Changes in Tree Swallow Phenology Due to Climate Change in Alaska

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Contents

Preface

There are several people I would like to thank for helping me to complete this honors thesis. Steve Matsuoka for getting me involved with studying tree swallows. David Tessler for hiring me to study tree swallows and other bird species. Audrey Taylor for training me in the field. Julie Hagelin for hiring me, introducing the idea for this thesis to me, and helping me along the way. Tricia Blake and April Harding Scurr at the Alaska Songbird Institute for providing me with the data used in this thesis. All of the volunteers that helped to collect the data that I used. My thesis advisers Dan Doak, Alex Cruz, and Dale Miller for statistical, editorial, and general help in writing this thesis.

Abstract

Ecological effects of climate change are beginning to be seen across the globe. In avian species, these effects often manifest in earlier breeding dates. Tree swallows in the temperate zones of North America advanced their laying date by nine days between 1959 and 1991. However tree swallows in more arctic regions, where climate change is occurring more rapidly, have not yet been studied. Additionally, two important climate variables, wind and precipitation, have been largely ignored in climate change studies to date. I used tree swallow nest records from Fairbanks, Alaska to examine how climate change is affecting these birds in the northern part of their range. To provide a more comprehensive view on how tree swallows are being affected by climate change, I looked at effects from wind and precipitation in addition to temperature. I found an advance in laying date and a decrease in incubation time, resulting in a greater advance in hatch date, associated with increasing temperatures and decreasing wind

speeds. I conclude that tree swallows in Alaska are hatching earlier and that this shift is likely caused by increasing temperatures and decreasing wind speeds in May and June.

Introduction

This document is an honors thesis written for the students of the University of Colorado, especially those in Environmental Studies. The purpose of this thesis is to explore the effects of climate on the timing of important reproduction events in tree swallows in Fairbanks, Alaska. It then makes predictions on what may happen to this species as the climate changes in the future. In this work, I test the hypothesis that warming spring temperatures in Alaska have caused tree swallows to start laying their eggs earlier in the season and having shorter incubation times.

Data for this study came from tree swallow nest boxes at two sites in Fairbanks, Alaska between the years 2000 and 2013. The Alaska Department of Fish and Game and the Alaska Songbird Institute installed nest boxes and began monitoring the species in 1999 at Creamer's Field Migratory Wildlife Refuge in Fairbanks, Alaska. A second site was added at the University of Alaska, Fairbanks in 2009. I became involved in 2013 by setting up and monitoring a nest box site on the Joint Base Elmendorf Richardson in Anchorage, Alaska. This site only has one year of data so it will not be used in my analysis.

Data were collected mainly by citizen scientists who volunteered to help with this study. The relevant data collected were the date of first egg laying for each active next box (laying date), the date that the chicks hatched for each active nest box (hatch date) and the number of eggs in each nest (clutch size). I used regression and AIC analyses to ask whether these dependent variables can be predicted by different climatic factors that vary between years, including temperature, wind and precipitation.

Background

Climate change is an important factor to consider in any attempt to predict the behavior of individuals or the dynamics of entire populations. There is substantial evidence that climate change is already affecting many species throughout the world. These effects include range and phonological shifts (Walther *et al.* 2002).

For bird species, one of the most striking effects of climate change has been the link between increasing spring temperatures and advancement in laying date. This effect has been seen in several species of temperate birds (Dunn and Winkler 1999; Crick *et al.* 1997, Doxa *et al.* 2012, Heath *et al.* 2012, D'Alba *et al.* 2010). Tree swallows, the focal species for my study, advanced their laying date by nine days from 1959 to 1991 in the continental United States (Dunn and Winkler 1999).

My study expands this research into more northern latitudes and uses more recent data. Alaska has warmed twice as fast as the rest of the United States over the past 50 years (EPA 2014; "National Climate Assessment" 2014). While population estimates of tree swallows (*Tachycineta bicolor*) in Alaska are not available, overall tree swallow populations in the continental United States and Southern Canada have declined by 36% since 1966, and the majority of this decline took place in the northern section of the area studied (figure 1) (Sauer *et al.* 2013). It is not clear if these two phenomena are linked, but they provide a strong reason to examine the effects of climate change on this species in Alaska. Based on these data, I hypothesized that there will be a more pronounced change in tree swallow reproductive phenology in Alaska than in the rest of the United States, and also that interannual changes in spring climate will predict these shifts in reproductive events.

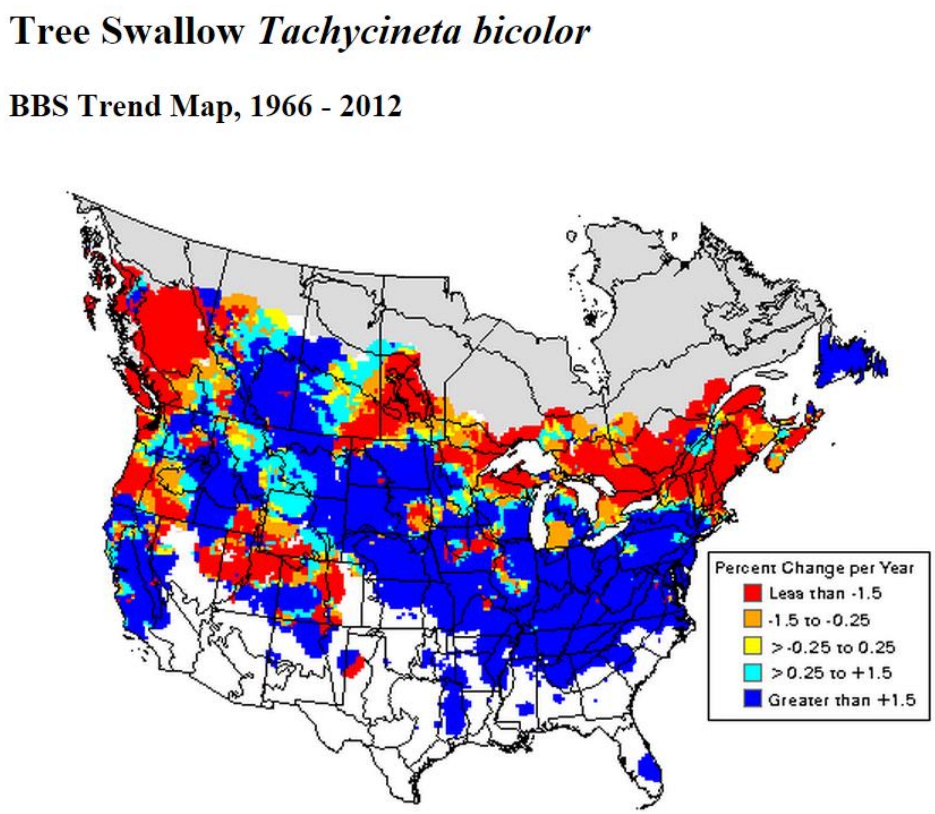


Figure 1 - Image taken from The North American Breeding Bird Survey – Results and Analysis

Tree Swallows

Tree swallows are cavity nesting birds and nest in open areas such as marshes, fields, shorelines and swamps that have standing dead trees. They nest in vacated cavities made by other species and availability of these cavities is often the limiting factor in their reproduction. Tree swallows will therefore readily nest in man-made nest boxes and thus are a very well-studied species and a good candidate for new studies (Robertson et al., 1992).

Tree Swallows primarily eat flying insects, but can also survive on nuts and seeds for extended periods of time, allowing them to spend more time in more northern areas than other species. Their breeding range includes much of the United States and Canada, up to tree line. In the winter they migrate to the southern edge of the United State and Mexico (Robertson et al., 1992).

Tree swallows almost always lay only one brood per season which usually contains between 4 and 7 eggs. They lay one egg per day and usually do not start incubating their eggs until the penultimate egg has been laid, this allows all the eggs to hatch on the same day (Robertson et al., 1992).

Climate Change

Generally, the energy entering and leaving the planet is within a similar range. When this balance is upset, the climate changes. Several things can affect this balance, and since the Industrial Revolution, humans have been affecting it by emitting greenhouse gases such as carbon dioxide, methane and nitrous oxide (EPA, 2014). Increased concentrations of these gases in the atmosphere cause an increase in the greenhouse effect, which is partially responsible for warming the earth.

Through the process of evolution, each species on earth has adapted to fit the environment that it inhabits. These adaptations include how species determine when to breed, how they choose a mate, when they migrate and what migratory paths they take (Hoffmann and Sgro, 2011). For this reason, even small changes in the environment can have drastic consequences for organisms. We are already starting to see these consequences, 74-91% of species that have undergone changes in recent years have done so in accordance with climate change predictions (Parmesan and Yohe, 2003). In birds, the main change we are concerned with is advancing phenology, which is the timing of important activities throughout the season (Walther, 2002).

Temperature Changes

Warming temperatures are the most easily observed and most well known effects of climate change. They are also the cause of some of the other effects of climate change.

Temperature changes are especially important in Alaska which is warming at twice the rate of the rest of the United States resulting in an increase of 1.9° C over the past 50 years and the temperature is projected to increase at least that much in the next 50 years (Figure 2) (Overland *et al.* 2014, EPA 2014). In the Northern Hemisphere, the 30-year period from 1983 to 2012 was the warmest in the last 1400 years and the average global land and ocean surface temperature has risen by 0.85° C since 1880 (IPCC, 2014).

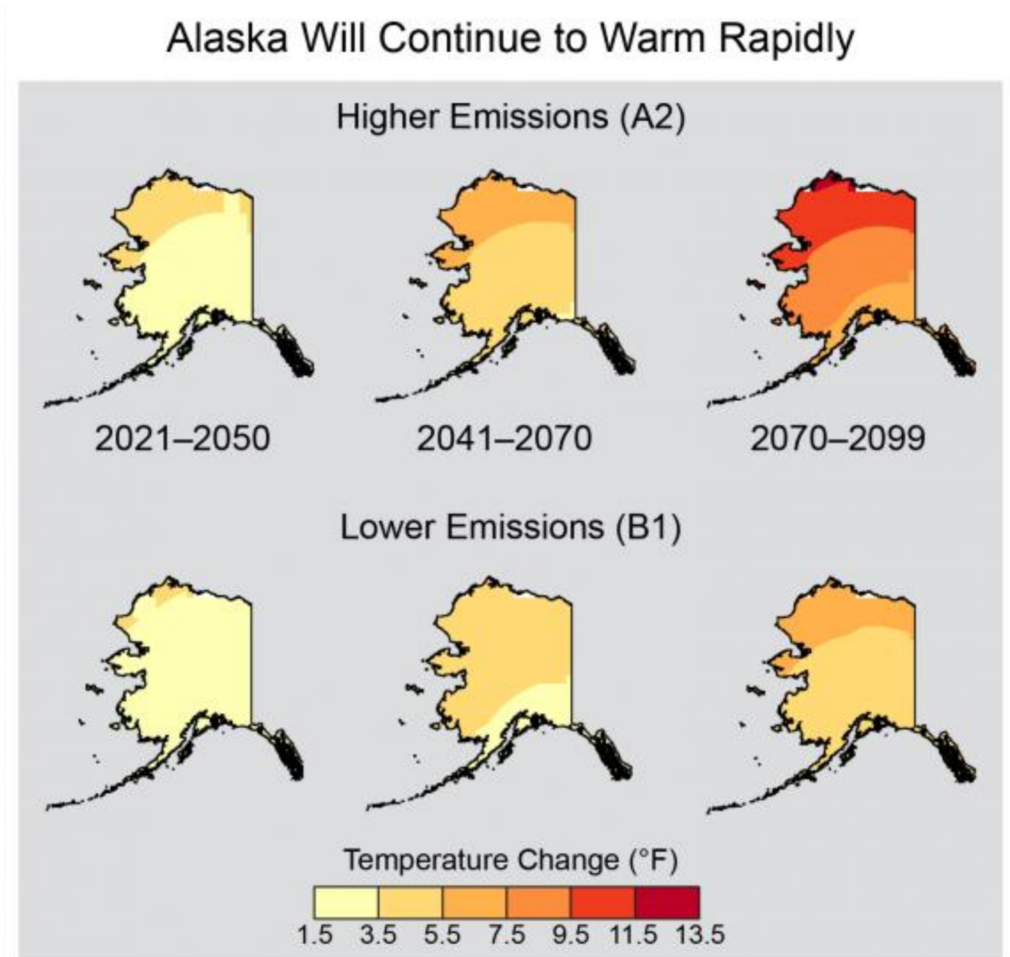


Figure 2 - Image taken from GlobalChange.gov

However, these global averages do not adequately represent the regional changes that are being felt by organisms. Minimum temperatures are increasing twice as fast as maximum temperatures causing a lengthening of freeze-free periods in northern regions and decreasing snow cover and ice extent (Walther et al., 2002) and causing the snow and ice to melt earlier in the season. This affects the hydraulic cycle (IPCC, 2014), and nutrient availability in lakes (Rouse et al., 1997), which could cause changes throughout the ecosystem. In northern regions, climate change is also causing permafrost to thaw which in turn causes lakes and ponds that are not stream-fed to shrink substantially (EPA, 2014).

Precipitation and Water Cycle Changes

Precipitation has not changed significantly in Alaska. Models predict that Alaska will have wetter winters in the future, however warmer summer temperatures will cause more evaporation and dryer summers. Rivers and lakes in the Arctic are in a delicate balance with the water cycle and this balance is easily altered by changes in precipitation and temperature. The spring thaw of snow and ice replenishes lakes and in turn determines the aquatic habitat and nutrients available to organisms in the spring. A warming climate would diminish this spring thaw, and many lakes, ponds and wetlands would likely disappear – causing habitat loss for the species who depend on them. In addition, a longer growing season and warmer temperatures would affect the nutritional, mineral and chemical makeup of lakes and ponds. These changes would cause effects throughout the food chain (Rouse et al., 1997).

Wind Changes

Climate change can also change the large-scale atmospheric circulation. This will have different effects on wind direction and speed throughout the world. There are several models that have tried to predict what the effects on wind speeds will be. Most agree that the Southeast part of Alaska will experience greater wind speeds, while the rest of the state is unclear. There is greater consensus in the models when looking only at the summer months, where it appears that most of the state will experience an increase in wind speeds (figure 3). Even in the areas where the models agree there will be an increase, this increase is expected to be very small (Eichelberger et al., 2008).

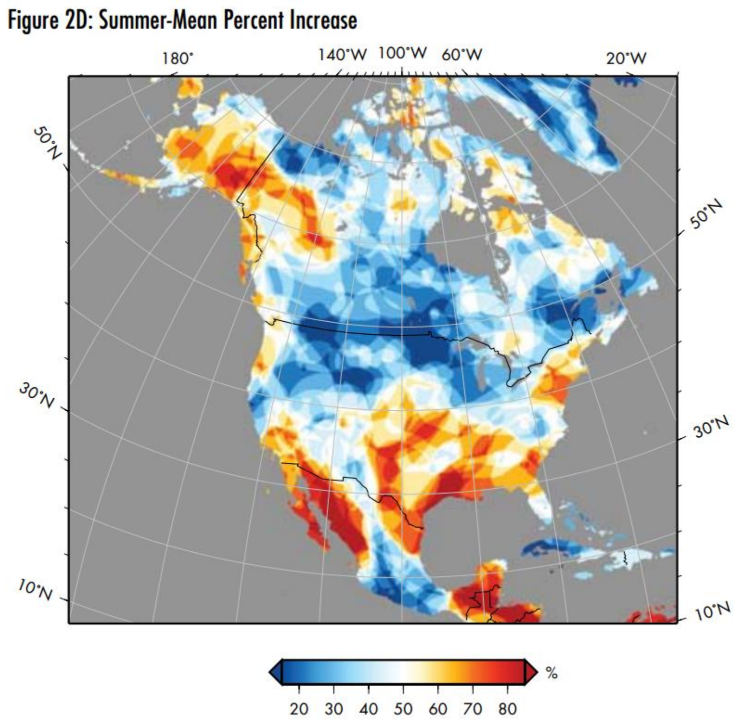


Figure 3 - Projected increase in summer wind speeds. Percentages represent percentage of models that agree that wind will increase.

Image taken from Eichelberger – Climate Change Effects on Wind Speed

Extreme Events

Changes in extreme weather-related events are another aspect of climate change. Since the 1950s the changes we have seen include: a decrease in cold temperature extremes, an increase in warm temperature extremes, an increase in extreme high sea levels and an increase in heavy precipitation (IPCC, 2014). These extremes have important ecological consequences because they can make it more difficult for organisms to survive and reproduce.

Causes of Climate Change

Climate change can be a natural phenomenon, and the earth has experienced much climate variation in its history. However, more than half of the warming we are now experiencing can be attributed to anthropogenic emissions. Since 1750, greenhouse gas emissions, such as carbon dioxide, methane, and nitrous oxide, have been increasing due to human activities. The decade from 2000 to 2010 experienced the highest emissions in history and the concentrations of these gases are the highest they have been in at least 800,000 years (IPCC, 2014).

Literature Review

Climate can influence several different areas of birds' lives including: geographic ranges, seasonal activities, migration patterns, abundances and breeding times (IPCC, 2014; Dunn, 2004; Ardia et al., 2006; Both et al., 2006; Brown and Brown, 2000; Crick et al., 1997; Crick and Sparks, 1999). Of these, timing of breeding is likely the most important factor in reproductive success in birds. It can be influenced by several things including: temperature, body size, diet, life history, and breeding preparation time (Dunn, 2004).

Another important point is that climatic change affects insects, tree swallow's food supply, as well as the swallows themselves. When the insects respond differently to these forces than the birds, it leads to an adaptive mismatch and can have negative results for the birds.

Effects of Temperature Changes on Birds

There have been several studies conducted on the effects that warming temperatures are having on birds species. This is an important factor as temperature is strongly correlated with the timing of breeding (Hussell, 2003) and arrival time for migratory birds (Brown and Brown, 2000). Dunn and Winkler (1999) found that tree swallows advanced their laying date by as much as nine days between 1959 and 1991. The authors hypothesized that this could be due to an advance in peak insect availability as insect abundance is directly related to temperature (Roeder, 1953). Another explanation for this phenomenon could be shortening migration distances, also due to climate change (Visser et al., 2009). In a meta-analysis of similar studies in other bird species, 60% of the studies found a long-term advance in lay dates.

For many species it remains to be seen if rising temperatures will have a negative or positive effect. However, there are some studies that give us insight on this. Ardia et al. (2010) found that experimentally cooling eggs resulted in nestlings that had lower body mass and a lower ability to kill bacteria, even in later developmental stages. Another study found that experimentally heated nestlings had greater survival rates, faster early growth rates and greater body mass than the control (Dawson et al., 2005). These studies suggest that rising temperatures could result in greater success for some species.

Effects of Precipitation Changes on Birds

Precipitation can affect both the arrival time, and laying date of bird species, but is not as strong a force as temperature (Rubolini et al., 2007; Crick and Sparks, 1999; Przybylo et al., 2000; Sayago and MacGregor-Fors, 2010). Migration of birds can also be affected by climate indices such as the North Atlantic Oscillation Index (NAOI) and the Southern Oscillation Index (SOI). These indices include temperature, precipitation and wind speeds, so it can be difficult to determine which of those variables has the greatest effect (Miller-Rushing et al., 2008).

In a study on barn swallows, Sayago and MacGregor-Fors (2010) found that precipitation one month before arrival date in the swallows' wintering grounds had a positive relationship with spring arrival time. They hypothesized that this was due to slowed flying due to the rain.

Effects of Wind Changes on Birds

Wind speed and direction have important implications for migration routes. Data from geolocators (small devices that can be put on birds and used to track their position on the globe) on tree swallows revealed that when migrating south, they travel over the Gulf of Mexico on days when there is a favorable (southern) wind. When the swallows return in the spring, they instead take a much longer, land route to avoid unfavorable winds over the Gulf (Bradley et al.). If wind direction or speed change due to climate change, this could have implications for migrating birds including reduced survival and changing migration times and distances.

When the birds arrive to their destination, wind can still play a role as it affects foraging ability. Since birds need to forage to feed themselves and their young, wind speeds can affect their success (Rose, 2009).

Food Mismatch

Birds time their breeding so that the time that their nestlings hatch lines up with the peak food availability since the nestlings have a very high demand for food (Dunn et al. 2010; Lack, 1968; Visser et al., 1998). This is an important consideration because relative resource abundance is related to larger clutch sizes, (Dunn et al., 2000) and chick development (McCarty and Winkler, 1999).

There is a lot of time between the decision to lay eggs and when the nestlings hatch, so the birds must rely on other cues to decide when to lay (Visser et al., 1998). With warming temperatures and other changes due to climate change, both birds and insects are changing their phenology, however we have no reason to suspect that they may change at the same rate (Visser et al., 2004). Both (2006) found that in bird populations where the insect populations peaked early, the bird population had not advanced enough to match it, and they faced declines up to 90%. Clutch size in tree swallows is affected by food availability so changes in timing or quantity of food availability could affect their breeding success (Winkler et al., 2014).

In some environments, there is not a peak in food supply, but rather a consistent supply throughout the breeding season. In these environments, the timing of egg laying in tree swallows is correlated with the amount of food during laying. In this instance tree swallows are undergoing selection to breed earlier, because earlier breeders generally produce more young, and not because of an earlier peak in food abundance (Dunn et al., 2010). However, if there is food available earlier in the season, this could allow them to breed earlier than would otherwise be possible.

Phenotypic plasticity, the ability of an organism to change its characteristics to fit changes in its environment, is an important factor when considering how species will adapt to climate change, and may allow them to survive in a rapidly changing environment (Gienapp et al., 2013, Nussey et al., 2005). In great tits (*Parus major*), the variation in the individual plasticity of timing of breeding is heritable and selection for more plastic individuals is increasing. As this selection continues, it may help the birds cope with the mismatch between their breeding time and peak food availability (Nussey et al., 2005).

Methods

All methods for data collection follow the protocols in "The Golondrinas Handbook" provided by Golondrians de las Americas ("The Golondrinas Handbook," 2010).

Site Setup

The two study sites used in the study were selected first by visiting areas that looked like favorable tree swallow habitats. These are open areas such as marshes, fields, shorelines and swamps. These areas were visited in the spring, when the swallows first arrived and had not yet made their nests, and then again later in summer when they had nested. Areas with abundant swallows in the spring and few in the summer were selected as study sites, as this indicated that swallows used those areas, but the areas were lacking in breeding cavities. The two sites that provided data for my work are both located in Fairbanks, in central Alaska. These sites are Creamer's Field Migratory Waterfowl Refuge (Creamer's Field) and the University of Alaska Fairbanks (UAF) and were set up in 1998 and 2008, respectively, and data were collected from 2000 and 2009 until 2013.

Nest boxes were constructed in accordance with the Golondrinas de las Americas protocols. They were installed on poles roughly 1.5 meters high, at least 20 meters apart, and away from any shrubs or trees. This placement provides protection from predators as well as ample space for territories. The setup of the sites took place the year before monitoring began, as the boxes could not be installed until late in the season when the ground was not frozen. The Creamer's Field site had 220 nest boxes and the UAF site had 110, although this number varied slightly between years due to damaged or added boxes.

Data Collection

The methods described below are the ideal scenario, however because of staffing shortages and other factors, nests were not always able to be checked as often. In these cases, laying date and hatch date had to be estimated as described below.

Nest Checks

All boxes were checked every three days starting in mid-May. When a nest was found in a box, the stage of the nest was recorded. The nest would then be checked every day until the first egg was laid, this was marked as the laying date. Once laying began, the nest would not be checked again until day eight of incubation, which is the best time to capture the female. The box would then be checked every day until the eggs hatched, this was marked as the hatch date. The box would then be checked every three days to measure the chicks until they were 10 days old.

After the chicks were 12 days old, the box could not be checked anymore for fear of causing the chicks to fledge prematurely.

Due to multiple factors, this schedule was not always followed when nest checks were performed. Because of this, some dates had to be estimated from the contents of the nest. Tree swallows lay one egg per day, therefore it is easy to calculate the laying date of an incomplete clutch by counting back the number of days using the number of eggs in the nest. Hatch date can also be estimated by the predicted hatch date (incubation initiation date plus 12, the average incubation time) and the age of the chicks when the nest is checked. An accuracy number was recorded along with these dates, this was equal to the number of days after the date of recorded nest activity that the nest was observed.

Data Analysis

Each site was considered separately in the models. Only nest records with a date recorded for both laying date and hatch date were used, so that any nests that were abandoned before the chicks hatched would be excluded. Since nest boxes were not checked every day, there were many dates that had to be estimated using the one egg per day rule as explained above. Some boxes that were found with already complete clutches had to be estimated using the hatch date and the average incubation time. To ensure accuracy of these estimates, I ran correlations between laying date and year using all of the data and then using only the data where the accuracy could have been determined using the one egg per day rule. The difference in the output was 0.003 signifying that the dates estimated with less accuracy did not need to be removed from the data set. The final data set included 126 total nest records for UAF and 348 total nest records for Creamer's Field across all the years of the study. All analyses used the individual nests for each year and not the average date across all nests per year.

We tested alternative statistical models to examine the effects of climate on two dependent variables: laying date and incubation duration. Incubation duration was calculated by adding the clutch size to the laying date and subtracting one, since tree swallows usually start to incubate the day before their last egg is laid (Robertson et al., 1992). This number was then subtracted from the hatch date. Clutch size was also used as a predictor for incubation duration because it was used to calculate incubation duration and could therefore have an effect on it.

We regressed laying date on the weather during May and incubation duration on the weather during the incubation period, defined as starting when the first nest at a site started incubation and continuing for three weeks. This period contained the majority of the incubation periods for all nests. I used weather data published on the NOAA website for the weather station at the Fairbanks International Airport. The weather variables used were average daily temperature, average daily precipitation, average daily precipitation squared, average daily wind speed, number of days with precipitation (precipitation days), number of days that were above average windiness (windy days), and number of days that were one standard deviation above average windiness (very windy days), with average windiness being calculated over the 14 years of the study. I also regressed all weather variables on year to look for temporal trends.

To test the support for different weather variables as factors influencing laying date or incubation duration, I created a set of alternative models that contained different weather variables. I started by creating models that only used one weather variable and then combined reasonable variables to build complexity. Lists of all models tested are in the appendix in Tables 1 – 4. I fit each of these different models using the glm function in R, and used AICc values to judge the support for each model. I also calculated summed AICc weights to judge the support for each independent variable across the suite of models. Models were fit separately for each of the two sites because the average laying date was consistently later at UAF than at Creamer's Field. In addition to these results, I report regression coefficients to show the direction of the effect of weather variables. Finally, I regressed both dependent variables against year to quantify the temporal trends in nesting phenology.

Results

Data from this study are presented below in a series of tables for each site and each variable measured.

Summary Tables

	Average Temperature	Average Wind Speed	Average Precipitation	Days with Precipitation	Windy Days	Very Windy Days	Precipitation Squared	Adjusted R-Squared	AICc	k	AICc weight
CF Laying Date	x					x	x	0.169	2030.175	5	0.485
CF Incubation Duration	x	x						0.212	1573.417	4	0.291
UAF Incubation Duration			x		x			0.078	347.43	5	0.185
UAF Laying Date	x	x		x				0.232	672.88	5	0.147

Table 1. Models with lowest AICc values for each scenario

	UAF Laydates	CF Laydates	UAF Incubation Duration	CF Incubation Duration
Average Temperature	0.75	1	0.56	1
Average Wind Speed	0.23	0.01	0.15	0.93
Average Precipitation	0.21	0.34	0.49	0.19
Days with Precipitation	0.47	0.18	0	0.27
Windy Days	0	0	0.72	0.04
Very Windy Days	0.77	0.99	0.09	0
Precipitation Squared	0.43	0.84	0.61	0.42

Table 2. Summed AICc weights

	UAF Laydates	CF Laydates	UAF Incubation Duration	CF Incubation Duration
Average Temperature	-0.24	-0.44	0.003	-0.28
Average Wind Speed	3.58	2.25	0.37	1.4
Average Precipitation	-4.67	1.14	0.19	-0.47
Days with Precipitation	-0.65	0.01	-0.01	-0.1
Windy Days	0.85	0.15	0.08	0.26
Very Windy Days	0.2	0.68	0.06	0.35
Precipitation Squared	-5.55	0.49	-0.26	-0.3

Table 3. Regression Coefficients

May Climate Trends

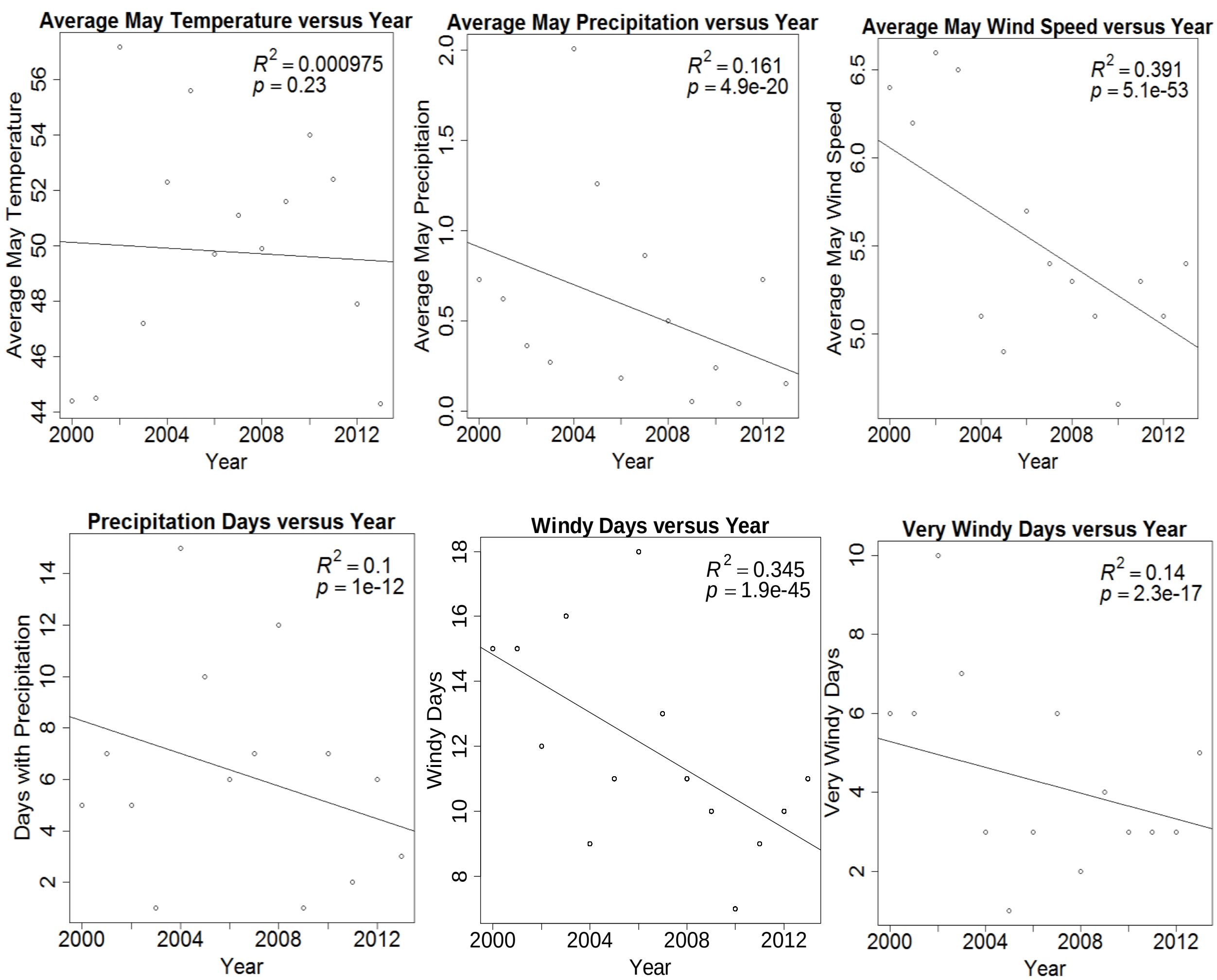


Figure 4. Weather in May over time

Average May temperature in Fairbanks has not increased in the last 14 years, however wind and precipitation have decreased considerably (Figure 4; see figure panels for statistical results). Very windy days decreased less than windy days and average wind.

Laying Dates

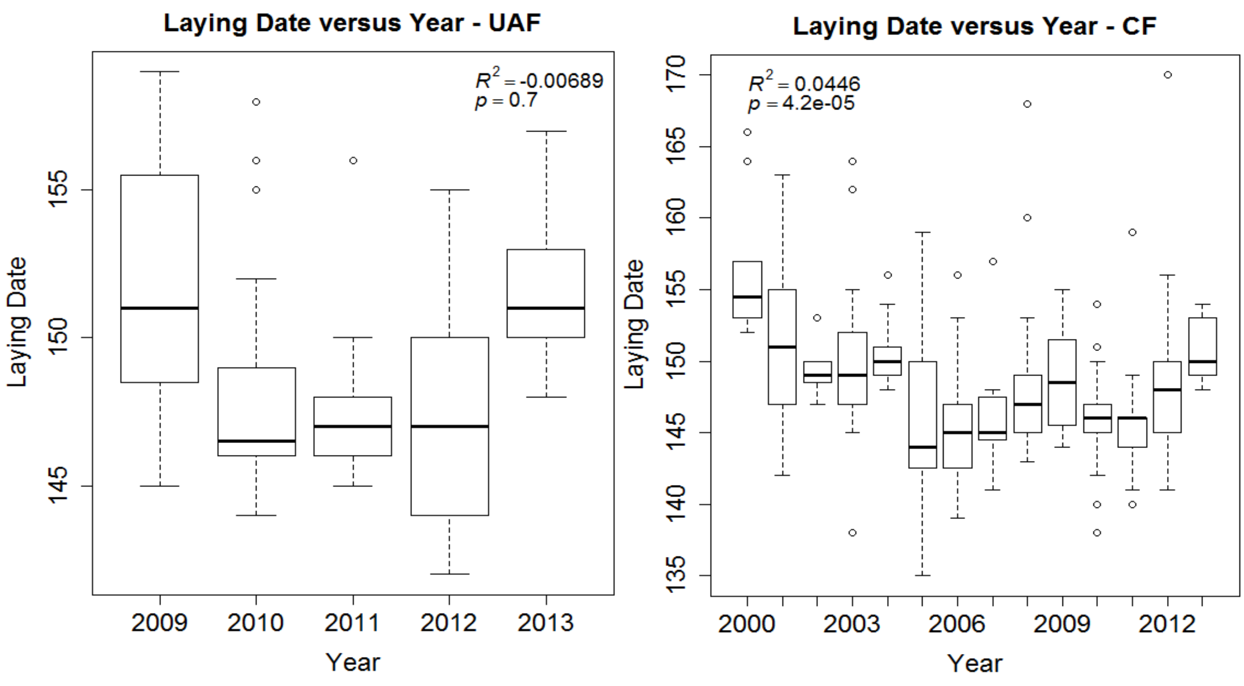


Figure 5. Laying Date over Time for University of Alaska, Fairbanks and Creamer's Field. The box plots show the results for individual nest box data in each year. The r-squared and p-values are from regressing year against laying date.

Laying dates have not advanced significantly over time at UAF and have advanced very little over time at Creamer's Field (Figure 5, see figure panels for statistical results).

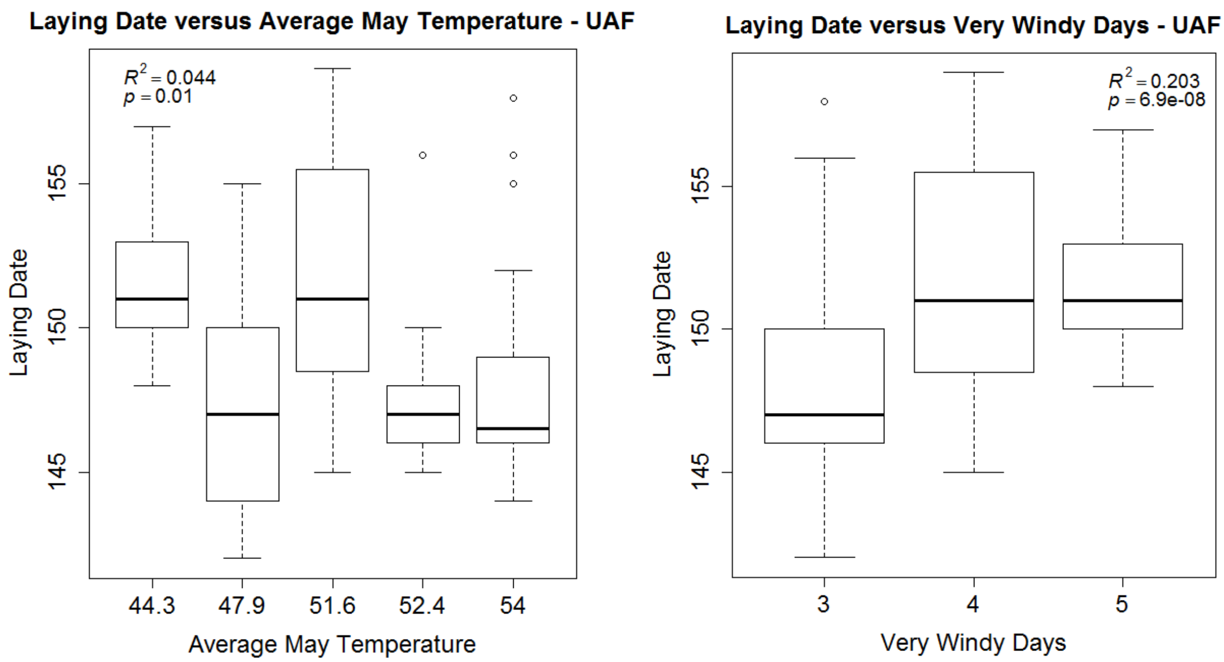
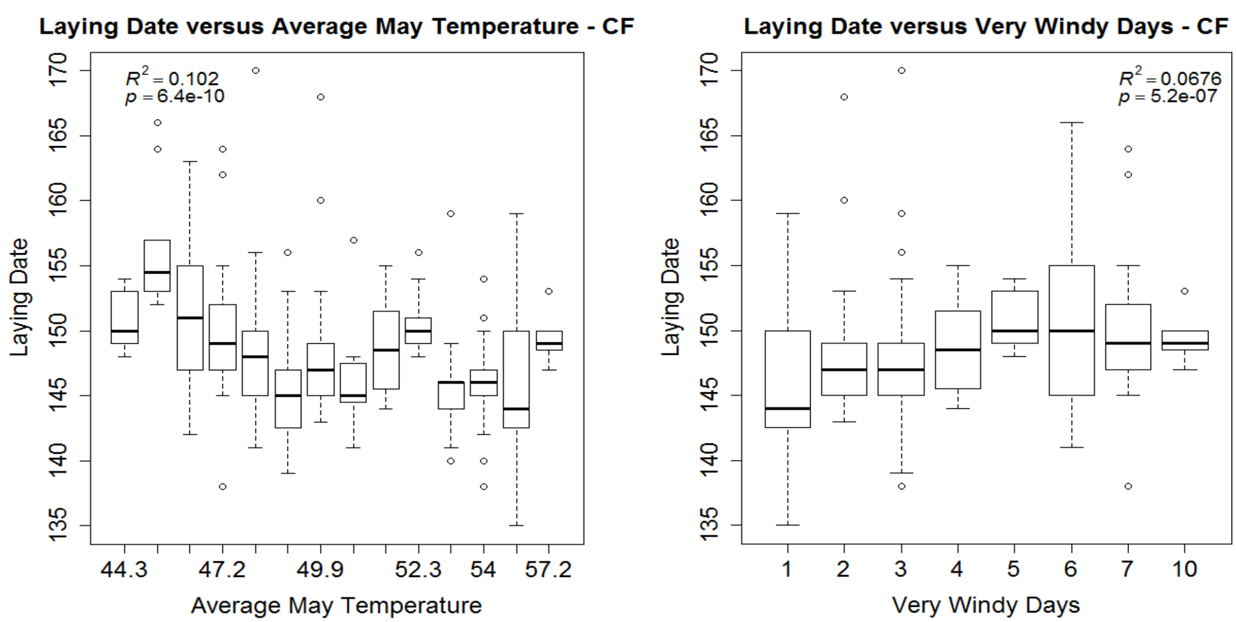


Figure 6. Laying date versus climate variables – University of Alaska, Fairbanks. The box plots show the results for individual nest box data in each year. The r-squared and p-values are from regressing temperature and then very windy days separately against laying date.



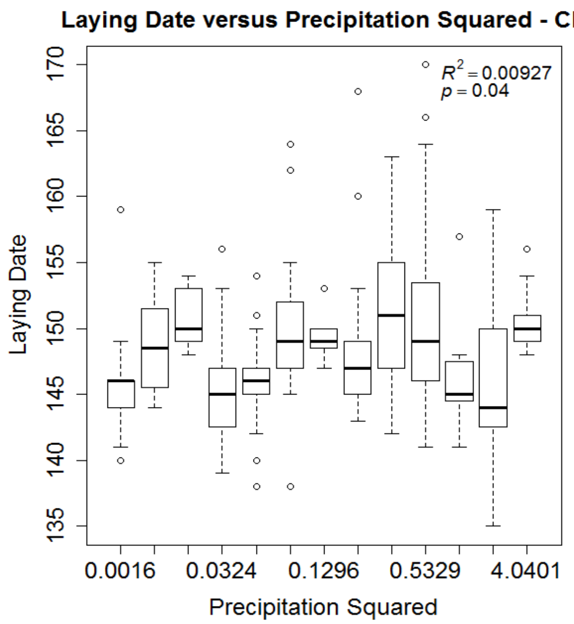


Figure 7. Laying date versus climate variables – Creamer's Field Migratory Waterfowl Refuge. The box plots show the results for individual nest box data in each year. The r-squared and p-values are from regressing temperature, very windy days, and precipitation squared separately against laying date.

All of the best models (models with low AICc values) for both sites include a negative effect of temperature, signifying that increased temperatures cause earlier laying dates (Figures 6 and 7, see figure panels for statistical results). The majority of the best models also include the number of very windy days (days with wind speeds more than one standard deviation above the average) as a positive effect, signifying that increased windiness causes laying dates to be later (Figures 6 and 7). Precipitation did not show as strong an effect. The UAF site had a negative effect of number of days with precipitation (Table 3). In contrast, the Creamer's Field site saw stronger support for a positive quadratic effect of average precipitation than for a positive linear effect of average precipitation and little support for a positive effect of days with precipitation (Figure 7, Tables 2 and 3).

Incubation Period Climate Trends

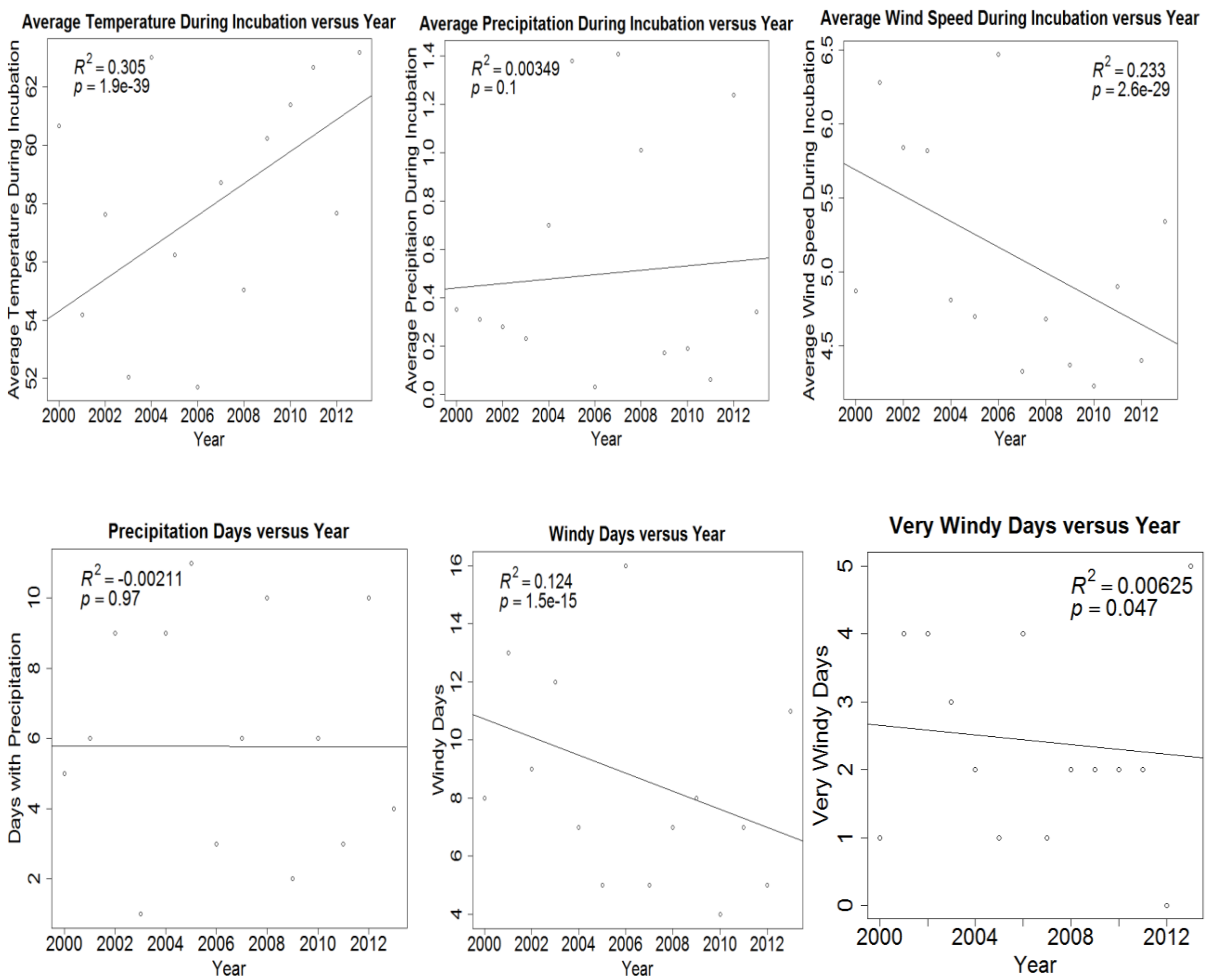


Figure 8. Weather during the incubation period over time

During the incubation period, temperature has increased, while precipitation has stayed largely the same and wind has decreased (Figure 8, see figure panels for statistical results). Very windy days decreased less than windy days and average wind.

Incubation Duration

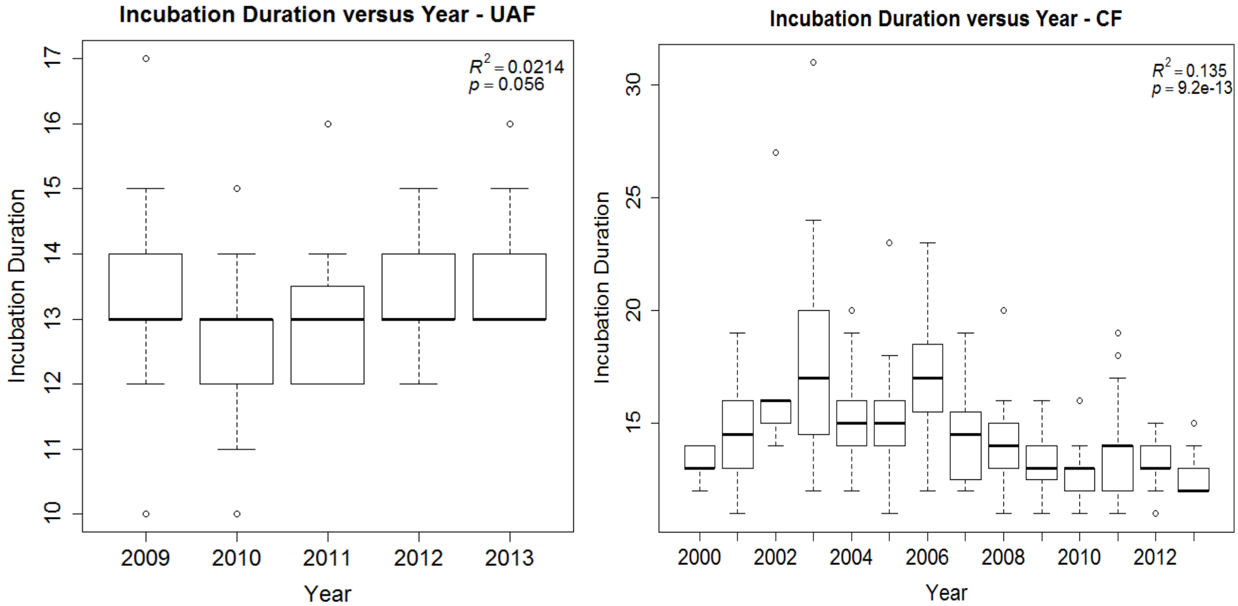


Figure 9. Incubation duration over time for University of Alaska, Fairbanks and Creamer's Field. The box plots show the results for individual nest box data in each year. The r-squared and p-values are from regressing year against laying date.

Incubation durations show no trend at UAF, but have decreased significantly at Creamer's Field (Figure 9, see figure panels for statistical results). It is important to note that the minimum incubation times have not decreased, but there are fewer long incubation times, causing the average incubation time to decrease.

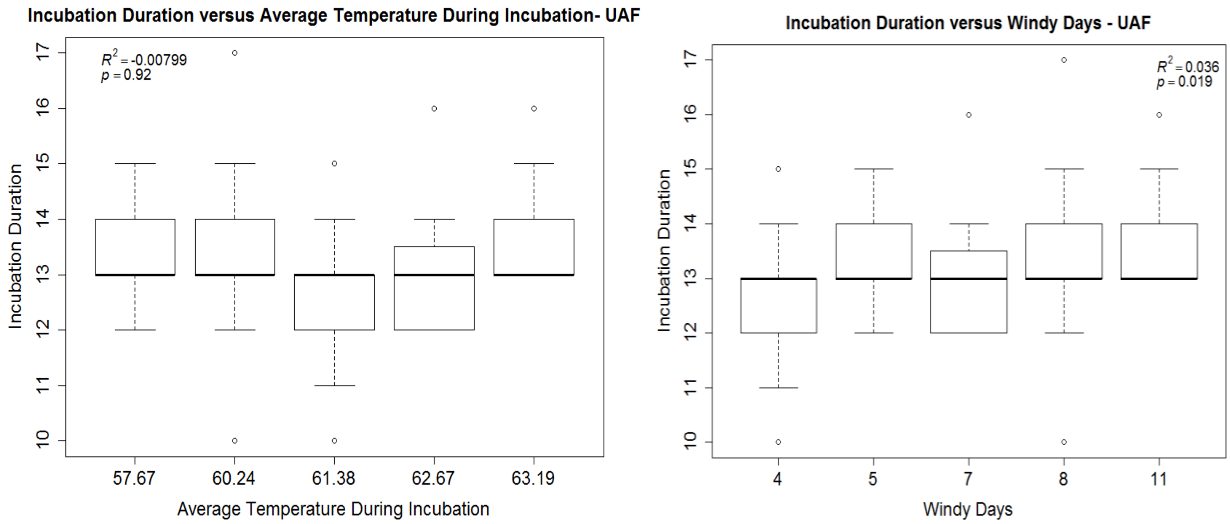


Figure 10. Incubation duration versus climate variables - University of Alaska, Fairbanks. The box plots show the results for individual nest box data in each year. The r-squared and p-values are from regressing temperature and windy days separately against laying date.

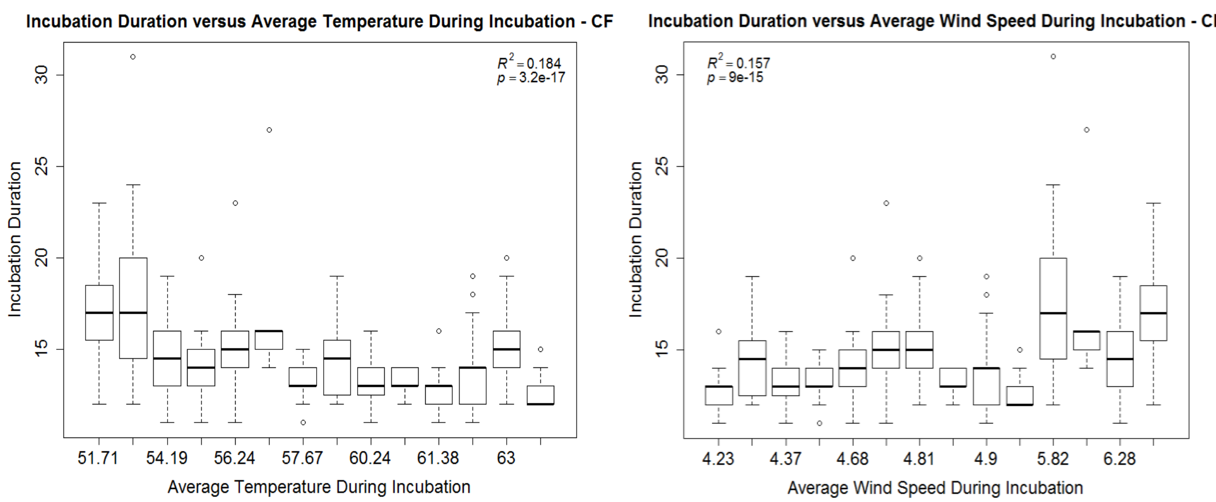


Figure 11. Incubation Duration versus climate variables – Creamer's Field. The box plots show the results for individual nest box data in each year. The r-squared and p-values are from regressing temperature and average wind separately against laying date.

Incubation durations at UAF and Creamer's Field are affected differently by climate, with Creamer's Field showing much stronger correlations to climate. Temperature appears as a negative effect in all of the best models for Creamer's Field, and most of the best models for UAF (Figures 10 and 11, Tables 2 and 3, see figure panels for statistical results). The most important variable for UAF, causing a positive effect in all of the best models is number of windy days (days with wind above average) (Figure 10, tables 2 and 3). While at Creamer's Field, average wind was in all of the best models, causing a positive effect as well (Figure 11, Tables 2 and 3). Precipitation had a smaller effect at both sites. Average precipitation was in the best model for UAF, but was not in any of the other best models, did not have a high summed AIC weight, and did not show a strong trend when regressed against incubation duration (Tables 2 and 3). At Creamer's field, number of days with precipitation had greater support than average precipitation, but only appeared in one of the best models, did not have a high summed AIC weight, and did not show a strong trend when regressed against incubation duration (Tables 2 and 3).

Hatch Date

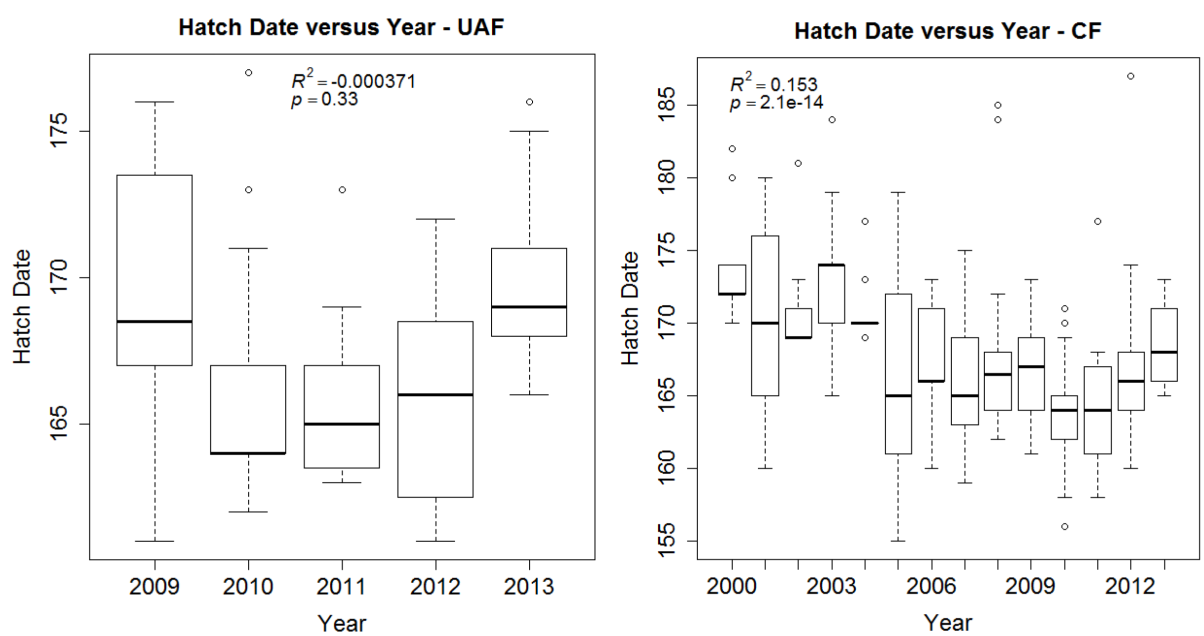


Figure 12. Hatch date over time – Creamer's Field. The box plots show the results for individual nest box data in each year. The r-squared and p-values are from regressing year against laying date.

Hatch dates show a stronger relationship between laying date and time at Creamer's Field than either laying dates or incubation duration (figure 12, see figure panels for statistical results).

This is because both the date of egg laying and the incubation duration affect the hatch date, so we would expect to see an additive effect from them.

Discussion

I found that climate is an important factor in tree swallow phenology, explaining up to 23% of the variance in laying date and 21% of the variance in incubation durations between years. The date of first egg laying has advanced slightly through time and overall incubation durations have decreased. It is possible that this shift was due to changes in data collection, but the same protocols were followed every year of the study so this is not likely. Additionally, temperature showed an inverse relationship with earlier laying dates and shorter incubation durations while wind was positively related to each. Thus, the temporal trends in laying date and incubation duration are likely caused, at least in part, by increasing temperatures and decreasing wind speeds. Precipitation does not have a very strong effect in either direction, with the exception being laying date at UAF where increased precipitation was correlated with earlier laying dates. However, since we only see this pattern here, and there were not many years of data for that site, this could be a spurious effect.

Contrary to climate change projections and other areas of the state (Overland *et al.* 2014, EPA 2014), May temperature did not change in Fairbanks from 2000 to 2013, and therefore the shift in laying date has been slight. However the small advancement in laying date combined with decreasing incubation times have caused a larger advancement in hatch dates at Creamer's Field. Hatch dates at UAF do not show a temporal trend, likely because there were only five years of data for that site. Notably, the data show that wind can have an effect as large as, or larger than, temperature.

Dunn and Winkler (1999) found a greater advancement in laying date (nine days versus three days) and a greater effect of temperature on laying date ($r^2 = 0.75$ versus $r^2 = 0.10$). This is likely because their study used the mean laying date for each year, while our study used each individual laying date. By using the mean laying data, much of the variability is removed which results in higher correlations, but less power. Rose (2009) found that average daily wind speed had a significant negative effect on the rate that adult swallows feed their young and wet, cold and windy conditions have been seen to cause delays in egg laying and incubation in other studies on tree swallows (Wang and Beissinger 2011, Kuerzi 1941). This shows that the effect of wind observed in this study was likely not just a spurious event. Wind not only makes it more difficult for tree swallows to forage, it also creates a wind chill, which makes it more difficult for the birds to keep warm. Both of these effects can cause delays in egg laying and incubation.

Alaska is projected to warm by 2 to 4° C by 2050 (Overland *et al.* 2014, EPA 2014). Wind and precipitation are harder to predict. Precipitation is expected to increase, however with decreased snowmelt and increased evaporation due to higher temperatures summers may become drier (EPA, 2014). Most models agree that wind speeds will increase in the Fairbanks area, but the amount of increase is unsure (Eichelberger, 2008). However, in the years of our study, Fairbanks saw a decrease in both wind and precipitation (Figures 4 and 8). If temperatures continue to increase, but wind increases as well, it will be difficult to predict the effect that this will have on tree swallows since the former will cause advancement in phenology and the later will cause a retreat. If both temperatures increase while wind continues to decrease then we will likely see a greater advancement in phenology. During the years of this study, average temperature was negatively correlated with all measures of windiness for both the month of May and the incubation period (Appendix – Tables 4 and 5). If this correlation holds true in the future then we would expect to see windiness continue to decrease as temperatures increases, resulting in greater advancements in tree swallow phenology.

However, tree swallows are a migratory bird (Winkler et al. 2011). Therefore this shift in phenology is constrained by the time that the birds arrive in Alaska. Since Alaska is farther away from their wintering grounds than most of their other breeding locations, tree swallows arrive in Alaska relatively late in the season. The swallows are therefore constrained in how early they can breed by their migration, unless their migration time changes as well. Additionally, much of the advancement in phenology seen so far can be attributed to decreasing incubation durations. During the years of this study, incubation times likely decreased because the incubation period was warmer and less windy, so there were fewer delays to incubation. However, there is a biologically determined minimum incubation duration (11 days in tree swallows) that the climate will not affect (Winkly et al. 2011). This will also constrain the advance in phenology that we would expect to see in the future.

Climate change has received much of attention in recent years, and numerous studies have been conducted to determine the effects that is it having and will have on various species around the world. Few studies, however, have looked at such a widely dispersed species as tree swallows. The combined results of our study and the Dunn and Winkler (1999) study show an effect of climate change on tree swallows throughout much of the continental United States, Canada and Alaska. Another important aspect of our study that has been largely ignored in other similar studies is the effect of wind. Our study clearly shows that wind plays an important role on the phenology of tree swallows and thus brings to light the importance of taking this variable into account in future climate change studies.

Questions for Further Research

The frequency of extreme events is another aspect of climate expected to increase with climate change. Because of the shorter length of our dataset, we were not able to look for effects from extreme events, but this could be an important variable to consider in future studies.

Insectivorous long-distant migrant species have been seen to decline in areas with a seasonal peak insect availability due to an increasing mismatch between the timing of chick hatching and peak food availability. However, species that live in areas with a more constant food supply did not face declines (Both et al. 2010). The later situation was found to be the case for tree swallows in Southern Canada and the Northern and Eastern United States (Dunn et al. 2010). Studies on insect availability in Alaska are needed to determine if and how continuing changes in climate will affect tree swallow reproductive success.

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Appendix

Average Temperature	Average Wind	Average Precipitation	Precipitation Days	Windy Days	Very Windy Days	Precipitation Squared	Adjusted R-Squared	Delta AICc	k	AICc weight
X							0.04	25.35	3	0
	X						0.06	23.77	3	0
		X					0.1	18.34	3	0
			X				0.13	14.02	3	0
				X			0.08	20.31	3	0
					X		0.2	2.36	3	0.05
						X	0.09	18.79	3	0
X					X		0.22	0.26	4	0.13
X		X					0.17	8.13	4	0
X			X				0.15	11.95	4	0
		X			X		0.21	2.31	4	0.05
			X		X		0.22	1.51	4	0.07
	X					X	0.13	14.13	4	0
					X	X	0.21	2.87	4	0.03
X						X	0.17	9.20	4	0
			X			X	0.14	13.90	4	0
X	X	X					0.17	9.38	5	0
X		X			X		0.22	1.87	5	0.06
X			X		X		0.22	1.49	5	0.07
X	X		X				0.23	0.00	5	0.15
X					X	X	0.23	0.55	5	0.11
		X			X	X	0.21	3.58	5	0.02
			X		X	X	0.21	3.34	5	0.03
X		X			X	X	0.23	1.27	6	0.08
X			X		X	X	0.23	1.27	6	0.08
X	X		X			X	0.23	1.27	6	0.08

Table 1. Table of all models run for laying date at UAF – Blue spaces represent p-value < 0.05, yellow space is the model with the lowest AICc value.

Average Temperature	Average Wind	Average Precipitation	Precipitation Days	Windy Days	Very Windy Days	Precipitation Squared	Adjusted R-Squared	Delta AICc	k	AICc weight
X							0.1	24.79	3	0
	X						0.07	38.89	3	0
		X					0.01	57.59	3	0
			X				*-0*	63.19	3	0
				X			0.01	59.89	3	0
					X		0.07	37.89	3	0
						X	0.01	58.99	3	0
X					X		0.12	18.54	4	0
X				X			0.11	24.44	4	0
X	X						0.11	22.94	4	0
X		X					0.13	13.04	4	0
X			X				0.11	23.64	4	0
		X			X		0.1	26.54	4	0
			X		X		0.09	32.34	4	0
	X	X					0.09	29.54	4	0
X						X	0.14	11.04	4	0
	X					X	0.09	29.54	4	0
					X	X	0.1	27.74	4	0
		X				X	0.01	59.24	4	0
			X			X	0.02	56.74	4	0
X	X	X					0.15	9.60	5	0
X		X			X		0.16	2.30	5	0.15
X			X		X		0.14	10.20	5	0
X		X				X	0.14	13.10	5	0
X					X	X	0.17	0.00	5	0.48
X			X			X	0.14	10.80	5	0
X	X	X				X	0.15	9.07	6	0.01
X		X			X	X	0.17	2.07	6	0.17
X			X		X	X	0.17	2.07	6	0.17

Table 2. Table of all models run for laying date at Creamer's Field – Blue spaces represent p-value < 0.05, yellow space is the model with the lowest AICc value.

Average Temperature	Average Wind	Average Precipitation	Precipitation Days	Windy Days	Very Windy Days	Clutch Size	Adjusted R-Squared	Delta AICc	k	AICc weight
X							-0	8.95	3	0
	X						0.02	5.12	3	0.01
		X					-0	8.04	3	0
			X				-0	8.92	3	0
				X			0.04	3.32	3	0.04
					X		0	7.46	3	0
						X	0.02	4.82	3	0.02
X					X		0.04	4.53	4	0.02
X		X					0.01	7.82	4	0
X				X			0.06	1.2	4	0.1
X	X						0.05	3.23	4	0.04
		X			X		0.03	5.11	4	0.01
			X		X		0	8.97	4	0
		X		X			0.06	1.51	4	0.09
X						X	0.02	6.93	4	0.01
				X		X	0.05	2.64	4	0.05
		X				X	0.03	5.23	4	0.01
	X					X	0.04	3.77	4	0.03
X	X	X					0.05	4.27	5	0.02
X		X			X		0.03	6.39	5	0.01
X		X		X			0.05	3.13	5	0.04
X					X	X	0.06	2.98	5	0.04
X				X		X	0.08	0.37	5	0.15
		X		X		X	0.08	0	5	0.18
X	X	X				X	0.07	2.86	6	0.04
X		X		X		X	0.07	1.95	6	0.07

Table 3. Table of all models run for incubation duration at UAF – Blue spaces represent p-value < 0.05, yellow space is the model with the lowest AICc value.

Average Temperature	Average Wind	Average Precipitation	Precipitation Days	Windy Days	Very Windy Days	Clutch Size	Adjusted R-Squared	Delta AICc	k	AICc weight
X							*0.18*	10.95	3	0
	X						*0.16*	21.75	3	0
		X					*0*	80.05	3	0
			X				*0.01*	76.65	3	0
				X			*0.12*	36.65	3	0
					X		*0.03*	70.65	3	0
						X	*0*	80.15	3	0
X					X		*0.19*	8.2	4	0
X		X					*0.19*	7.5	4	0.01
X				X			*0.2*	5.6	4	0.02
X	X						*0.21*	0	4	0.29
X			X				*0.19*	7.6	4	0.01
		X			X		*0.03*	72	4	0
			X		X		*0.03*	71.9	4	0
		X		X			*0.14*	31.8	4	0
	X	X					*0.17*	18.1	4	0
X						X	*0.19*	11.2	4	0
				X		X	*0.12*	36.8	4	0
			X			X	*0.02*	76.3	4	0
	X					X	*0.16*	22.4	4	0
X	X	X					*0.21*	2.059	5	0.1
X	X		X				*0.21*	1.359	5	0.15
X				X		X	0.2	8.459	5	0
X		X				X	*0.2*	7.959	5	0.01
X				X		X	*0.2*	6.059	5	0.01
X	X					X	*0.21*	0.659	5	0.21
X			X			X	*0.2*	7.959	5	0.01
X	X	X				X	*0.21*	2.73	6	0.07
X	X		X			X	*0.21*	2.03	6	0.11

Table 4. Table of all models run for incubation duration at Creamer's Field – Blue spaces represent p-value < 0.05, yellow space is the model with the lowest AICc value.

	Avg. Temp	Avg. Precip	Avg. Precip^2	Rainy Days	Avg. Wind	Windy Days	Very Windy Days
Avg. Temp	1.000	0.174	0.254	0.250	-0.547	-0.509	-0.410
Avg. Precip	0.174	1.000	0.950	0.801	-0.168	-0.152	-0.211
Avg. Precip^2	0.254	0.950	1.000	0.734	-0.227	-0.235	-0.239
Rainy Days	0.250	0.801	0.734	1.000	-0.318	-0.194	-0.451
Avg. Wind	-0.547	-0.168	-0.227	-0.318	1.000	0.795	0.791
Windy Days	-0.50	-0.152	-0.235	-0.194	0.795	1.000	0.454
Very Windy Days	-0.410	-0.211	-0.239	-0.451	0.791	0.454	1.000

Table 5. Table of correlations between all weather variables during the month of May.

	Avg. Temp	Avg. Precip	Rainy Days	Avg. Wind	Windy Days	Very Windy Days
Avg. Temp	1.000	-0.063	0.045	-0.612	-0.567	-0.187
Avg. Precip	-0.063	1.000	0.801	-0.472	-0.552	-0.641
Rainy Days	0.045	0.801	1.000	-0.381	-0.541	-0.491
Avg. Wind	-0.612	-0.472	-0.381	1.000	0.942	0.771
Windy Days	-0.567	-0.552	-0.541	0.942	1.000	0.804
Very Windy Days	-0.187	-0.641	-0.491	0.771	0.804	1.000

Table 6. Tables of correlations between all weather variables during the incubation period.