology on a seasonal basis in different migratory populations in the northern hemisphere (Williams et al. 1977, Erni et al. 2002, Kemp et al. 2010, Studds and Marra 2011). Similar patterns have been observed with intermediate-scale climate trends and migration phenology.

1.5.1 Intermediate-Scale Climate Trends

Intermediate-scale trends in weather are often associated with annual and multiyear fluctuations such as the El Niño/Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO). ENSO and NAO are complex climate phenomenon that can be summarized in a numerical index (Hurrell 1995, Timmermann et al. 1999, Both 2010). ENSO is also referred to as the Oceanic Nino Index (ONI) or Southern Oscillation Index (SOI) in the literature. The phenomenon and the index will be referred to as ENSO in this review.

ENSO is an index used to classify sea surface temperature regimes and atmospheric pressure differentials in the Pacific Ocean (Graf et al. 2014). The ENSO index has two components. The first component is the Southern Oscillation, which is the difference in atmospheric pressure readings on the island of Tahiti and in the city of Darwin, Australia, and the second component is the sea surface temperatures in the equatorial Pacific region.

Because weather in eastern North America is predominately driven by the Jet Stream, which brings weather systems across North America from west to east, variation in ENSO can be a strong determinant of weather across the continent (Hurrell 1995). ENSO fluctuations are correlated to variations in precipitation in the Midwest, southeastern U.S., and Caribbean, as well as the northeast U.S. During years with high ENSO index values (El Niño), rainfall generally increases across the southeastern U.S.; in years with lower ENSO index values (La Niña), precipitation is generally less abundant in the southeast U.S. (Herring 1999, Welker 2012).

Differences in atmospheric pressure in the North Atlantic Ocean (i.e., NAO) noticeably affect seasonal temperature and precipitation regimes in western Europe (Hurrell 1995). These pressure differentials also affect weather in eastern North America. A higher NAO index, which corresponds to lower low pressure over Iceland and higher high pressure over the Azores, usually correlates with an increase in the prevalence of southwesterly winds over the eastern U.S. and Canada due to changes in the location and intensity of the North American jet stream. Increased intensity of the Jet Stream as a result of the higher North Atlantic pressure gradient allows cold arctic continental air, primarily situated over Canada, to be carried off the continent, thus preventing cold dry air from building up and draining south, allowing warmer, wetter conditions to dominate. Increased Jet Stream intensity from NAO often manifests as warmer and wetter than average winters in the New England region of the U.S. and elsewhere in eastern North America (Hartley and Keables 1998). The opposite effect is also noticeable when the NAO index is low (i.e., the difference in atmospheric pressure between Iceland and the Azores is less pronounced), resulting in more severe and longer winters in the northeastern U.S. because the lower intensity pressure gradient over the North Atlantic is less efficient at drawing cold continental air off northern North America, and thus cold dry air vortices can form and stagnate over eastern North America (Hartley and Keables 1998).

NAO is a complex atmospheric weather phenomenon summarized by a simple index. NAO is a measure of intensity of atmospheric pressure differentials above the southern and northern North Atlantic Ocean. Specifically, NAO is a value that tracks the difference in magnitude of high pressure at Ponta Delgata, Azores, Portugal and low pressure near Stykkisholmur, Iceland (Hurrell 1995). NAO values fluctuate based on the difference in atmospheric pressure across a given length of time and range from -1 to 1 (Hurrell 1995). Both the NAO phenomenon and index will be described as NAO herein.

1.5.2 Intermediate-Scale Trends and Corresponding Changes in Phenology

Changing patterns in the fluctuation and magnitude of both ENSO and NAO have been linked strongly to rapid human induced climate change and are thought to play a role in driving migration timing (Hurrell 1995, Timmermann et al. 1999, Karl and Trenberth 2003, Donat et al. 2014, Sydeman et al. 2014). Intermediate-scale climate trends such as ENSO and NAO explain some variation in migratory activity over 3 - 8 year periods, although the extent of variation in spring arrival timing that can be explained by these phenomena is not consistent in the literature (Cotton 2003, Hüppop and Hüppop 2003, Marra et al. 2005, Wilson 2007, MacMynowski and Root 2007).

Wilson (2007) used observational data of spring migrants collected by volunteers to analyze the relationship between NAO and median spring arrival dates of passerine migrants with quantile regression. They included the fluctuation of NAO index values in their model of spring migration phenology in Maine and demonstrated a clear relationship between NAO and the behavior of some, but not all, passerine migrant species (Wilson 2007). Of the 105 species included in Wilson's 12-year study, only 10 species' arrival dates were related to variation in NAO, yet in a clear majority of the species (60 species out of 105 total) there was a relationship with at least one climatic factor. Thus NAO explained variation in spring migration phenology for 25 of the 105 species, but temperature explained in spring migration for 30 of the 105 species.

Marra et al. (2005) evaluated changes in phenology of long-distance migratory birds in North America using a long-term data set consisting of 32 passerine species captured in Louisiana and captured again at two other mist-netting locations 2,500 km to the north in the eastern U.S.A. and Canada. They sought to understand how climate change might affect the timing and rate of migration, and how arrival times may be related to plant growth (common lilac [*Syringa vulgaris*] was used as a surrogate for native vegetation because of the abundance of data on their flowering phenology) and NAO (Marra et al. 2005). Marra et al. (2005) showed that NAO explained a significant amount of variation in migration behavior for multiple species, but not all.

The effect of NAO on spring migrant capture dates varied, with data from some species negatively correlated with NAO (n = 17) and dates for other species positively correlated with NAO (n = 28). The only statistically significant correlations were positive relationships between NAO and mean capture dates in three species (Marra et al. 2005). The author concluded that long-distance passerine migrants in North America adjusted timing and rate of migration to match annual variations in ambient temperature, and that some species are affected by intermediate-scale climatic trends such as NAO.

Although Marra et al. provide evidence of a relationship between NAO and migration phenology in some species, other authors found no conclusive evidence of the effects of NAO or ENSO on spring migration phenology. For example, Cotton (2003) analyzed spring migration of 20 species in the United Kingdom over a 30 year period from 1971 through 2000. Cotton used the first arrival date of trans-Saharan migrants (i.e., species that overwinter in sub-Saharan Africa but breed in the U.K. and elsewhere in Europe) to evaluate the effect of NAO and ENSO on spring migration. Migrants arrived earlier in the U.K., by approximately eight days over the 30 year period, but was not able to show a statistically significant correlation between that phenological response and either NAO or ENSO. Cotton suggested that changes to migration phenology are a result of variation in seasonal duration at wintering grounds and not NAO or ENSO at breeding grounds (Cotton 2003). The use of first arrival date, instead of mean or median arrival dates, as a metric of spring migration may have biased Cotton's results because of the effects of inter-annual changes in demographics on first arrival numbers. Nonetheless, other researchers working with similar species using a broader geographic area and long duration data sets have observed a strong relationship between NAO and migration and have attributed these changes to rapid human induced climate change (Hüppop and Hüppop 2003).

Hüppop and Hüppop (2003) used a continuous 41-year dataset on passerine migratory behavior from the island of Helgoland in the North

Sea to describe the relationship between NAO and mean spring arrival times of birds migrating to northern Europe. The study focused on arrival time of 24 species at a common *en route* migratory stopover site. Species included both long- and medium-distance migrants, representing tens of thousands of individuals. Hüppop and Hüppop used Student's t-test to test for a relationship between NAO variations and mean spring arrival times. Furthermore, they used species-specific migration periods as opposed to generic spring migration periods used by other researchers, to avoid biases that could result from fitting all species to the same migration period model. By using species specific migration models their assessment was more sensitive to inherent interspecific differences in migration period.

Of 24 species, 23 species had arrival times that trended earlier during the study period, and these earlier arrival times were attributed to higher NAO values. The relationship between earlier arrival dates and higher NAO values was statistically significant in 21 species. Furthermore, NAO was a disparately greater factor (i.e., contributing to later and earlier arrival times depending on the NAO values) in the arrival time of long-distance migrants compared to medium-distance migrants.

Similar to Hüppop and Hüppop's work in Europe, researchers have characterized the long term response trend of migratory birds to NAO patterns in the U.S.A. (MacMynowski and Root 2007). A dataset spanning

21 years of observations from Chicago provides evidence of the relationship between NAO and spring migration phenology in North America (MacMynowski and Root 2007). The authors used data from 22 species to evaluate the relationship between NAO and spring arrival times, and they also modeled this relationship separately for each sex and different migratory strategies. The researchers obtained capture data from the Field Museum of Natural History in Chicago, U.S.A. from 1979 – 2000 and used three different temporal metrics of migration from the Chicago dataset: first arrival, onset of continuous migration, and median of migration period. In addition to climate indices of NAO and ENSO, they used regional averages of mean temperature anomalies, species, sex, and different time periods in their regression models to account for other sources of variation. Seventy-three percent of the long-distance migrant species' spring migrations were correlated with NAO compared to all species combined (45%) and short-distance migrants (18%). This trend was most prevalent in males, with up to 75% of male migration correlated significantly with NAO. The trend was different for responses to temperature. A large proportion (73%) of short-distance migratory species showed statistically significant correlations between migration timing and regional mean temperature, compared with long-distance migratory species (18%) and all species (45%).

Similar to NAO, the response to temperature variation was disproportionately statistically significant for males. Thus, NAO may be responsible for more variation in migration phenology of long-distance migrants, whereas small-scale trends such as regional temperature trends may account for more variation in short-distance migrants.

Regardless of variability in the magnitude of the effect of intermediate-scale climate trends on migration behavior as described in the literature, a clear pattern of increasingly earlier arrival dates is evident. This tendency is especially clear in long-term studies (Hüppop and Hüppop 2003), which showed advances in arrival dates of 0.05 - 0.25 days per year.

1.6 Large-Scale Trends and Responses

The effects of human induced climate change are most evident at large spatio-temporal scales. Climatological trends discussed in the previous sections occur primarily at small and intermediate-scales, but those trends also indicate global climate patterns that we now understand as human-induced climate change (Maclean et al. 2017). Small and intermediate-scale climate trends clearly affect spring migration; therefore, it is important to account for the variability induced by those factors, such as temperature, precipitation, and NAO, to determine if an underlying large-scale trend drives spring migration phenology.

1.6.1 Large-Scale Climate Trends

In this review I define large-scale climate trends as multi-year and multi-decade changes in fundamental climate processes. I also included associated responses in a biological system observed over long periods of time in this definition. Large-scale trends in this context can be represented by the variable "year". Migration responses to small-scale and intermediate-scale trends may be susceptible to confounding factors, such as variability in weather conditions that doffer across multiple geographic locations along migration routes or to stochastic variation within years. Large-scale phenomena affecting the entirety of the earth's system and operating over multiple years or decades should be less susceptible to confounding factors and artefacts in observational data sets because metrics of global scale are compilations of data from thousands of locales. Likewise effects of anthropogenic climate change on migration phenology are clearly evident when climate variables and associated biological responses are observed over multiple decades.

1.6.2 Large-Scale Climate Trends and Corresponding Changes in Phenology

Increases in global temperature as a result of greenhouse gas emissions and other pollutants from human activities are manifested in the temporal advancement of migration and breeding (Bradley et al. 1999, Hüppop and Hüppop 2003, MacMynowski and Root 2007). Higher global temperatures are resulting in earlier spring conditions that are in turn followed by earlier arrival dates (Bradley et al. 1999).

Although birds cannot judge weather conditions of destinations prior to embarking on migration, autocorrelation of climatic variables, including temperature, occurs across large spatial areas (Gordo 2007). Warmer conditions at departure points and along migration routes generally correlate to warmer weather conditions at breeding grounds, and these associations may lead to migrants arriving earlier at their breeding destinations (Gordo 2007).

Researchers working in southern Wisconsin, U.S.A. used a unique dataset spanning a 61 year period to evaluate effects of human induced climate change on phenology (Bradley et al. 1999). They used observations of spring migration made by Aldo Leopold from 1936 to 1947 coupled with observations made by the researchers from 1976 to 1998. This long-duration study period, although not continuous, included observations of 55 different annual phenomenon (i.e., phenophases) of plants and birds, including spring arrival dates. The researchers used lake ice trends as a substitute for regional temperature.

The large temporal scale of the data set allowed Bradley et al. (1999) to develop robust models of phenophases and annual spring temperature trends. Although other taxa, not just birds (arrival of birds comprised 16 of 55 phenophase observations), exhibited a significant change in arrival date across the study period, 6 avian species (37.5%) arrived earlier, and overall 19 (35%) of the phenophases evaluated showed increases in "earliness" (Bradley et al. 1999).

Bradley et al.'s research demonstrates the effects of climate change (i.e., increasing temperature) on spring migration phenology, although not all bird species in the study exhibited the same response. Ward et al. (2016) compiled data on 16 migratory species across a 50 year study period from 1964 -2013. The researchers used the first arrival date of these 16 species at breeding grounds in the central Arctic Alaskan coast to demonstrate effects of climate change on migration phenology. Ward et al. also used small and intermediate scale trends in their model, but most of the variation was explained by year. Of particular interest was the magnitude of the response: birds arrived at the breeding grounds an average of 0.12 days earlier per year across the study period. Overall, all 16 species had significantly earlier first arrival dates.

Miller-Rushing et al. (2008) modeled migration phenology and climate change at the Manomet Research Station in coastal Massachusetts (1970-2002). The researchers modeled effects of climate change on migration by including ecological and climatological factors in a multi-decadal model of the migration timing of 32 species. The researchers sought to identify and quantify sources of variation in response to climate change. Miller-Rushing et al. included specific measures to avoid biases from not only climate factors, but also ecological factors such as migratory distance, breeding habitat, and food availability. They also avoided use of first arrival dates, which they contended are not reliably characteristic of the migratory cohort as a whole and can be biased by inter-annual fluctuations in population sizes.

Of the 32 species studied, 8 species had mean arrival dates statistically significantly earlier across the 33 year study, which was directly attributed to effects of climate change. In contrast, for those same 8 species, there was no statistically significant change in first arrival dates during the study period. There was also statistically significant intra-specific variation in arrival dates. Notably, during the 33 year study period, migratory population cohorts of 19 of the 32 species exhibited an average of a 34% decline in population size, which was attributed to effects of climate change, but is also relevant in the bias inherent with the use of first arrival dates as a metric for migration phenology.

Miller-Rushing et al. used multiple regression models including cohort size and either first arrival or mean arrival dates. Cohort size explained much of the variation in first arrival dates but not in mean arrival dates. The author explained that the decrease in cohort size caused a 1.6 day change in first arrival date during the study period, which was noted as an artefact of the bias in using first arrival dates and not a result of underlying climatological factors. Nonetheless, Miller-Rushing et al.'s study showed a clear change in mean arrival dates over the 33-year study period, which was not explained entirely by cohort size or migratory behavior, and which was attributed to human-induced rapid climate change (e.g., a 1.5° C increase in spring temperatures across the 33-year study period). They also noted inter-annual variation in migration advancement rates, with birds migrating generally earlier in warmer years, especially species migrating from wintering grounds in the Caribbean, Central American, and southern North America.

Usui et al. (2017) published a robust meta-analysis using 73 studies of migration phenology from 1749 - 2014 across 5 continents and 413 species. This meta-analysis builds on some themes evaluated in the Miller-Rushing et al. paper, as well as literature described in the Small-Scale and Intermediate-Scale sections. Usui et al. accounted for not only climatological variables and ecological variables, as did Miller-Rushing et al. and others, but they also included phylogeny in their meta-analysis of temporal shifts in migration phenology.

Usui et al. determined the slope values of spring migration changes within the 73 studies used in their meta-analysis. They used both first arrival dates and mean/median arrival dates of spring migrants (the researchers did not differentiate between mean and median), and they found highly statistically significant trends for earlier spring migration over the study period. They noted that the steepest advance in spring migration occurred between the 1920s and 1990s. Furthermore, advances in migration timing between breeding grounds and at stopover sites *en route* to breeding grounds did not vary significantly. Over time, on average, the species included in their multi-century meta-analysis advanced spring migration by 2.1 days per decade. Short distance migrants advanced their migration timing more than longer distance migrants did, but all species showed an advance in migration timing across the study period. However, migration timing was sensitive to changes in annual temperature, which affected the magnitude of the response across species and populations. For example, during warm years, migration may have advanced more than in cool years, although the overall trend was towards significant advances in spring migration. Similar to Miller-Rushing et al., Usui et al. concluded that first arrival dates exhibited more inherent bias that mean/median arrival dates.

CHAPTER 2 - QUANTITATIVE DATA EXPLORATION

2.1 Introduction

There have been few attempts to model climate change's effect on the migration phenology of Maine's bird populations, with the exception of Wilson 2007. As summarized in Chapter 1, advancement in spring migration has been observed in many regions of Europe and North America. I theorized that the same factors contributing to advancements in spring migration elsewhere are acting on birds breeding in the state of Maine. To explore the effects of climate change on migratory birds in Maine I present the results of a quantitative data modeling exercise which models the variation in phenology of a selection of neo-tropical migrant bird species and the same climatic factors evaluated in the literature as summarized in Chapter 1. I used publicly available and crowd sourced data to assess how climate change may be related to the advance in spring arrival dates of migratory birds in Maine. I used a model selection approach to develop a predictive model of spring migrant arrival dates. The results of Chapter 1 Literature Review guided the modelling approach employed in Chapter 2.

The goal of this exercise was to 1) determine the amount of variation in spring migration that can be explained by climate, and, 2) to model the median arrival dates of 29 species of bird from 1982-2014. I used climate variables including temperature, NOA, ENSO, and other climate indices, as well as year, to build a predictive model of spring migration arrival times. As documented in the literature collected in the Northern Hemisphere, I predicted that many migratory bird species in Maine are arriving increasingly earlier in spring, and that this earlier arrival is likely correlated to climate change.

Open source software and public data sets are advantageous because they are widely available to the broader scientific community and allow researchers to utilize the same methods. There is a growing movement for increased transparency of data collection and analysis in the scientific community, and measures that enable replication of studies by fellow researchers can be facilitated by using open source software and publicly available.

2.2 Methods

2.2.1 Data Sources

To model the effects of climate change on spring avian migration phenology in Maine, I accessed data from multiple publicly available sources, including data on arrival dates of spring migrants from eBird, and NAO, ENSO, and other weather variables and indices from the National Oceanic and Atmospheric Administration (NOAA;

www.ncdc.noaa.gov/extremes/cei/, and Table 2). I developed multivariate regression models and mixed linear-models, and, used model averaging.

For spring migration data, I was granted permission to access eBird data after submitting an inquiry to their website (www.ebird.org). The eBird dataset consisted of observations submitted to eBird by volunteers and citizen scientists from across Maine. Approximately 70% of eBird observations came from the more densely populated areas of the state including the southern, coastal, and central regions, giving the dataset geographic sampling biases.

The eBird dataset provided the full set of quality controlled records for all observations in Maine between 1982 and 2014. I selected a subset of these data for my analysis by truncating the data set and only including observations during the spring migration period from March through May 31, 1982–2014. By starting with data from March I was able to assure that any early first arrival migrants were included in the analysis. From this modified dataset I selected 50 migrant species (including species from the families Parulidae, Vireonidae, Icteridae, and Tyrranidae) that do not typically winter in Maine or elsewhere in New England or New York. I then excluded species that were not observed during at least 25 years in the study period (78%), resulting in 29 species (Appendix Table 1). I classified these species as either mid-distance migrants (n = 9; Appendix Table 1) or long-distance migrants (n = 20; Appendix Table 1). Mid-distance migrants included species known to winter south of Maine and primarily north of Florida. Long-distance migrants included species known to winter primarily south of Florida, including the Caribbean, Central America, and South America (Alerstam and Christie 1993). For these species arrival dates from eBird were converted into a Julian day format before calculating mean spring arrival date and median spring arrival date. For example, April 1 was converted to day 101 or 102 if it occurred in a leap year.

I calculated the mean spring passage date (MNSP) and median spring passage date (MDSP) using the Julian eBird bird observation dates for each spring. The MNSP was calculated by averaging the Julian date of all spring observations of a given species from March 1 through May 31 in a given year. The MDSP was calculated as the median Julian date of all spring observations of a given species from March 1 through May 31 in a given year. Ultimately, I chose to use MDSP as the response variable for data analysis based on previous research that demonstrated clear relationships between MDSP and NAO in European passerine populations (Hüppop and Hüppop 2003, Marra et al. 2005). Median arrival dates of spring migrants may be more representative than mean arrival date because they minimize the effect of first arrival date and demographic bias, which can bias phenology assessments using first arrival and mean arrival dates (Usui et al. 2017).

For covariates I used year as an indicator of large-scale trends, NAO and ENSO as intermediate-scale metrics, and 19 other regional weather and climate indices were evaluated for use as measures of small-scale trends. The NAO and ENSO index values used were normalized based on a rotated principal component analysis conducted by NOAA (Hurrell 1995). NAO and ENSO data included data from the year preceding the corresponding migration season; for example, for the 2014 spring migration season, the NAO and ENSO data included the 12 months prior to April 2014.

For small-scale predictor variables, I evaluated 19 datasets pre-summarized by NOAA for the Northeast U.S. (including Delaware and Pennsylvania and all other northeastern states north to Maine). NOAA data included extreme minimum and maximum temperatures, drought indices, and similar metrics and datasets included data from March through May for each year (Table 2). I used temperature data obtained from the NOAA Gardiner station in central Maine, because data from this station were selected because it was isolated from the effects of Maine's coast and inland mountains. The station was presumably the most representative of the temperature trends of the state as a whole.

In total the initial model included 21 regional weather and climate indices for my analysis of spring migration phenology (Table 2).

2.2.2 Data Analysis

Predictor Variable Selection

In preparation for model building, model selection, and model averaging, I evaluated the relationship and collinearity among the 21 candidate predictor variables (Table 2). Predictor variables were expected to be highly correlated with each other, e.g., the Climate Extremes Index is a composite measure of precipitation trends and temperature extremes, and thus it was likely to be correlated to those component variables. To avoid collinearity and to retain as much independence in predictor variables as possible, I evaluated correlation and collinearity among the 21 original predictor variables in R 2.3.4 using the Hmisc package (Harrell 2015). I used Hmisc to calculate the variance inflation factor (VIF) for a Durbin Watson Test for the 21 predictor variables (O'Brien 2007) (Table 3).

Results of the correlation, collinearity assessment, and Durbin Watson Test reduced the number of predictor variables to a final subset of predictor variables that had the least correlation to other variables (Table 2). The criteria for retaining a predictor variable was VIF < 10 and no statistically significant correlation with any other predictor variable. The 11 predictor variables retained for further analysis were the NOAA climate extremes index (spring only), NAO, ENSO, extreme maximum temperatures above normal for the Northeast region in spring, extreme minimum temperatures above normal for the Northeast region in spring, extreme minimum temperatures below normal for the Northeast region in spring, wet/dry conditions less even for the Northeast region in spring, wet/dry conditions more even for the Northeast region in spring, abnormally infrequent precipitation for the Northeast region, and abnormally frequent precipitation for the Northeast region (Table 3). In an effort to reduce covariance between these similar indices, I chose a combination of the two extreme temperature and wet/dry indices by calculating the difference of the extreme maximum and extreme minimum temperatures and precipitation indices, thereby reducing the total number of independent variables used in the model to 7 (Table 2). The independent variables used in the model included: year, ENSO, NAO, the Palmer Drought Severity Index for the Northeast monthly average per spring (PDSI), the difference between extreme maximum temperature above normal and extreme maximum temperatures below normal for the Northeast per spring of each year (Extreme Above Normal Temp), the difference between extreme maximum below normal temperature and extreme minimum below normal temperature for the Northeast per spring of each year (Extreme Below Normal Temp), and the number of extreme one day above normal precipitation events for the Northeast per spring of each year (Extreme Precipitation).

Table 2. Variance inflation factor amongst predictor variables.

Variable Title	Climate Extremes Index Per Spring (Mar. - May)	Northern Atlantic climate index	Pacific climate index	Extreme Maximum Temperatures Above Normal Per Spring	Extreme Maximum Temperatures Below Normal Per Spring	Extreme Minimum Temperatures Above Normal Per Spring	Extreme Minimum Temperatures Below Normal Per Spring	Wet/Dry Conditions Less Even in Region Per Spring	Wet/Dry Conditions More Even in Region Per Spring	Abnormally Frequent Precipitation-Spring	Abnormally Infrequent Precipitation-Spring
Climate Extremes Index Per Spring (Mar. - May)	1.00	0.09	0.12	0.09	-0.23	0.42	-0.05	-0.07	0.10	-0.11	-0.54
Northern Atlantic climate index	0.09	1.00	0.98	-0.25	0.05	0.20	0.00	0.46	0.33	0.09	-0.08
Pacific climate index	0.12	0.98	1.00	-0.23	0.02	0.23	-0.02	0.44	0.35	0.08	-0.08
Extreme Maximum Temperatures Above Normal Per Spring	0.09	-0.25	-0.23	1.00	-0.04	0.11	0.15	0.01	-0.18	-0.16	-0.13
Extreme Maximum Temperatures Below Normal Per Spring	-0.23	0.05	0.02	-0.04	1.00	-0.09	0.60	-0.11	-0.17	-0.21	-0.21
Extreme Minimum Temperatures Above Normal Per Spring	0.42	0.20	0.23	0.11	-0.09	1.00	-0.03	0.03	-0.17	-0.24	-0.21
Extreme Minimum Temperatures Below Normal Per Spring	-0.05	0.00	-0.02	0.15	0.60	-0.03	1.00	0.15	-0.31	-0.35	-0.10
Wet/Dry Conditions Less Even in Region Per Spring	-0.07	0.46	0.44	0.01	-0.11	0.03	0.15	1.00	-0.19	-0.33	0.01
Wet/Dry Conditions More Even in Region Per Spring	0.10	0.33	0.35	-0.18	-0.17	-0.17	-0.31	-0.19	1.00	0.51	-0.01
Abnormally Frequent Precipitation-Spring	-0.11	0.09	0.08	-0.16	-0.21	-0.24	-0.35	-0.33	0.51	1.00	0.38
Abnormally Infrequent Precipitation-Spring	-0.54	-0.08	-0.08	-0.13	-0.21	-0.21	-0.10	0.01	-0.01	0.38	1.00

Table 3. Description of predictor variables.

Variable Summary	Type	Time Period	Region	Category	Description
Climate Extremes Index Per Year (Jan. - Dec.)	Composite Index	Annual	North Eastern U.S.	Composite Measure of Regional Extremes	The CEI (Climate Extremes Index) is described by NOAA as an aggregate set of convectional climate extreme indicators and is the arithmetic average of the 5 other CEI indices. A value of 0% indicates no portion of the year was subject to extremes of temp or precipitation, a value of 100% indicates that the entire year was subject to extremes of temp and Precipitation.
Climate Extremes Index Per Spring (Mar. - May)	Composite Index	Spring	North Eastern U.S.	Composite Measure of Regional Extremes	As above but for spring only.
NAO Index	Composite Index	Annual	North Atlantic	Index of Hemispherical Climatological Trends	Index of North Atlantic Oscillation - Positive value causes warmer temperatures and increased rainfall in NE, Negative value causes cooler and drier winters in NE.
ENSO	Composite Index	Winter	Western Hemisphere	Index of Hemispherical Climatological Trends	Index of Southern Oscillation (El Niño/La Niña) during winter preceding spring of given year). Positive values cause warmer and drier than average winters in NE.
Palmer Drought Severity Index	Composite Index	Monthly (per year)	Northeast	Index of Drought Conditions	The Palmer Drought Severity Index (PDSI) is derived from temperature and precipitation to estimate relative dryness. It ranges from -10 (dry) to +10 (wet).
Extreme Maximum Temperatures Above Normal Per Year	Index based on observations	Annual	North Eastern U.S.	Warm Periods Abnormally Warm	The sum of the percentage of the NE states with maximum temperatures above normal for the entire year
Extreme Maximum Temperatures Above Normal Per Spring	Index based on observations	Spring	North Eastern U.S.	Warm Periods Abnormally Warm	The sum of the percentage of the NE states with maximum temperatures above normal for the spring (March - May) of a given year
Extreme Maximum Temperatures Below Normal Per Year	Index based on observations	Annual	North Eastern U.S.	Warm Periods Abnormally Cool	The sum of the percentage of the NE states with maximum temperatures below normal for the entire year
Extreme Maximum Temperatures Below Normal Per Spring	Index based on observations	Spring	North Eastern U.S.	Warm Periods Abnormally Cool	The sum of the percentage of the NE states with maximum temperatures below normal for the spring (March - May) of a given year
Extreme Minimum Temperatures Above Normal Per Year	Index based on observations	Annual	North Eastern U.S.	Cool Period Abnormally Warm	The sum of the percentage of the NE states with minimum temperatures above normal for the entire year
Extreme Minimum Temperatures Above Normal Per Spring	Index based on observations	Spring	North Eastern U.S.	Cool Period Abnormally Warm	The sum of the percentage of the NE states with minimum temperatures above normal for the spring (March - May) of a given year
Extreme Minimum Temperatures Below Normal Per Year	Index based on observations	Annual	North Eastern U.S.	Cool Periods Abnormally Cool	The sum of the percentage of the NE states with minimum temperatures below normal for the entire year
Extreme Minimum Temperatures Below Normal Per Spring	Index based on observations	Spring	North Eastern U.S.	Cool Periods Abnormally Cool	The sum of the percentage of the NE states with minimum temperatures below normal for the spring (March - May) of a given year
Wet/Dry Conditions Less Even in Region Per Year	Index based on observations	Annual	North Eastern U.S.	Wet/Dry Conditions Less Even in Region	The sum of NE states PDSI severe drought (i.e. the lowest tenth percentile) with above normal moisture surplus (for the entire year)
Wet/Dry Conditions More Even in Region Per Year	Index based on observations	Annual	North Eastern U.S.	Wet/Dry Conditions More Even in Region	The sum of severe drought (i.e., the lowest tenth percentile) with below normal moisture surplus (for the entire year)
Wet/Dry Conditions Less Even in Region Per Spring	Index based on observations	Spring	North Eastern U.S.	Dry Periods with Above Normal Moisture	The sum of NE states PDSI severe drought (i.e. the lowest tenth percentile) with above normal moisture surplus (for spring)
Wet/Dry Conditions More Even in Region Per Spring	Index based on observations	Spring	North Eastern U.S.	Dry Periods With Below Normal Moisture	The sum of severe drought (i.e., the lowest tenth percentile) with below normal moisture surplus (for spring)
Abnormally Frequent Precipitation	Index based on observations	Annual	North Eastern U.S.	Abnormally Frequent Precipitation	Sum of extreme one day precipitation events above normal per year
Abnormally Frequent Precipitation	Index based on observations	Spring	North Eastern U.S.	Abnormally Frequent Precipitation	Sum of extreme one day precipitation events above normal per spring
Abnormally Infrequent Precipitation	Index based on observations	Annual	North Eastern U.S.	Abnormally Infrequent Precipitation	Sum of extreme one day precipitation events below normal per year
Abnormally Infrequent Precipitation	Index based on observations	Spring	North Eastern U.S.	Abnormally Infrequent Precipitation	Sum of extreme one day precipitation events below normal per spring

I then used the 10 predictor variables and year to model MDSP in three discrete ways: simple linear regression, linear mixed-model, and model averaging.

Simple Linear and Multivariate Regression

The eBird data set was used to generate the MDSP for each species, resulting in 29 median arrival dates. To model each species' median arrival date, I first evaluated year as an overall effect on arrival date of each species:

$$\textbf{Arrival} = \beta_0 + \beta_1 \textbf{Year} + \epsilon$$

Each species' coefficient of Year (β_1) is a measure of that species' spring migration phenology trending earlier or later. Simple linear regressions of each species' arrival MDSP and year were modeled separately.

The individual species model described above estimates the effect of year on MDSP for each species but it can be considered as an estimate for a more general effect common to all species. I used the same regression model for the multivariate regression approach, but instead of generating 29 different simple linear regression models, i.e., one for each species, I used all 29 species at once to generate a multivariate regression. Then, I generated regression plots and used locally weighted scatterplot smoothing to visually depict the trend in the multivariate regression. Locally weighted scatterplots are used to fit scattered or noisy data to a line of best fit; it is a non-parametric approach that does not assume the data fit a pre-determined distribution and helps to show trends in continuous data sets (Cleveland 1979).

One drawback of the regression models is that errors are not independent because the dataset includes multiple species, not all of which have the same migratory behavior patterns. For example, species known to arrive earlier on average than all other species have a predictably negative error in all years; thus, all earlier arriving birds will have correlated errors. Correlated errors would indicate a lack of independence across variables.

Linear Mixed-Model

In addition to simple linear regression and multivariate regression, I developed a linear mixed-model of median spring arrival times. This linear mixed-model includes fixed and boot-strapped random effects. The model uses species' slopes (β_1) and intercepts (β_0) as the fixed effect, and the random effect is a random sampling of a distribution with a mean of 0 and some variance to generate the random slope (β_{1j}) and intercept (β_{0j}).

$$\mathbf{Arrival}_j = (\beta_0 + \beta_{0j}) + (\beta_1 + \beta_{1j})\mathbf{Year} + \in$$

The random intercept (β_{0j}) is such that some species may have a negative intercept, and some have a positive intercept; thus, they arrive earlier or later than other species. The random slope (β_{1j}) is also derived from a sampling of a population with mean of 0 and some variance, resulting in some species demonstrating a larger or smaller effect on MDSP from year. The linear mixed-model is a partial pooling among the individual species' models, whereas the multivariate regression model computes slope and intercept separately for each species.

Model Averaging

The model selection and model averaging approach is a fundamentally different approach to the scientific process than hypothesis testing, and it is well suited to describing complex ecological systems (Burnham and Anderson 2003). The model selection approach is based on the concept of multiple working hypothesis (Johnson and Omland 2004). Model selection allows inferences to be made about a given system or subject that are not mutually exclusive and therefore often present a more comprehensive description of a given system or subject without the constraints of hypothesis testing in the traditional sense. I used model averaging to develop a model of median spring arrival dates. This approach allowed me to incorporate multiple model parameters that affected the response variable. Traditional statistical approaches rely on a single model, for example regression analysis, whereas model averaging includes the results of multiple plausible models to develop a single comprehensive model. Model averaging can result in a reduction of model selection bias and can compensate for model selection uncertainty (Johnson and Omland 2004, Burnham and Anderson 2004).

After developing the simple linear regression, multivariate regression, and linear mixed-model, I included 3 other covariates (NAO, OSI, and the climate extremes indices) into a model of MDSP. I developed multivariate linear mixed models using year, NAO, OSI, and climate extremes indices, but because of lack of true independence among the variables, this approach had limitations in the ability to accurately model MDSP without substantial error. The model used for model averaging was:

$$\mathbf{Arrival} = \beta_0 + \beta_1\,\mathbf{Year} + \beta_1\,\mathbf{NAO} + \beta_1\,\mathbf{ENSO} + \beta_1\,\mathbf{PDSI} + \beta_1\,\mathbf{Extreme\ Above\ Normal\ Temperature} + \beta_1\,\mathbf{Extreme\ Below\ Normal\ Temperature} + \beta_1\,\mathbf{Extreme\ Precip} + \in$$

I then generated an average model using all 7 covariates and calculated weighted averages for each of the coefficients of variation in the models. I used the dredge function in MuMIn package in R to fit the set of sub-models containing all combinations of the predictor variables (Leonard et al. 2014). I then used the model average function to construct a single "best" model with model-averaged coefficients averaged over the entire set of submodels (Kang et al. 2003).

2.3 Results

Climate

Mean monthly temperature for spring (March - May) trended higher from 1982 to 2014; however, this trend was not statistically significant (R^2 = 0.001, Adj. R^2 = -0.03, p = 0.867). NAO had a statistically significant relationship with the NOAA Climate Extreme Index (R^2 = 0.305, Adj. R^2 = 0.2792, p = 0.001), extreme maximum above average spring temperatures in the Northeast (R^2 = 0.3566, Adj. R^2 = 0.3327, p = 0.0006), and other climate indices included in the global model. The full regression matrix of predictor variables is available in Appendix Table 2.

Simple Linear Regression

Median arrival dates for each species varied by year, but the general trend was toward increasingly earlier arrival dates for all species during the study period (1982 - 2014) (Figure 3, Appendix). Of the 29 species included, 26 exhibited gradually earlier arrival dates from 1982 to 2014, and only three species (blue-headed vireo [*Vieo solitarius*], eastern phoebe [*Sayornis phoebe*], and yellow-bellied flycatcher [*Empidonax flavientris*]) exhibited stable or later arrival dates for the same period. The trend in earlier median arrival dates for most species was not statistically significant ($p > 0.05$). However, song sparow (*Melospiza melodia*) (*Adj.* R^2=0.252, p = 0.003) and American redstart (*Setophaga ruticilla*) (*Adj.* R^2=0.127, p = 0.033) exhibited statistically significantly earlier median arrival dates (MDSP). For all species pooled, the trend was similar to that observed for individual species, with a negative relationship between median arrival data and year (Figure 9).

Different environmental predictors related to different species' MDSP patterns. Although species varied substantially, the largest mean coefficient value in the species-specific average model, among all species, was the Climate Extremes Index. For 1 unit change in the Climate Extremes Index (Appendix Table 2) median spring arrival dates changed across all species on average -0.23 days (SD = 0.31, SE = 0.06).

Species MDSP responded differently to the predictor variables. For example, only six species exhibited an earlier median arrival date in response to an increase in the Climate Extremes Index when all other predictor variables were fixed (blackpoll warbler [*Setophaga striata*], black-throated blue warbler [*Setophahga caerulescens*], black-throated green warbler [*Setophahga virens*], chimney swift [*Chaetura pelagica*], Eastern kingbird [*Tyrannus tyrannus*] and Eastern phoebe [Sa*yornis phoebe*]). For the "Cool Periods with Abnormally Cool Weather" index, most species (n = 21) exhibited a later average median arrival date. Conversely, most species (n = 21) had a corresponding earlier median arrival date response to "Warm Periods Abnormally Warm".

The goodness of fit for species-specific average models was also variable. All average models for each species had $R^2 > 0.16$, with a maximum of 0.64. The maximum R^2 for long-distance and middle-distance migratory species was 0.47 (black-throated green warbler) and 0.64 (brown thrasher [*Toxostoma rufum*]). Overall, the species-specific average models had a higher average R^2 across all models for middle-distance migratory species ($R^2 = 0.394$) than for long-distance migratory species ($R^2=0.311$).

Multivariate Regression

As described above, the MDSP of each species was modeled against year, resulting in 29 different regression models (Appendix Figures 1-29). When combined into the multivariate model using the coefficient for year for each species' model, the mean trend in arrival time over the 32 year period is a -0.19 change in MDSP per year, or -6 days over the 32-year period; 90% of bird species trended earlier during this period (Figure 5). However, these data are not independent because some species trend earlier than others.

The multivariate regression using all species and year as the independent variable demonstrates that there is a clear trend in MDSP across species from 1982-2014. The slope of the median arrival date across all species was estimated to be -0.123 (SE = 0.028, $p < 0.05$). However, there is a caveat to the estimated standard error and P-value, because there was a lack of independence of error in the dataset. For example, some species naturally migrate earlier than others, and thus the species' MDSP are not independent when pooled. A corrective factor to adjust for individual species' migration behavior could alleviate this lack of independence in future analyses.

The multivariate regression can be used to explore the eBird dataset more thoroughly (Figure 6). The MDSP data for each species was plotted in a simple linear regression of the MDSP against year for each species (Figure 7). The simple linear regression of MDSP and year for each species was then smoothed using locally weighted scatterplots smoothing, to demonstrate the trend in MDSP across all species (Figure 8).

Raw data have too much noise to be particularly useful or indicative of trends in the dataset across species (Figure 6). Simple linear regression is an overly simple view of MDSP trends for most species (Figure 7). Locally-weighted smoothing shows a more nuanced and complex trend in MDSP with a consistent pattern in earlier arrival dates (Figure 8 and 9).

Linear Mixed-Model

One challenge with the multivariate model is a lack of standard error because of the lack of independence between dependent variables. In the linear mixed-model, I combined fixed and random effects, resulting in a more appropriate and accurate estimate of standard error. By standardizing the residuals, I arrived at an estimate of the slope (-0.189) of median arrival date as a function of year (SE = 0.037). Put another way, based on the linear mixed-model, I estimated that median arrival dates are advancing by 0.189 days per year across all species.

I then included NAO and ENSO in the mixed model along with year, which resulted in an estimate of MDSP adjusted for NAO and ENSO. By including NAO and ENSO in the model, the original estimated change in MDSP of -0.189 days per year changed to -0.11 days per year. NAO and ENSO account for some variation in MDSP across year, but when adjusted we still see an advancement in migration of 0.11 days. ENSO had a positive effect on MDSP ($B = 1.736$) and NAO had a strong negative effect on MDSP ($B= -3.547$). The strong positive effect of ENSO is evident in MDSP trends in the late 1990's when the steady advancement of MDSP reversed for approximately 6 years (Figure 8 and Figure 9).

Following the inclusion of NAO and ENSO in the linear mixed-model I included the PDSI, Extreme Below Temperature, Extreme Above Temperature, and Extreme Precipitation variables. The "extremes" model had a slightly negative slope (-0.07) but deviated from the approximately -0.19 coefficient observed in the other models.

Average Model

Model averaging allowed me to fit all possible models of MDSP and year, NAO, ENSO and the 4 other predictor variables into a single model. The coefficient for year in the average model was -0.197, which corresponds to a 0.197 day advance in MDSP per year when accounting for the 6 other model covariates (Table 3). The year coefficient, of approximately -0.19, is consistent with year coefficient generated in the simple regression, linear mixed-model, and multiple regression models. Unlike the regression and models, the average model minimized error among all possible model combinations by averaging the coefficient for each parameter.

Table 4. The average model of MDSP and 6 covariates.

Covariate	Coefficient	Standard Error	p-Value
NAO	-0.987	0.573	< 0.001
Year	-0.197	0.042	< 0.001
PDSI	-0.088	0.178	< 0.001
Extreme Below Normal Temperature	-0.047	0.024	0.053
Extreme Precip	-0.037	0.019	0.057
Extreme Above Normal Temperature	0.024	0.021	0.26
ENSO	0.0576	0.196	0.77

Table 5. Coefficient for year in each model approach.

Modelling Method	Coefficient for year on MDSP
Simple Linear Regression	-0.19
Multivariate	-0.123
Linear-mixed model (not adjusted for NAO and ENSO)	-0.189
Linear-mixed model (adjusted for NAO and ENSO)	-0.11
Linear-mixed model (adjusted for NAO, ENSO, PDSI, Extreme Below Temperature, Extreme Above Temperature, and Extreme Precipitation variables)	-0.07
Model averaging	-0.197

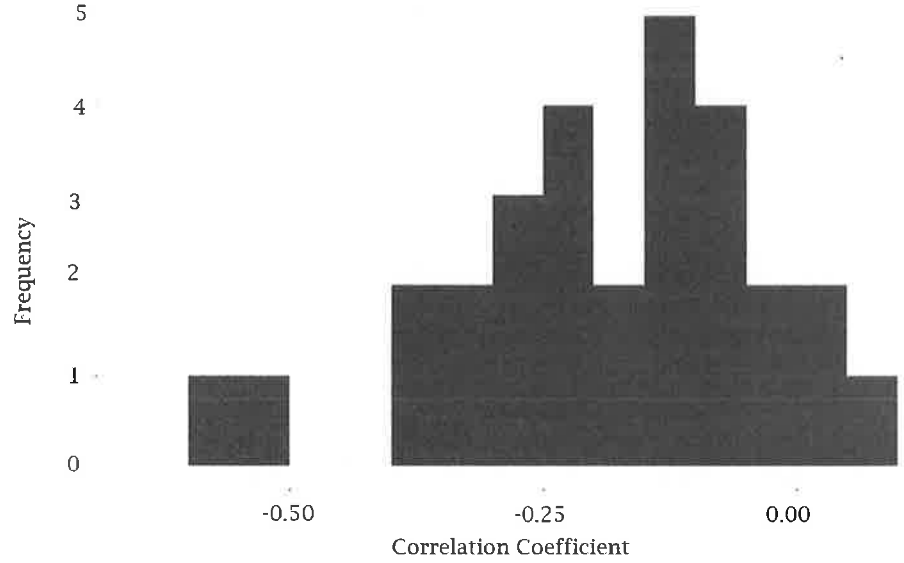

Figure 2. Frequency of median arrival dates and year, for 29 species, March – May 1982-2014 Maine.

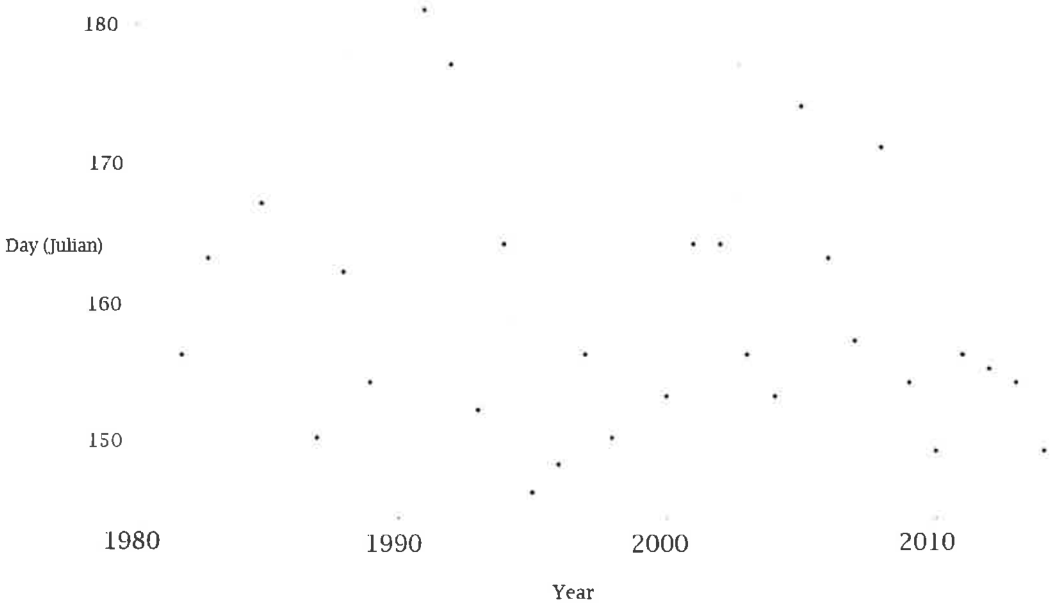

Figure 3. Distribution of coefficient of correlation of median arrival dates and year, for 29 species, March – May 1982-2014 Maine.

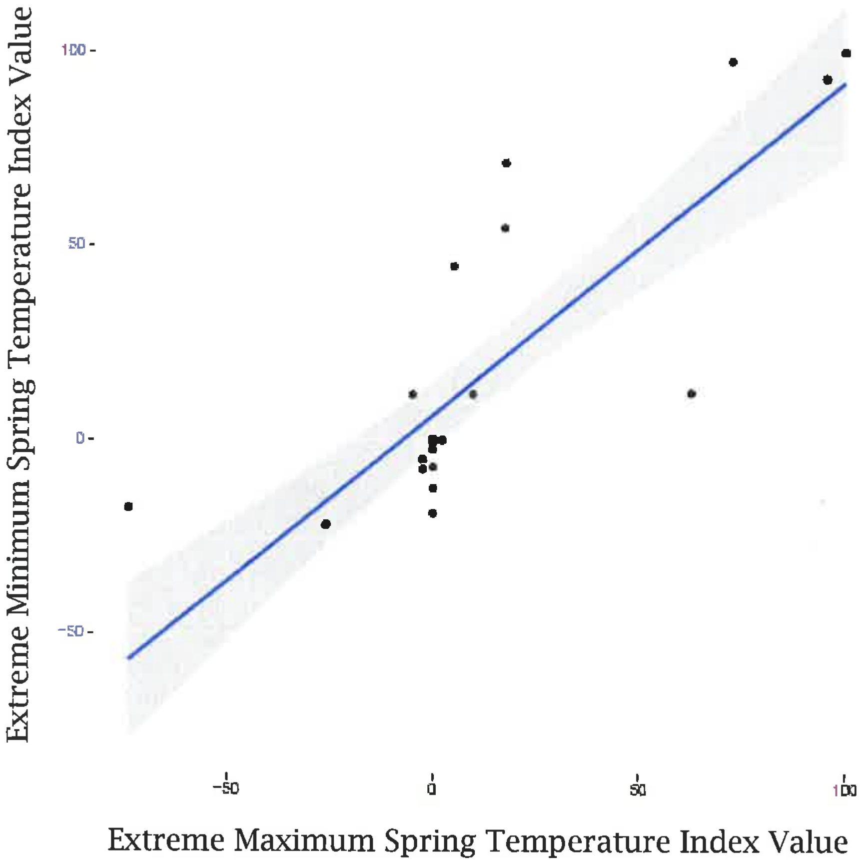

Figure 4. Plot of extreme minimum and extreme maximum temperatures for the spring period (March – May) in the northeast from NOAA. These variables exhibited collinearity. Blue line is the regression of the Extreme Minimum Spring Temperature Index against Extreme Maximum Spring Temperature. The grey area is the 95% confidence interval for the regression.

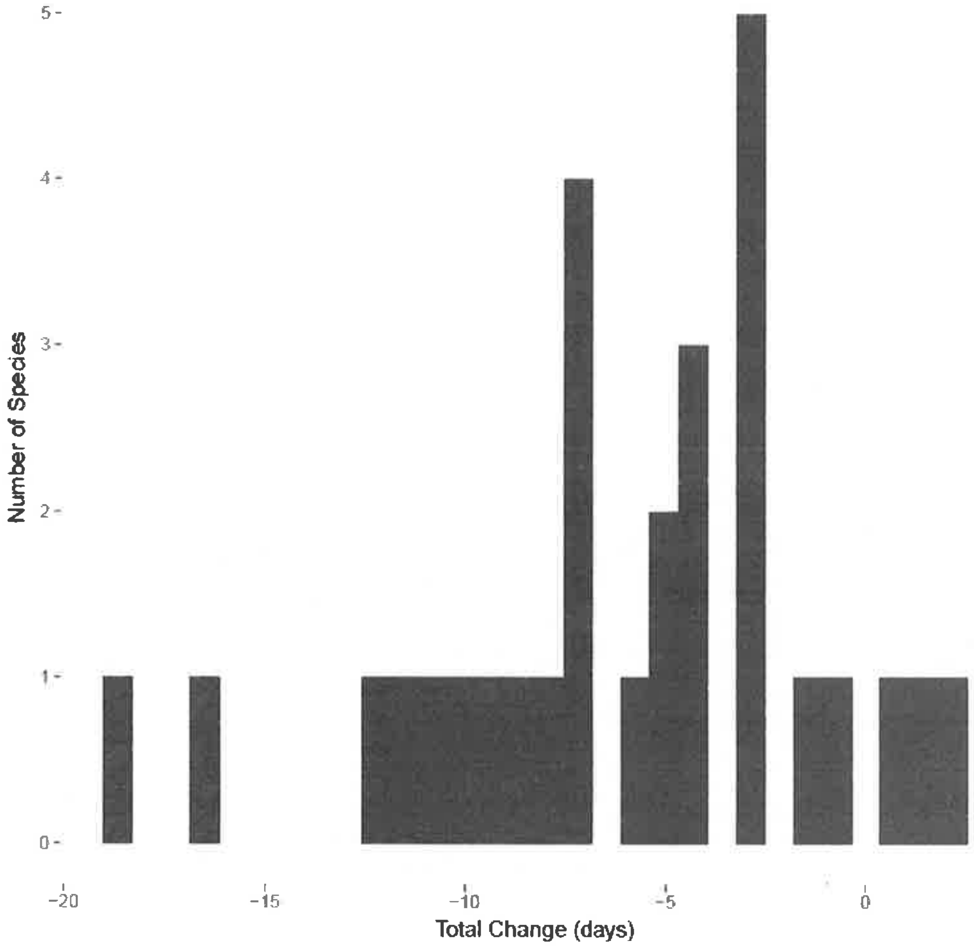

Figure 5. The change in median arrival date (MDSP) for 29 species, March – May 1982-2014 Maine.

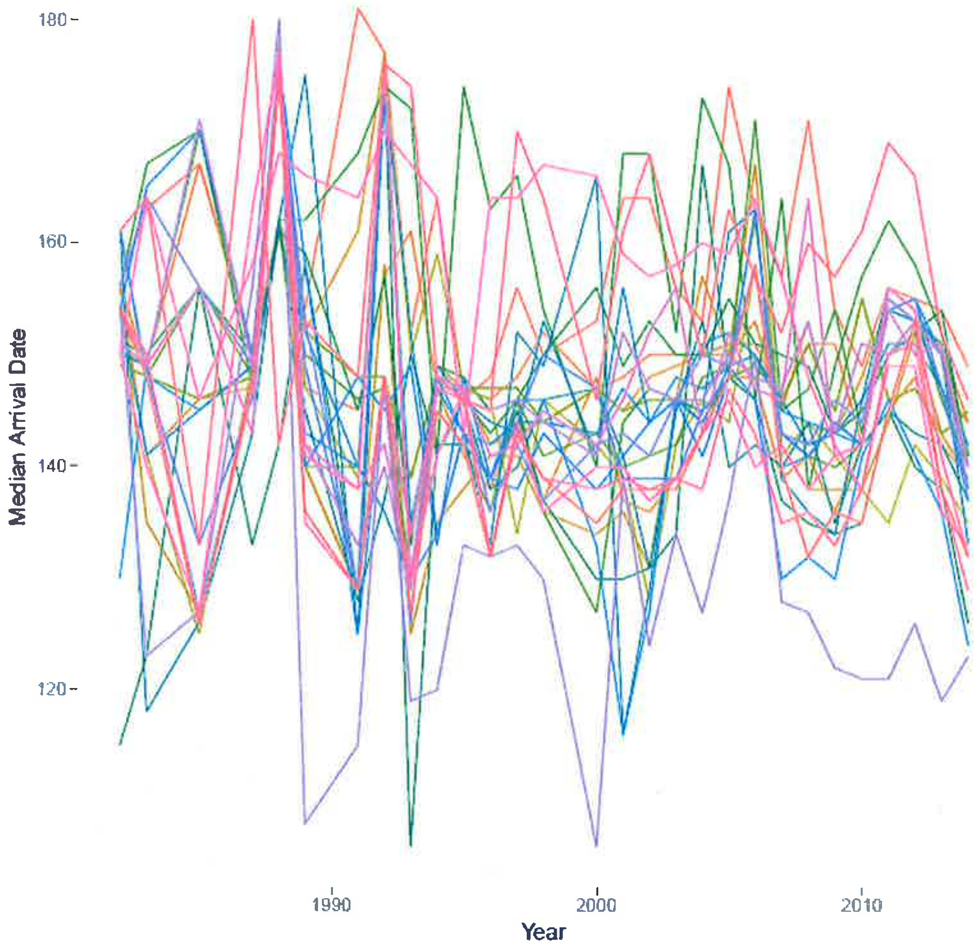

Figure 6. Julian date MDSP by year for 29 species, March – May 1982-2014 Maine. There is substantial variation by species and across years.

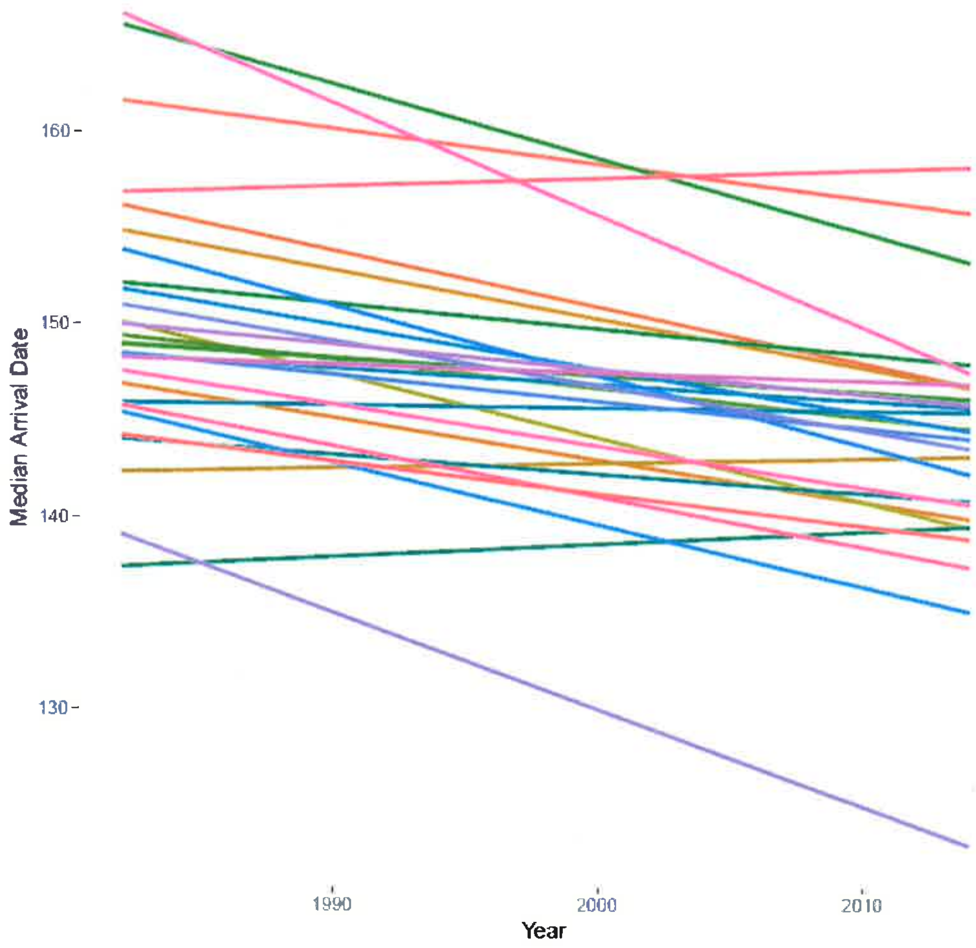

Figure 7. Simple linear regression for each bird species' Julian median arrival date by year, for 29 species, March – May 1982-2014 Maine. The declining trend in median spring arrival date is apparent in most species, and consistent across species. The variation among years is masked with the simple linear regression.

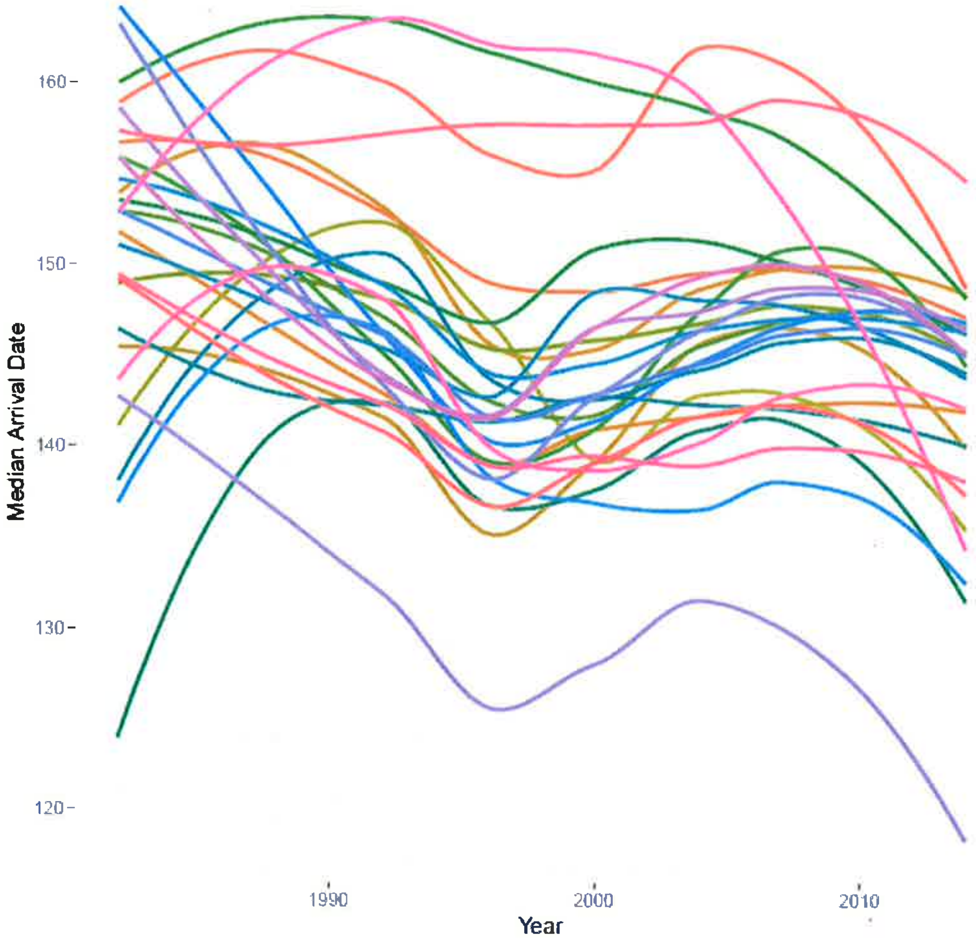

Figure 8. Species' median spring arrival date (MDSP) by year for 29 species, March – May 1982-2014 Maine. The trend is similar to Figure 7 and 8, but with the locally weighted scatterplots smoothing applied more of the variation across years is apparent. Despite the declining trend in MDSP shown in the simple linear regression, MDSP variation was not as uniform from year to year as the simple linear regression model shows.

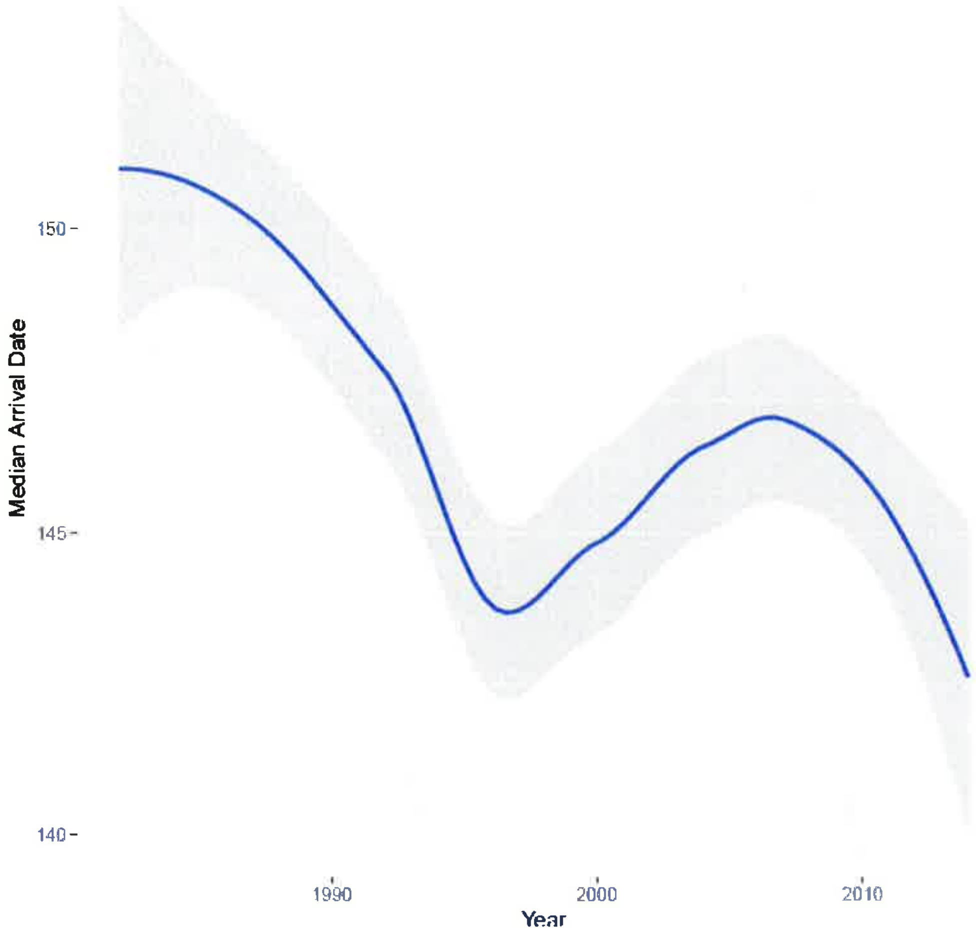

Figure 9. MDSP data, by year, from all species combined, using a multivariate regression model with locally-weighted smoothing, for 29 species, March – May 1982-2014 Maine. The gray shaded area is the SE. As with the species-specific Figures 7 and 8, this shows a clear advancement in MDSP (i.e., earlier MDSP) across the years, although there is a reversion back to later MDSP dates in the late 1990's this is then followed by earlier MDSP through 2014.

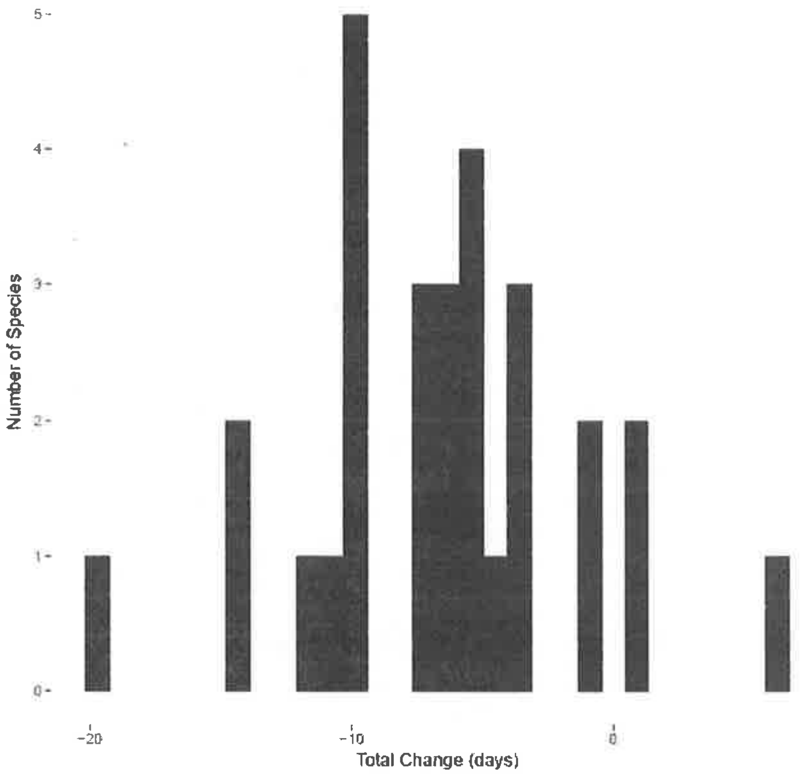

Figure 10. Histogram of the count of species and the estimated total change in the median spring arrival date in a linear mixed-model adjusted for NAO and ENSO.

CHAPTER 3 - DISCUSSION

3.1 The Observed Trend

Human induced climate change's effect on migration phenology is most evident at large temporal scales, such as across multiple decades, as observed in the literature and my own data analysis. Although there is variability in migratory activity on small temporal scales (i.e., hour to hour and day to day), this variation is masked by variation in patterns of migration at greater temporal scales (i.e., week to week, month to month, and year to year). Migration variation is partially a function of broader climatic trends, behavioral responses to environmental conditions, and stochastic factors (Able 1973).

Increasing mean annual temperatures measurably affected arrival times of 26 of the 29 species of spring migrants studied in Maine (Chapter 2), and long term observational datasets more fully elucidate such trends at regional and national scales (Wood et al. 2011). The three species, blue-headed vireo, eastern phoebe, and yellow-bellied flycatcher exhibited stable or later arrival dates for the same period. These three species are insectivores and sally for insects from a perch, although blue-headed vireo may occasionally eat fruits. It is possible that this reliance on insects, especially flying insects, may affect the plasticity of their migration phenology. These species may have less flexibility in adjusting their migration because of their reliance on a seasonally abundant food resource and a specific foraging method. Although, other factors including underrepresentation in the dataset caused by observation bias in the case of the yellow-bellied flycatcher, which is more difficult to identify and observe than many of the other species evaluated.

Changes in spring arrival dates can be linked directly to anthropogenic climate change when accounting for NAO and other abiotic variables (Laaksonen and Lehikoinen 2013, Usui et al. 2017). However, some studies do not reveal clear causal factors and are confounded by constraints on behavioral plasticity and demographics (Marra et al. 2005, Wilson 2007 Miller-Rushing et al. 2008).

In my quantitative data exploration, I found variation in the effect of year on median spring arrival dates, but in general I demonstrated an approximately -0.18-day change in median arrival date per year across all species during the study period.

The different modeling methods employed in my data exploration yielded slightly different results, which reflect variability also observed in the literature. Simple linear regression models for each individual species demonstrated a clear trend toward earlier MDSP over time among most species. Ward et al. (2016) demonstrated a similar average response, among all species studied of -0.12 days per year also using a simple-linear regression approach. The multivariate model resulted in a -0.19 change in MDSP per year during the study period. This model did not account for differences in individual species' migration strategy and phenology (e.g., some species arrive earlier than other species each year), which, for example, Laakosonen and Lehikonen's 2013 paper did account for, but Bradley et al.'s 1999 work did not. It's possible that by accounting for variation in relative migration behavior across species (e.g., accounting for earlier and later migrating species) I may have had different results; however, variation in MDSP was so consistent for 26 of the 29 species, it's probable that even if I accounted for the species specific migration behavior I would have observed the same trend in MDSP.

Results of the linear mixed-model were not substantially dissimilar to the multivariate and simple linear regression models and documented a change in median arrival date of approximately -0.19 days per year across all species. In the linear mixed-model, I combined fixed and random effects similar to Miller-Rushing et al.'s (2008) study, resulting in a more accurate standard error. When I accounted for confounding variables such as NAO and ENSO, I ended up with a reduced estimate of change in annual arrival date of -0.11 days per year. Many studies in Usui et al.'s (2017) meta-analysis accounted for these same confounding factors. When I included other variables, such as temperature and precipitation, the estimate of annual change in MDSP reverted back to the estimate observed in the simple linear regression models, approximately -0.18 days per year. The average model resulted in a similar coefficient for year, of -0.197 days per year (or -1.97 days per decade) during the study period, which demonstrates that NAO and ENSO may have a larger effect on MDSP than other weather variables, but that year is still the driving force behind the observed advancement in MDSP. The observed advancement in MDSP is consistent with Usui et al. (2017) who concluded in their multi-century meta-analysis that on average most migratory species have advanced spring migration by 2.1 days per decade. Both my data analysis and Usui et al. (2017) demonstrate that advancements in migration phenology is driven by year, which is a manifestation of climate change.

The trend of declining MDSP is evidence of the large-scale effect of global climate change driving median arrival date across years and decades. The variation observed across years in the late 1990s where the trend in MDSP changes from negative to positive for a period of approximately 8 years may be a result of variation in small-scale weather conditions or more likely in intermediate-scale phenomenon of ENSO and NAO. For example ENSO was particularly strong in 1998.

3.2 Implications of the Trend

Each year migrants experience effects of a changing climate at wintering grounds, during migration, and upon arrival at breeding grounds. As clearly demonstrated, climate and weather conditions vary on local, regional, and global scales (Meentemeyer 1989) and may change hourly, daily, or at much longer temporal intervals (Emanuel et al. 1985). Numerous studies support advancement of spring migration phenology as a result of human induced climate change, although the magnitude of different species' response to climate change varies based on their migration strategy, foraging behavior, and other life history traits (Usui et al. 2017).

Effects of climate change on the phenology of spring migration have been observed on 5 continents (Morris et al. 1994, Hurrell 1995, Morris et al. 2003, Wood et al. 2011, Usui et al. 2017). These changes in arrival times have implications for individual survival and population viability, because arrival times are often associated with changes in reproductive success (Saino et al. 2010). Declines in populations of long-distance migratory birds in the northern boreal forests of Finland have been linked to climate change (Laakosonen and Lehikonen 2013). Late arrivals are less competitive at finding mates, and they may have arrived at a time when typically, seasonally abundant food resources are not at peak availability (Laakosonen and Lehikonen 2013). The consequences of changes in spring migration phenology on fitness are poorly understood because of complex demographic factors (e.g., recruitment and emigration) that confound attempts to link changes in phenology and population declines (Hurrell 1995, Wood et al. 2011).

Laakosonen and Lehikonen (2013) studied population growth trends of 94 boreal bird species in multiple habitats in Finland to determine effects of climate change and corresponding changes in habitat on species of conservation concern. The researchers collected data from 1986 - 2012 using traditional point count observational methods during the spring breeding period (May 20 - June 20). Laakosonen and Lehikonen divided the species into seven migratory classes and compared them across eight habitat types. The researchers then developed general linear models of population size and growth, with habitat and migratory strategy as covariates. They concluded that long-distance migrants and species with northern distributions had the lowest population growth. They attributed the lower rate of population growth to long-distance migrants becoming out of sync with the phenology of seasonally abundant food resources at breeding grounds (Laakosonen and Lehikonen 2013). These observed reductions in population growth rates of long-distance migrants may be a consequence of the observed advancement in arrival dates for long-distance migrants arriving and breeding in Maine. I observed earlier arrival dates for 90% of the long and middle distance migrants.

There are likely to be severe consequences from earlier migration if birds arrive on spring breeding grounds too early or too late relative to peak food resource availability (Usui et al., 2017, Laakosonen and Lehikonen 2013). For example, the timing of leaf out, a major ecological event in temperate forest ecosystems, coincides with an increase in availability of invertebrate prey species. If migrants time their arrival with leaf out incorrectly, population growth rates may be reduced. Birds that feed invertebrate prey to their young may experience strong selective pressure to track changes in the timing of leaf out.

Other research has explored biological constraints on migratory behavior, which can result in birds becoming maladapted to a rapidly changing climate. Timing of spring arrival and physical condition of birds when they arrive on the breeding grounds are important determinants of reproductive success and fitness. Pied flycatchers (*Ficedula hypoleuca*) can adapt migration and breeding to climate and weather conditions, but this adaptation can be masked by physical migratory constraints (Both 2010). Both explains that although migrants have been repeatedly observed arriving earlier to breeding grounds, earlier arrival dates do not necessarily correspond to individuals breeding earlier (Both 2010). Both observed strong evidence of earlier migration departure dates, but earlier departure dates were not strongly related to earlier arrival dates at breeding grounds, which was attributed to the confounding factors of environmental constraints encountered during migration (Both 2010). Earlier arrival dates seem to occur but are not always associated with earlier departure dates, suggesting that the complexities of migration *en route*, and not just at departure or arrival, can be a confounding factor in our understanding of climates' effect on passerine migration. This conclusion is similar to Hüppop and Hüppop's research (2003), which suggests that adaptation to climate change is primarily a manifestation of phenotypic plasticity and not necessarily evidence of emerging changes in genotypes as expected if selection were occurring (Charmantier and Gienapp 2014). As climate change intensifies (Delworth et al. 2016), new research may explain the relationship between changing weather patterns, migratory behavior, and breeding success.

Effects of climate change on the phenology of spring migration will continue to be observed throughout the Northern Hemisphere, and given the potential for changes in selective pressure on earlier migrants, greater plasticity in migratory behavior may manifest. Selective pressures due to climate change also may occur on a rapid time-scale, consistent with the pace of climate change, and some bird populations may not be successful in fully adapting to the changing climate.

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APPENDIX A

Appendix A. Table 1.

Mid-Distance Migrants

Common Name	Species Name
Brown Thrasher	*Toxostoma rufum*
Eastern Towhee	*Pipilo erythrophthalmus*
Hermit Thrush	*Catharus guttatus*
Northern Flicker	*Colaptes auratus*
Palm Warbler	*Setophaga palmarum*
Song Sparrow	*Melospiza melodia*
Swamp Sparrow	*Melospiza georgiana*
White-throated Sparrow	*Zonotrichia albicollis*
Yellow-rumped Warbler	*Setophaga coronata*

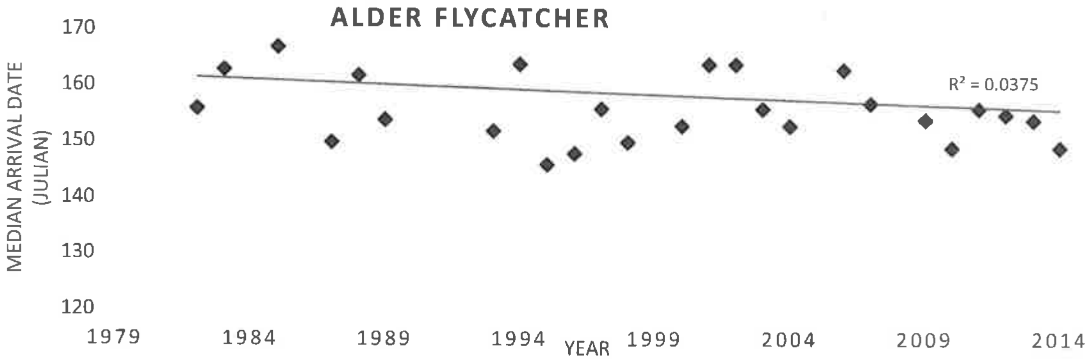
Long-Distance Migrants

Common Name	*Species Name*
Alder Flycatcher	*Empidonax alnorum*
American Redstart	*Setophaga ruticilla*
Black-and-white Warbler	*Mniotilta varia*
Blackburnian Warbler	*Setophaga fusca*
Blackpoll Warbler	*Setophaga striata*

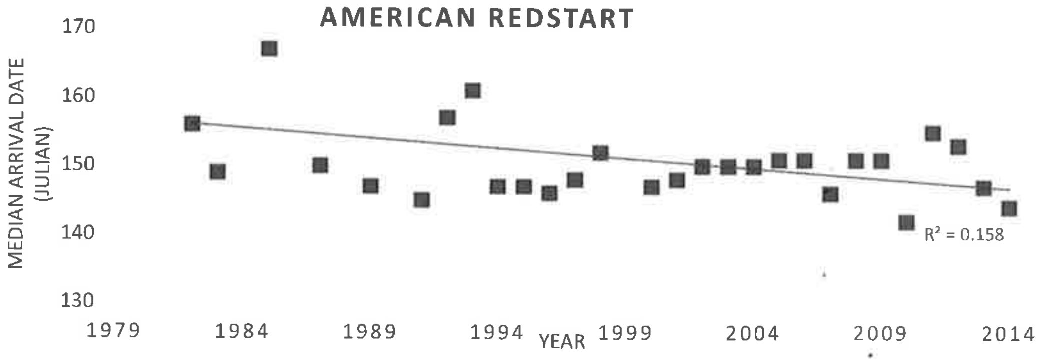
Black-throated Blue Warbler	*Setophaga caerulescens*
Black-throated Green Warbler	*Setophaga virens*
Blue-headed Vireo	*Vireo solitarius*
Chimney Swift	*Chaetura pelagica*
Cliff Swallow	*Petrochelidon pyrrhonota*
Eastern Kingbird	*Tyrannus tyrannus*
Eastern Phoebe	*Sayornis phoebe*
Least Flycatcher	*Empidonax minimus*
Magnolia Warbler	*Setophaga magnolia*
Nashville Warbler	*Oreothylpis ruficapilla*
Northern Parula	*Setophaga americana*
Ovenbird	*Seiurus aurocapilla*
Ruby-throated Hummingbird	*Archilochus colubris*
Scarlet Tanager	*Piranga olivacea*
Yellow-bellied Flycatcher	*Empidonax flaviventris*

Appendix A. Table 2.

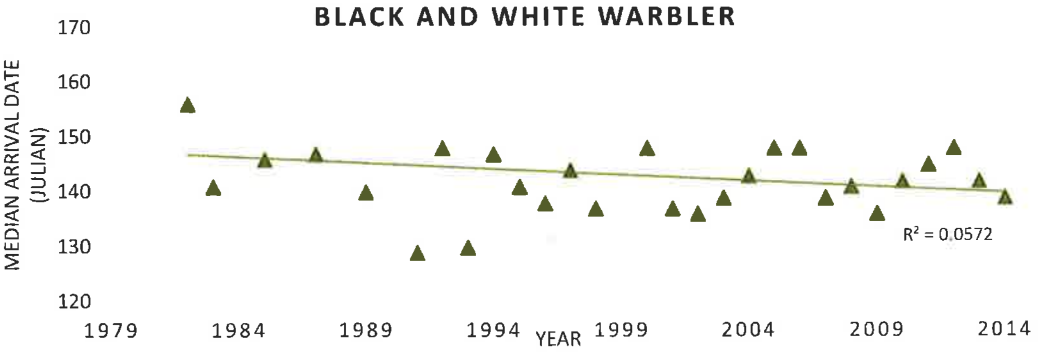
Variable	Climate Extremes Index Per Spring (Mar. - May)	Northern Atlantic climate index	Pacific climate index	Extreme Maximum Temperatures Above Normal Per Spring	Extreme Maximum Temperatures Below Normal Per Spring	Extreme Minimum Temperatures Above Normal Per Spring	Extreme Minimum Temperatures Below Normal Per Spring	Wet/Dry Conditions Less Even in Region Per Spring	Wet/Dry Conditions More Even in Region Per Spring	Abnormally Frequent Precipitation-Spring	Abnormally Infrequent Precipitation-Spring
Climate Extremes Index Per Spring (Mar. - May)	1.000	0.088	0.116	0.089	-0.229	0.424	-0.049	-0.069	0.097	-0.114	-0.544
Northern Atlantic climate index	0.088	1.000	0.981	-0.247	0.053	0.200	-0.003	0.460	0.328	0.086	-0.076
Pacific climate index	0.116	0.981	1.000	-0.232	0.022	0.227	-0.017	0.437	0.353	0.083	-0.082
Extreme Maximum Temperatures Above Normal Per Spring	0.089	-0.247	-0.232	1.000	-0.038	0.108	0.149	0.015	-0.181	-0.164	-0.132
Extreme Maximum Temperatures Below Normal Per Spring	-0.229	0.053	0.022	-0.038	1.000	-0.091	0.603	-0.109	-0.170	-0.210	-0.212
Extreme Minimum Temperatures Above Normal Per Spring	0.424	0.200	0.227	0.108	-0.091	1.000	-0.027	0.031	-0.171	-0.239	-0.213
Extreme Minimum Temperatures Below Normal Per Spring	-0.049	-0.003	-0.017	0.149	0.603	-0.027	1.000	0.146	-0.315	-0.354	-0.105
Wet/Dry Conditions Less Even in Region Per Spring	-0.069	0.460	0.437	0.015	-0.109	0.031	0.146	1.000	-0.189	-0.333	0.013
Wet/Dry Conditions More Even in Region Per Spring	0.097	0.328	0.353	-0.181	-0.170	-0.171	-0.315	-0.189	1.000	0.515	-0.008
Abnormally Frequent Precipitation-Spring	-0.114	0.086	0.083	-0.164	-0.210	-0.239	-0.354	-0.333	0.515	1.000	0.377
Abnormally Infrequent Precipitation-Spring	-0.544	-0.076	-0.082	-0.132	-0.212	-0.213	-0.105	0.013	-0.008	0.377	1.000



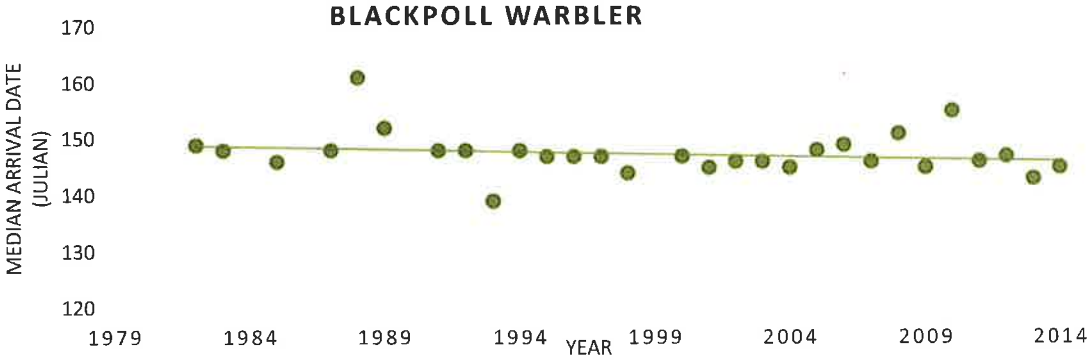
Appendix Figure 1. Alder Flycatcher median arrival dates by year 1979 - 2014



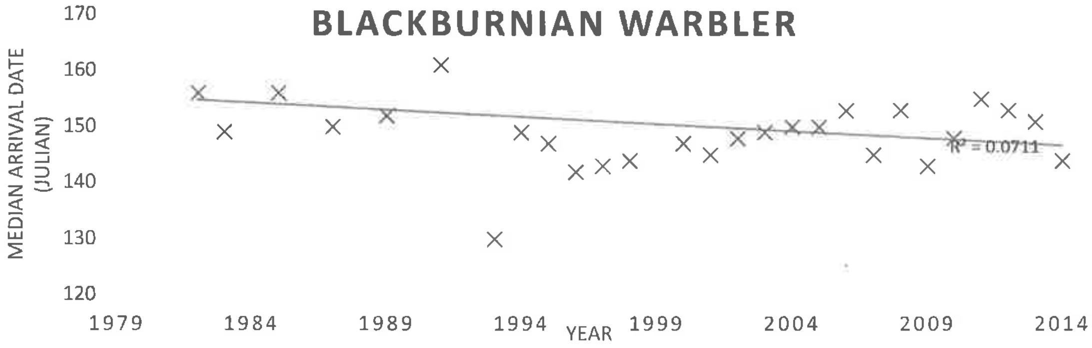
Appendix Figure 2. American Redstart median arrival dates by year 1979 - 2014



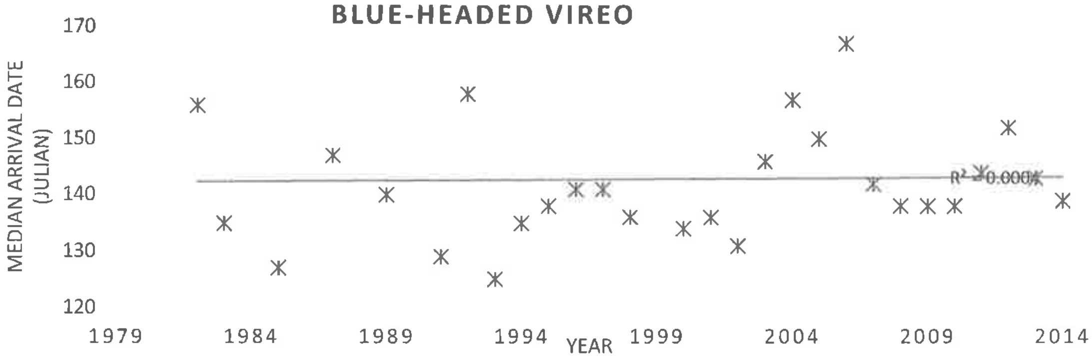
Appendix Figure 3. Black and White Warbler median arrival dates by year 1979 - 2014



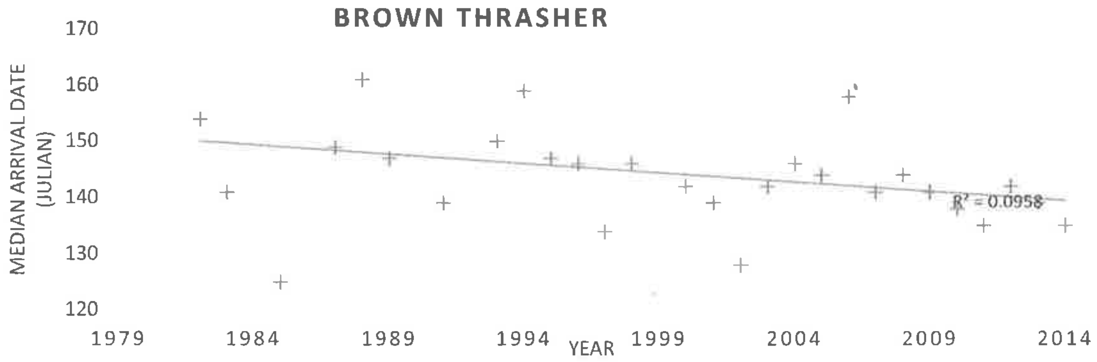
Appendix Figure 4. Blackpoll Warbler median arrival dates by year 1979 - 2014



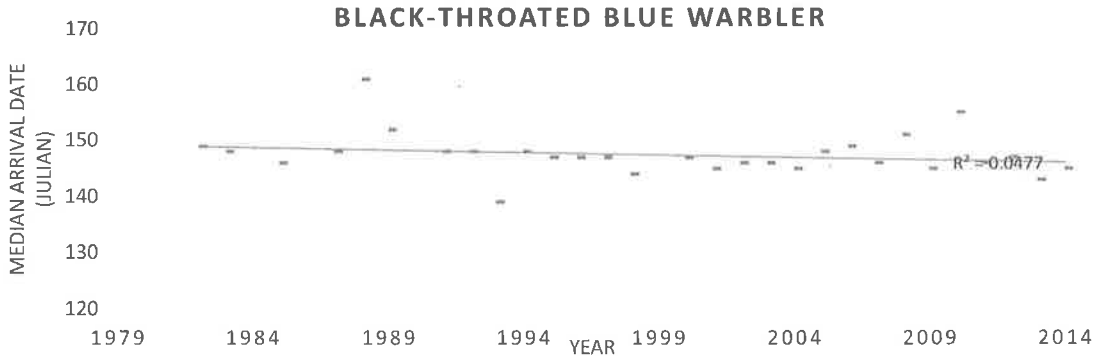
Appendix Figure 5. Blackburnian Warbler median arrival dates by year 1979 - 2014



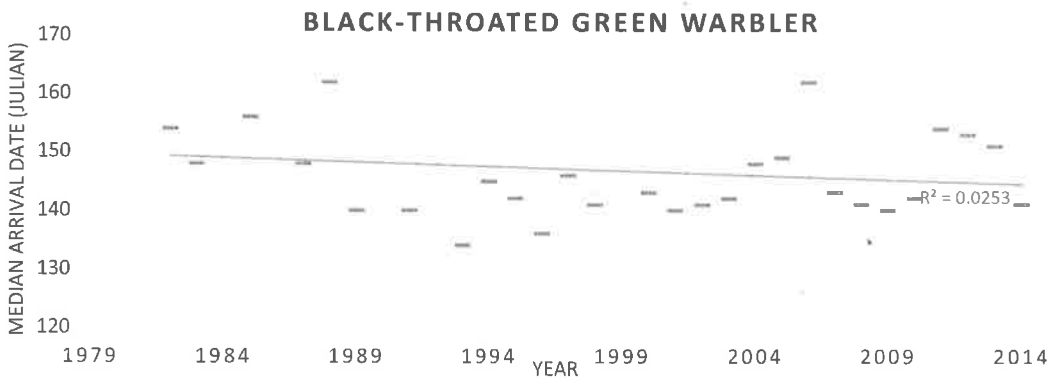
Appendix Figure 6. Blue-Headed Vireo median arrival dates by year 1979 - 2014



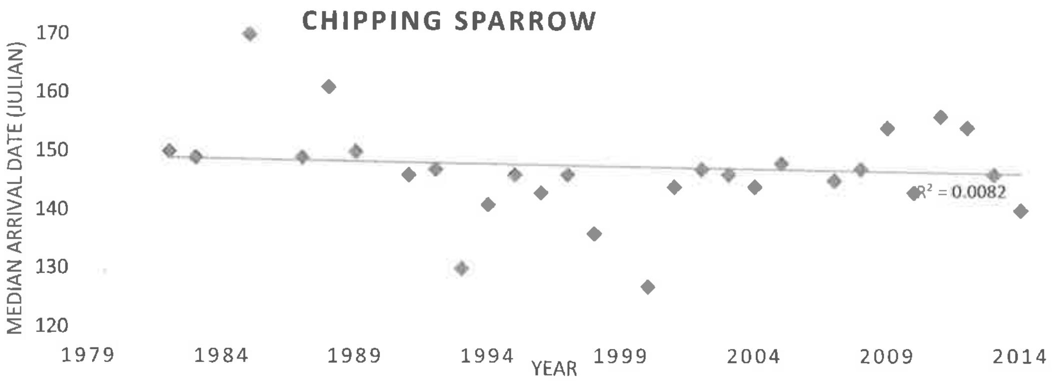
Appendix Figure 7. Brown Thrasher median arrival dates by year 1979 - 2014



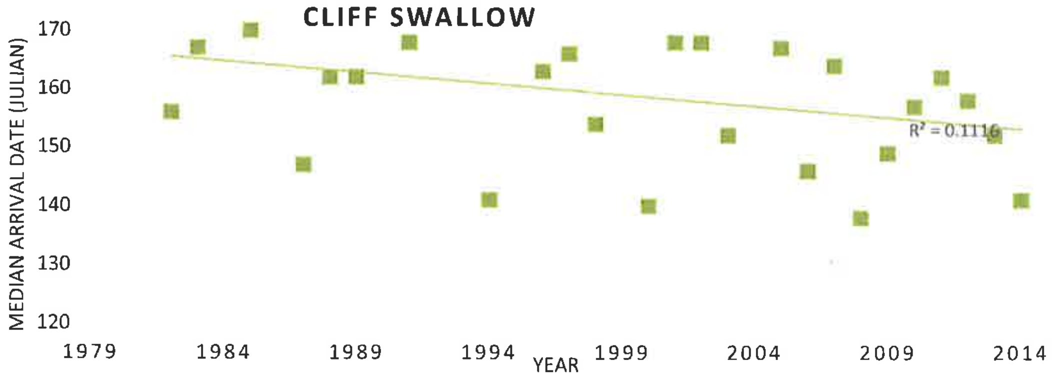
Appendix Figure 8. Blue-Throated Blue Warbler median arrival dates by year 1979 - 2014



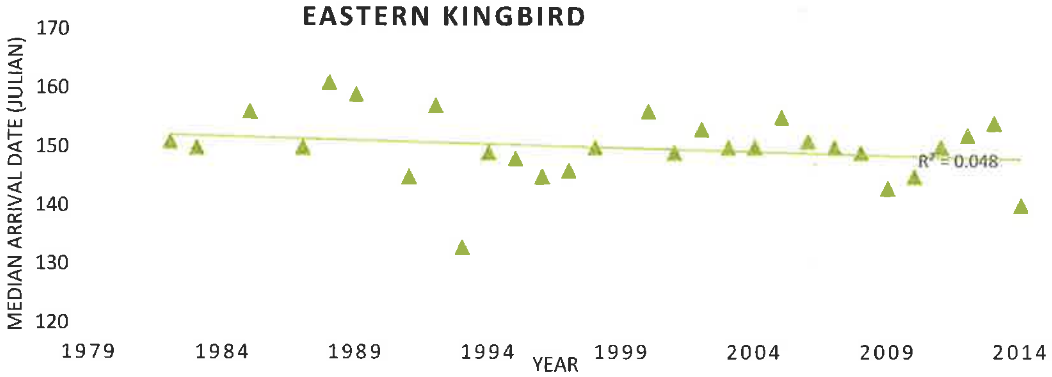
Appendix Figure 9. Black-Throated Green Warbler median arrival dates by year 1979 - 2014



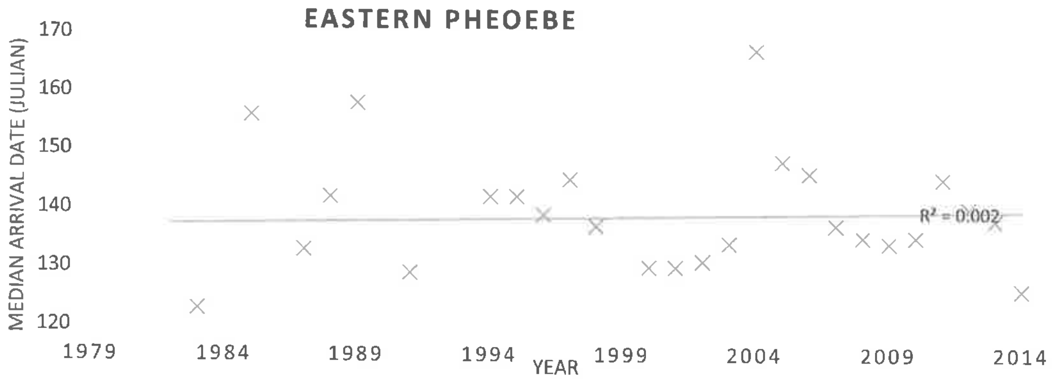
Appendix Figure 10. Chipping Sparrow median arrival dates by year 1979 - 2014



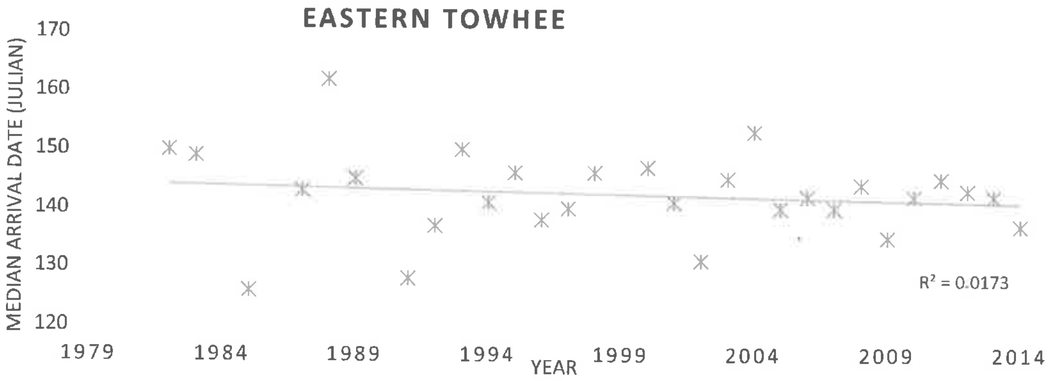
Appendix Figure 11. Cliff Swallow median arrival dates by year 1979 - 2014



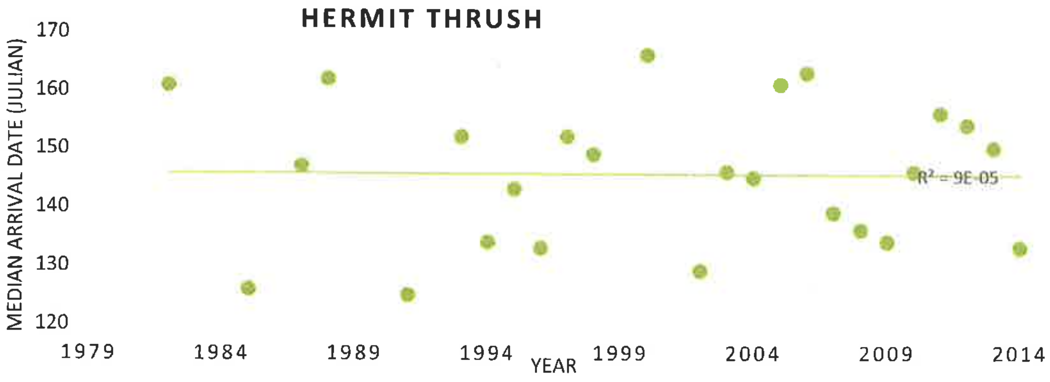
Appendix Figure 12. Eastern Kingbird median arrival dates by year 1979 - 2014



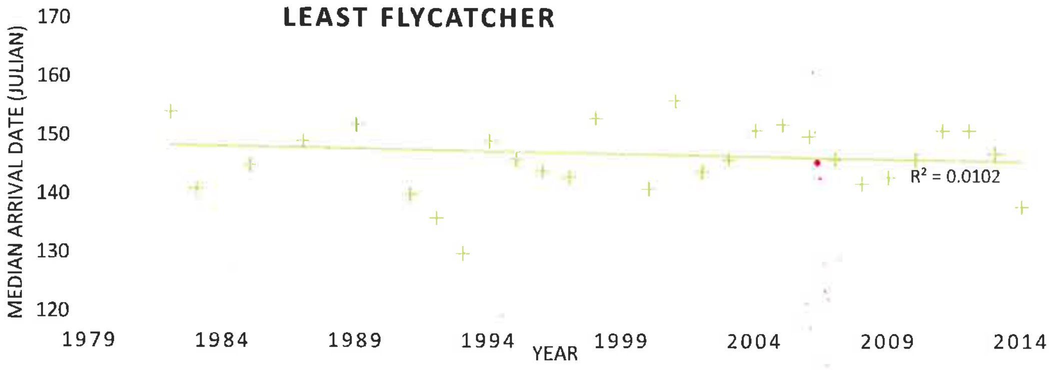
Appendix Figure 13. Eastern Phoebe median arrival dates by year 1979 - 2014



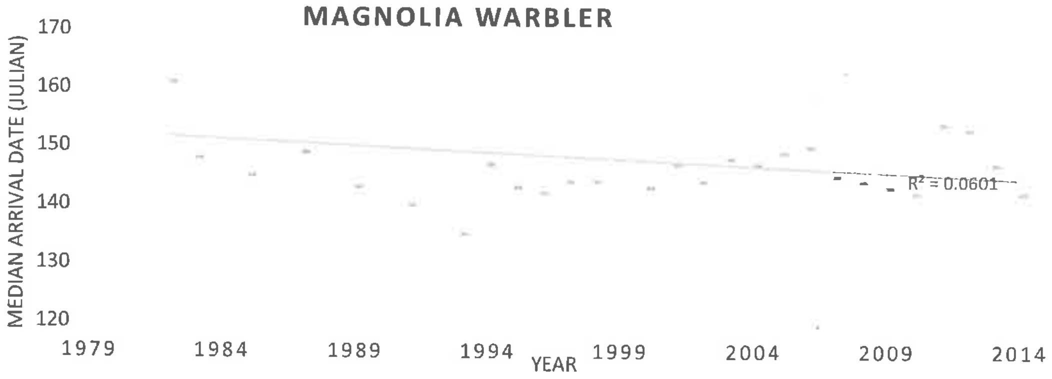
Appendix Figure 14. Eastern Towhee median arrival dates by year 1979 - 2014



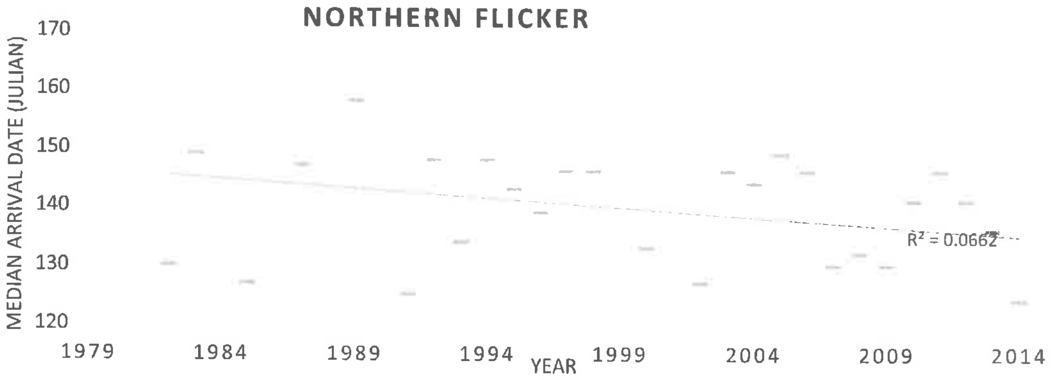
Appendix Figure 15. Hermit Thrush median arrival dates by year 1979 - 2014



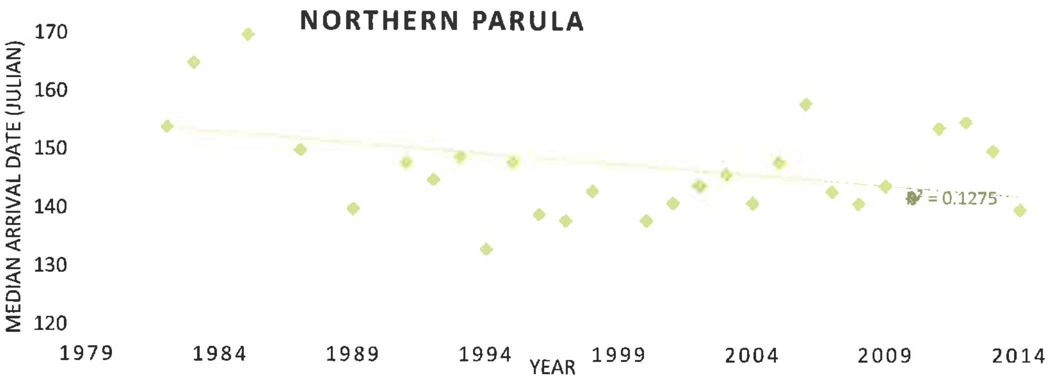
Appendix Figure 16. Least Flycatcher median arrival dates by year 1979 - 2014



Appendix Figure 17. Magnolia Warbler median arrival dates by year 1979 - 2014



Appendix Figure 18. Northern Flicker median arrival dates by year 1979 - 2014

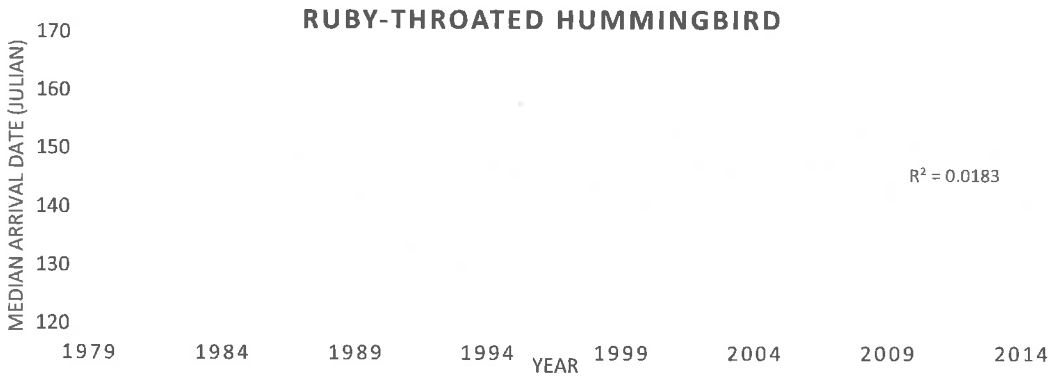


Appendix Figure 19. Northern Parula median arrival dates by year 1979 - 2014

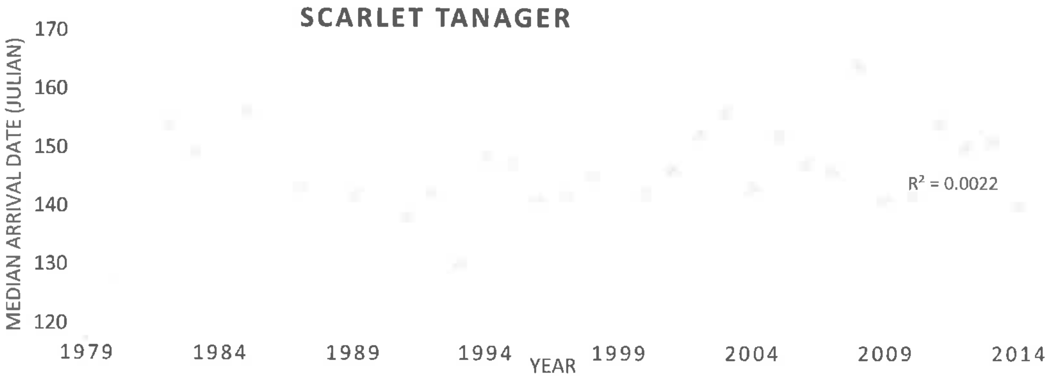
Appendix Figure 20. Nashville Warbler median arrival dates by year 1979 - 2014

Appendix Figure 21. Ovenbird median arrival dates by year 1979 - 2014

Appendix Figure 22. Palm Warbler median arrival dates by year 1979 – 2014

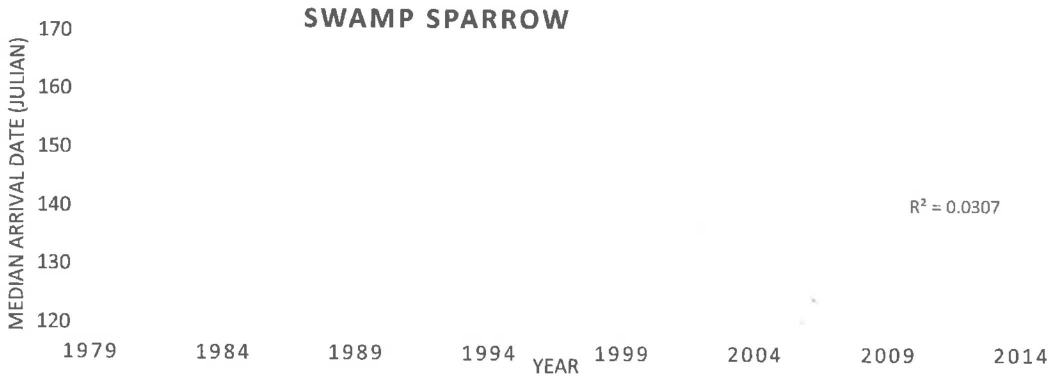


Appendix Figure 23. Ruby-Throated Hummingbird median arrival dates by year 1979 - 2014

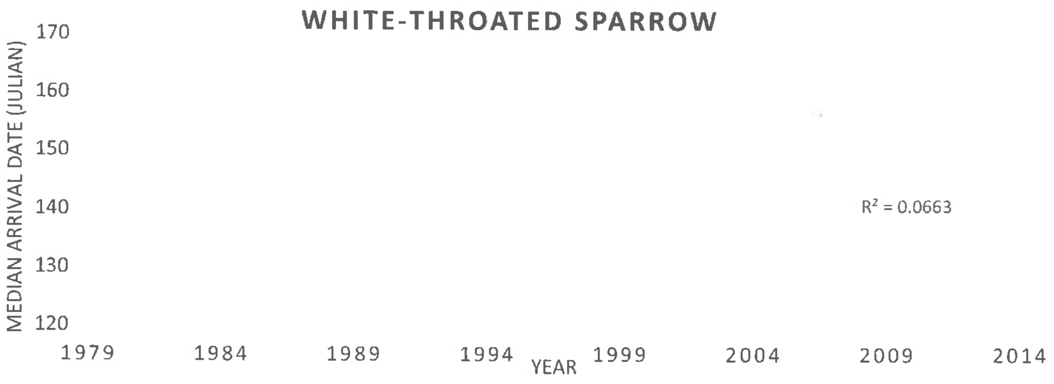


Appendix Figure 24. Scarlet Tanager median arrival dates by year 1979 – 2014

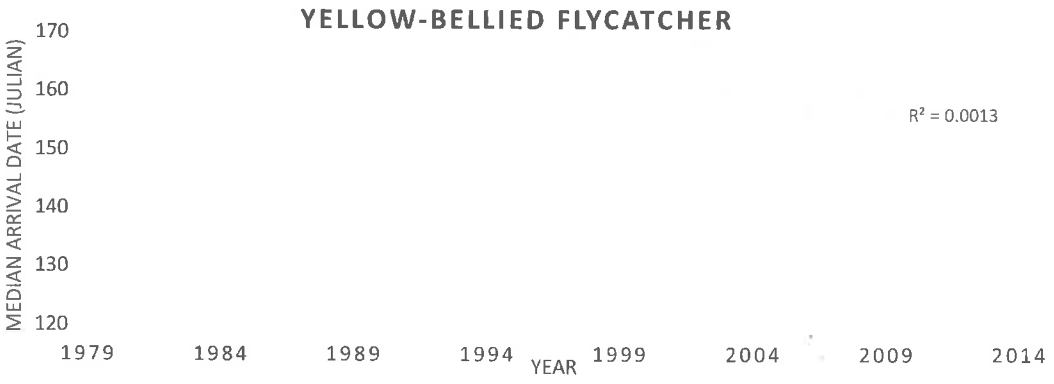
Appendix Figure 25. Song Sparrow median arrival dates by year 1979 - 2014



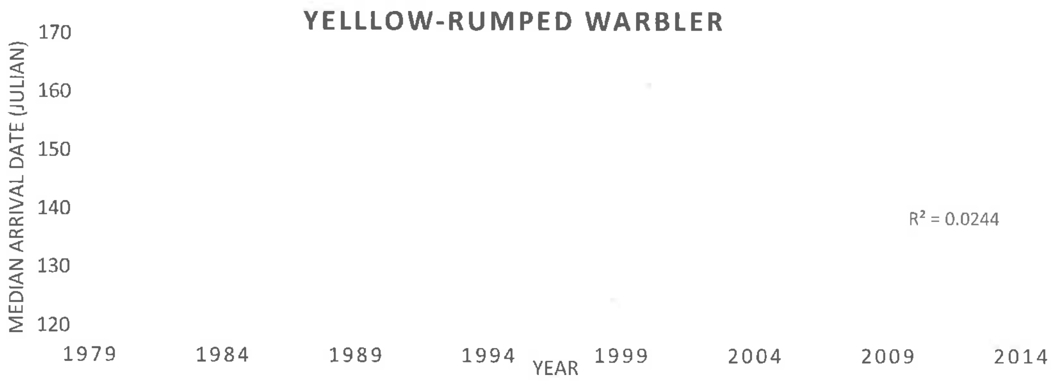
Appendix Figure 26. Swamp Sparrow median arrival dates by year 1979 – 2014



Appendix Figure 27. White-Throated Sparrow median arrival dates by year 1979 - 2014



Appendix Figure 28.Yellow-Bellied Flycatcher median arrival dates by year 1979 – 2014



Appendix Figure 29. Yellow-Rumped Warbler median arrival dates by year 1979 - 2014