

The Relationship Between Temperature, Rainfall, and Tree Swallow Fledging Times

By

Caleb Gruber

David Aborn  
Professor of Environmental Science  
(Chair)

Thaddeus McRae  
Associate Professor of Environmental  
Science  
(Committee Member)

Loren Hayes  
Professor of Biology  
(Committee Member)

The Relationship Between Temperature, Rainfall, and Tree Swallow Fledging Times

By  
Caleb Gruber

A Thesis Submitted to the Faculty of the University of Tennessee at Chattanooga in Partial  
Fulfillment of the Requirements of the Degree of Master of Science:  
Environmental Science

The University of Tennessee at Chattanooga  
Chattanooga, Tennessee

May 2023

## ABSTRACT

Weather effects such as temperature and precipitation are known to affect reproductive success of many avian species. Weather variables can directly or indirectly influence the fledging success of nestlings. I investigated the effect of minimum temperature, maximum temperature, average temperature, maximum rainfall experienced in one day during a fledging period, and average daily rainfall on how long it takes tree swallow nestlings in Tennessee to fledge using multi-linear regression and linear mixed-effects modeling. I found that minimum temperatures, maximum temperatures, maximum rain experienced in a one-day period, and total rain all had a significant relationship on the time it takes for tree swallow chicks to fledge ( $p < 0.05$ ). The best model includes these weather variables and can account for about 20-21% of the variation seen in the time it takes tree swallow chicks to fledge.

## ACKNOWLEDGEMENTS

First, I would like to thank my wife Haleigh. Her support carried me through my graduate experience much more than I could have accomplished alone. I would like to thank the Cornell Lab of Ornithology and their Nestwatch program. Without the contribution of the Nestwatch data, this project would have been less likely to make it off the ground. I would also like to thank my committee members, Drs. David Aborn, Thaddeus McRae, and Loren Hayes for providing their time, support, and knowledge towards my growth as an academic.

## TABLE OF CONTENTS

ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
LIST OF TABLES.....	vii
CHAPTER.....	1
I.    INTRODUCTION.....	1
II.   METHODS.....	5
Tree Swallow Data.....	5
Weather Data.....	6
Multi-Linear Regression.....	7
Linear Mixed-Effects Modeling.....	7
Model Analysis.....	8
III.  RESULTS.....	9
Model Comparison.....	9
Variance Inflation Factor.....	11
IV.  DISCUSSION AND CONCLUSION.....	12
Overall Summary.....	12
Temperature Effects.....	12
Precipitation Effects.....	14
Conclusion.....	16
REFERENCES.....	19

## APPENDIX

A. R Model Code and Output .....	24
VITA .....	29

## LIST OF TABLES

TABLE 1. P-values of the RBase1 model as well as the coefficients, confidence intervals, and r-squared values .....	10
TABLE 2. The VIF scores for model RBase1 .....	11

## CHAPTER 1

### I. INTRODUCTION

Global climate change is predicted to lead to greater variation in temperature extremes as well as unpredictability in precipitation patterns (IPCC, 2013). Additionally, the frequency in periods of abnormally high or cold temperatures are expected to increase, as well as increased periods of rain due to climate change (Rahmstorf & Coumou, 2011; Wuebbles et al., 2014). These changes in weather brought on by climate change are having detrimental effects on many avian species. A recent study reported that 419 migratory bird species in on North America have experienced population declines due to environmental changes, many of which are human induced (Rosenberg et al., 2019). These environmental changes are part of the reason why we are seeing that bird species are currently the vertebrate group that have the highest proportion of overall species with populations of less than a thousand. (Ceballos et al., 2020).

Changing weather patterns leading to more extreme temperatures and increased variability in precipitation may impact the reproductive success of many avian species (Crick, 2004; de Zwaan et al., 2019). For instance, extreme high temperatures are shown to reduce fitness in avian species, and are predicted to decrease biodiversity in years to come due to its sublethal effects (Bourne et al., 2020; Conradie, 2019; Greño et al., 2008; Riggio et al., 2023). One study showed how higher temperatures increased mortality rates in young across three development rates of egg, nestling and fledging likely caused by heat stress (Bourne et al., 2020). Another effect of extreme high temperatures is that they may also reduce fertility in avian



species because egg and sperm production were shown to be sensitive to temperature extremes (Schou, 2021). On the other end, extreme minimum temperatures, often identified as cold snaps specific to the region the study is done, are shown to reduce food availability and subsequently fledging success in avian species (Garrett et al., 2022; Winkler et al., 2013).

The amount of precipitation a nestling experiences can also impact its fitness by leading to reduced weights and increasing energy allocation towards thermoregulation (Morrison, 2002; Radford, 2003). Excess rainfall can reduce the number of visitations by parents to provide food to nestlings as well as negatively affect the overall health condition of parents, especially during cold snaps (Öberg, 2015, Robinson, 2017). Because of this, rainfall then indirectly impacts the growth rates of fledglings by preventing these chicks from being fed by parents who are unable to provide for them (Dawson, 2000). Another study showed how cold periods with extended rainfall led to an increase in nest abandonment (Martin, 2017). This fact leads to direct mortality of chicks and is concerning in the face of climate change. Furthermore, there may be detrimental effects occurring during the post-nestling period from these weather factors and can lead to long-term reduced fitness (Naef-Daenzer, 2001). Climate change has the potential to increase these detrimental effects since it is projected that temperature extremes will increase, there will more periods of rainfall, and variation in temperature and rainfall will become more unpredictable.

Part of the reason as to why these environmental changes are occurring comes from alterations in seasonality brought on by climate change. For example, it has been shown that the last frost of spring happens 7 days earlier and the first frost of autumn happens about 5 days later when compared to the previous 100 years in the continental U.S. (Kukal & Irmak, 2018). These changes in seasonality are suspected to contribute to hardship in many migratory species who

may be unable to compensate and find suitable environments for shelter, food availability, and breeding sites (Crick, 2004; Visser et al, 2004). There is also the potential for asynchronicity between breeding times and food availability due to climate change. Thomas (2001) shows how a population of blue tits (*Parus caeruleus*) in Corsica had a reduced number of breeding pairs since the cost of raising chicks was too high due to a food availability mismatch.

One avian species susceptible to climate change and weather variability is tree swallows (*Tachycineta bicolor*). Tree swallows are cavity-nesting insectivores that migrate throughout most of America and Canada during their breeding season. Since they are cavity nesters, this makes them ideal species for acquiring data as they are easily observable. As insectivores, they could be more directly impacted by weather effects such as intense periods of rainfall since prey items are likely to be less active (English, 2017; Wheelwright, 2022; Winkler, 2013). Tree swallows are also of concern since climate change is shifting their breeding dates, leading to earlier breeding times in the year (Dunn, 1999). Earlier breeding time may potentially lead to asynchronicity between breeding times and prey availability, although this is not well tested and has yet to be shown for tree swallows (Visser, 1998; Visser, 2004). The combination of this species being cavity nesters plus likely being more sensitive to variability in weather makes tree swallows an ideal species of study to observe how climate change is affecting avian species.

I sought to determine if precipitation and temperature influence the time it takes tree swallow chicks to fledge. My hypothesis is that increases in maximum temperatures, minimum temperatures, maximum rainfall experienced in one day, and average daily rainfall affects the time it takes tree swallow chicks to fledge. To test this, a multi-linear regression and mixed-

effects model-making approach was used to find if precipitation and temperature effects influence how long it takes Tree Swallow chicks to fledge in Tennessee.

## II. METHODS

### Tree Swallow Data

Two sets of data were used in looking at fledging dates and locations of tree swallow chicks for this study. The first data set was collected by Dr. David Aborn, an ornithologist and professor at the University of Tennessee at Chattanooga. These data span the years 2014 through 2022. The second data set was provided by Nestwatch, which is a citizen-science project led by The Cornell Lab of Ornithology. Citizens record nest parameters for any nest they find and monitor ([nestwatch.org](http://nestwatch.org)). The information citizens submit must follow a strict protocol laid out by Nestwatch's Nest Monitoring Protocol. The data from both data sets consists of observations of tree swallow nests in Tennessee. The list of variables extracted from Dr. Aborn's and Nestwatch's data consists of day of hatch of first chick, day of fledge of first chick, year in which chick fledged, and location of the nest. These data were used to calculate the time the first chick in each nest hatched to the time the first chick fledged to establish a fledging period for each nest. Nestwatch provided coordinates for each nest, and these were put into to ArcGIS Pro as points. A Tennessee county shapefile was then downloaded so that coordinates could be easily placed within a county. Dr. Aborn's work was all done in Hamilton County, so no GIS work was necessary for that data set. Days to fledge for each nest was then calculated by subtracting the date of the first egg to hatch from the date of the first chick to fledge. The days to fledge is considered the dependent variable when comparing it to weather effects. It is important to note the fledging data from Dr. Aborn's field sampling is not used for the years 2014 and 2018. This

is because the data were not readily available, or observations were too far apart from each other to gain conclusive evidence of true fledging times. Additionally, even though it was available, we did not use the data from 2014 and 2018 from the Nestwatch data to avoid sample size biases in the mixed effects models as these years had significantly less observations.

#### Weather Data

Weather data was obtained from the National Oceanic and Atmospheric Administration (NOAA) (<https://www.noaa.gov>). The NOAA data includes minimum daily temperatures °F, maximum daily temperatures °F, average daily temperatures °F, and daily rainfall (in.). Data tables for these variables were requested at the county level from the years 2014-2022 so that nests were getting relatively local weather data while at the same time all the necessary weather variables were available. Because not all the Nestwatch data was in a county in which all weather factors were recorded, only seven counties had usable data. The counties are Anderson, Davidson, Hamilton, Knox, Loudon, Marion, and Sullivan. If data tables were requested at a more localized level than county, it was often the case that the five necessary weather variables were not all available. This data selection procedure allowed me to maximize spatial resolution with maximizing sample size.

The minimum daily temperatures, maximum daily temperatures, average daily temperatures, maximum rainfall observed in one day, and average daily rainfall across fledging period were calculated for each tree swallow chick in relation to their hatch date through their fledge date with the acquired NOAA weather data in Excel. This led to the reduction of observations used in the model-making process since I wanted all the points to have all five weather criteria. This ultimately led to a sample size of 485 observations for the 7-year study period.

## Multi-Linear Regression

Multi-linear regression was performed in R using the base statistics package (v4.1.2 R Core Team, 2023). This package was used to calculate the significance of minimum daily temperatures °F, maximum daily temperatures °F, average daily temperatures °F, max rainfall observed in one day (in.), and average daily rainfall on days to fledge through considering all five independent variables at the same time. These models include the full model with all five variables and subsets of variables, for a total of 12 multi-linear regression models. While the dependent variable remained days to fledge and can be seen in Table 1 of the appendix. It was found that when considering all independent variables at once, average temperature was not significant ( $p > 0.05$ ). This led to the removal of average temperature for the other 11 models. With the remaining weather variables, all possible combinations considering 3 weather variables were made into models. Then all combinations of multi-linear regression considering only 2 weather variables were made into models. *AIC* was calculated for each model using the base stats package (v4.1.2 R Core Team, 2023). Summaries of the best models were made using the base R package that show the p-values of an ANOVA test as well as multiple and adjusted r-squared values (v4.1.2 R Core Team, 2023). Interacting terms were evaluated, and this led to lower *AIC* scores. However, no term in these models was statistically significant, so only the non-interacting term models are reported in this study.

## Linear Mixed-Effects Modeling

Linear mixed effects modeling considers random effects in the model-making process. Using the lme4 package, 12 linear mixed-effects models were made to assess which model had the best fit and predictive power (Bates et al., 2015). The year of fledge for each sample was considered as a random effect. The weather effects of minimum daily temperatures °F, maximum

daily temperatures °F, average daily temperatures °F, max rainfall observed in one day (in.), and average daily rainfall were considered fixed effects in the same combinations as the multi-linear regression models, except that all models considered year as a random effect (see appendix Table 1).

### Model Analysis

After all the 12 multi-linear regression and the 12 mixed effects models were completed, the *AICs* were then calculated using the base stats package (v4.1.2 R Core Team, 2023). The models were evaluated to see which models had the lowest *AIC* score. Further analysis then looks at the p-values related to the overall multi-linear regression models as well as the p-values for the individual independent variables within the model. R-squared values are also assessed for the models to see how much of the variation of the dependent variable can be accounted for through the independent variables. The best model is selected based on being within 6 *AIC* of the lowest *AIC*, using the least number of variables to explain similar amounts of variation, and how significant the model and independent variables are ( $p < 0.05$ ) (Richards, 2005). Once the best model was identified, the variance inflation factor (*VIF*) was calculated for the independent variables to check for collinearity. If the independent variables were collinear ( $VIF > 5$ ), then removing the variable with the highest *VIF* score would have been considered.

### III. RESULTS

#### Model Comparison

Table 2 in the appendix shows all the model abbreviations and their corresponding *AIC* scores. Based on the *AIC* scores being within 6 *AIC* of the lowest *AIC* model, and using the model with least number of variables to explain similar amounts of variation, RBase1 is determined to be the best model. RBase1 is a multi-linear regression model that considers average daily rainfall, maximum rainfall, maximum temperatures, and minimum temperatures as independent variables. The reason RYAM1 was not chosen as the best model, even though it has a lower *AIC* score, is because it considers more variables through considering year as a random effect but does not account for much more variation than the simpler Rbase1 model. A table including relevant statistical information similar to Table 1 for RYAM1 is included in the appendix (Table 3). The insignificance of average temperature ( $p>0.05$ ), having more variables to consider in a model, and the higher *AIC* score also leads to the conclusion that both ABase and YAM should not be considered as the best models even though they are within 6 *AIC* of the lowest *AIC* model.



Table 1 P-values of the RBase1 model as well as the coefficients, confidence intervals, and r-squared values

<u>Table 1</u>			
<i>RBase1</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Entire model	n/a	n/a	< 2.2E-16
Intercept	-18.285	-23.575 – -12.997	0.001013
MinTemp	-0.228	-0.259 – -0.197	7.44E-13
MaxTemp	0.498	0.428 – 0.568	4.9E-12
MaxRain	2.823	2.384 – 3.262	3.18E-10
AvgRain	-10.616	-13.541 – -7.691	0.000314
Multiple R-squared		0.2109	
Adjusted R-squared		0.2043	
Observations	485		

Each independent variable, the intercept, and the overall model are significant ( $p < 0.05$ ) (Table 1). We can also see the type of relationship each independent variable has on the days to fledge. Minimum temperatures and daily average rainfall have a negative relationship with days to fledge. This means that as minimum temperatures and daily average rainfall increase, days to fledge in tree swallow chicks decreases. Maximum temperatures and maximum rainfall have positive correlations with fledging times.

The multiple and adjusted r-squared values are 0.2109 and 0.2043, respectively. This means that maximum rainfall, average daily rainfall, minimum temperatures, and maximum

temperatures can account for 20-21% of the variation in time it takes tree swallow chicks to fledge.

#### Variance Inflation Factor

Table 2 The *VIF* scores for model RBase1

<u>Table 2</u>				
<u>RBase1</u>	<u>MinTemp</u>	<u>MaxTemp</u>	<u>MaxRain</u>	<u>AvgRain</u>
VIF Score	2.1663	2.037	1.969	2.261

Table 2 shows the *VIF* calculations for the independent variables in RBase1. There are no significant concerns for collinearity indicated by the *VIF* values as none of the values are above 5.

## IV. DISCUSSION AND CONCLUSION

### Overall Summary

The hypothesis that precipitation and temperature influence time to fledge for tree swallow chicks in Tennessee is supported through the models. The evidence from the models demonstrates that 4 of the 5 weather criteria have a significant relationship with the time it takes tree swallow chicks to fledge. Average temperature is the only weather variable that is excluded from the best model.

### Temperature Effects

Research supports that extreme maximum temperatures and extreme minimum temperatures can negatively impact nestling fitness. High temperature variation is a constant theme in nestling survival. (Dawson et al., 2000; McCarty, 1999; Riggio et al., 2023). For instance, a recent study done in the California Central Valley showed how increased temperature extremes likely had detrimental effects on nestling weight and reproductive success in conjunction with rainfall patterns in cavity-nesting birds, including tree swallows (Riggio et al., 2023). A reason for this may be that extreme high temperatures reduces prey availability (Barras, 2021). Extreme high temperatures can also induce heat stress on nestlings, reducing weight and the probability of survival (Andreasson, 2018; Bourne, 2020).

Other studies indicate that minimum temperatures can have a greater effect on reproductive and fledging success in tree swallows than maximum temperature (Garrett et al, 2022; Winkler et al. 2013). This is also likely due to reductions in food availability, which may also reduce overall provisioning of nestlings (Dawson, 2000; Dawson, 2008, Garrett et al, 2022). Quinney (1986) found that food availability had direct impacts on nestling growth and survival of tree swallows when comparing two similar sites with differences in food availability. Two studies experimenting with heated nests found warmer temperatures led to increased fitness in nestlings. This may be because heated tree swallow nests reduce the necessity for energy expenditure for thermoregulation in nestling and parents (Dawson, 2005, Perez et al., 2008). Less energy spent on thermoregulation could then be allocated to more growth in the nestlings (Perez et al, 2008). Being able to grow more rapidly likely leads to earlier fledging times. In my best model, we see a general trend of increasing minimum temperatures leading to a decrease in fledging times in Tennessee. This indicates that low minimum temperatures may inhibit the ability to grow faster which may lead to longer fledging times, which is supported by the aforementioned Winkler and Garrett studies which are done in colder regions like New York (2013, 2022). Inversely, my best model also shows how an increase in maximum temperature may lead to increases the in time it takes to fledge. These finding are more like the 2019 Riggio study done in the California Central Valley that found that high maximum temperatures had negative effects on nestlings. Riggio suggested that environmental differences on where studies take place impact whether warmer or colder temperatures are more detrimental to fledging success based on the adaptations of the tree swallows in those regions, which is why there might be confounding reports across similar studies.

Tree swallows in my study may experience more of a balance in temperatures between the more northern studies, which indicated low minimum temperatures are detrimental, and the California study which indicated maximum temperatures are more detrimental. Here, I show that extremes in maximum temperature and minimum temperature are both significantly impacting the time it takes tree swallow chicks to fledge, which means they may be experiencing some of the detrimental effects of both low minimum temperature and high maximum temperatures previously described.

### Precipitation Effects

The amount of precipitation experienced during a nesting season has also been shown to affect fledging success in other studies. For instance, a study was done with another cavity-nesting bird that showed lower nesting success on the wet breeding season (Radford, 2003). Radford showed that total rainfall during wet breeding seasons alone accounted for 25% of the variation in fledging success for green woodhoopoes *Phoeniculus purpureus*. This could be due to either nest flooding or adults found other shelter to avoid water-logged feathers (Radford, 2001; Radford, 2003). For tree swallows, rainfall seems to have increased during their spring breeding season (Cox et al., 2019). It is suspected that this increase in precipitation leads to a reduction in prey items for tree swallows during rainy periods in conjunction with cold periods when minimum temperatures surpass a certain threshold for an elongated period (Cox et al., 2019; Gruebler, 2008; Wheelwright et al., 2022). However, this reduction likely comes from more intense rain events rather than overall increases in precipitation since large rain events can wash away insects during flooding events (Shrestha, 2019). Additionally, herbivore insect abundance may decrease in extreme weather events due to destruction of vegetation (Shrestha,

2019). A reduction in prey availability leads to a reduction in nestling growth because the parents cannot provide enough food for themselves and for the nestlings (Cox et al., 2019).

One comparative study between tree swallows and savannah sparrows (*Passerculus sandwichensis*) found that tree swallow nestlings were much more sensitive to temperature, rainfall, and windy conditions which impacted fledging success (Wheelwright et al, 2022). This study concluded that the primary differences come from the reduction in the tree swallow's capability to forage in inclement weather when compared to a ground-foraging species.

Wheelwright also observed abandoned nestlings during rainstorms after the rest of the brood had fledged. This shows that the parents, likely due to the stress of rainy and windy conditions, either died, had to make the decision to abandon the last of the nestlings or risk personal harm, or some other factor that prevented them from coming back to the nest. This study aligns with my results, which indicate that increases in maximum rainfall led to longer fledging times. Rainfall may impact the time to fledge by reducing growth and requiring more energy for thermoregulation during periods of stress.

We see in my study that there is a positive correlation between high rainfall events and tree swallow fledging times. Conversely, I show that an increase in average daily rainfall during a fledging period is negatively correlated with tree swallow fledging times. This could mean that intense periods of rain have direct impacts on thermoregulation and reduction of food availability. However, steady periods of rain, without getting too extreme, may be necessary for insect activity and insect food availability such as plants for herbivorous insects. Average rainfall also likely does not have the same direct effects as extreme rain events during a fledging period.

## Conclusion

Minimum temperature, maximum temperature, maximum rainfall, and average daily rainfall have significant impacts on the time it takes tree swallow chicks to fledge. These relationships are not surprising, as other areas of research indicate how these weather variables can impact food availability and have direct and indirect impacts on nestling and parental fitness. This study highlights the implications climate change is having on tree swallows. By increasing variability in weather patterns, having increased extremes in minimum and maximum temperatures, and increasing the variation in rainfall, climate change seems to be a contributor to longer fledging times in tree swallow chicks. This could mean an overall increase in energy expenditure from both parent and offspring to have a successful fledging from a tree swallow chick since it is taking chicks longer to fledge in extreme conditions. With chicks staying in the nest longer, parents are having to spend energy caring for the chicks for a longer period and there is a longer time for predation to occur. Chicks are also allocating more energy to thermoregulation instead of growth. By having more areas of energy allocation for chicks, it makes sense that the overall energy required for fledging is increased. If this is true, it could mean that it is becoming harder for tree swallow chicks to fledge in the face of climate change since more energy is required to do so. If it is becoming more difficult for chicks to fledge, then we may see declines in future populations of tree swallows due to a decrease in fledging success.

It is important to note that both sets of data, even though protocols of gathering samples are nearly identical, there are inherent differences on how each observer interpreted their observation. Some observers may have made mistakes in determining which chick was the first to fledge, which skews the time for an observation. Some people may have visited nests every day, although the requirement was at least every three days. This then could lead to different

accuracies in observations. Additionally, the NOAA data is not as localized as it could be to get a true sense of the weather effects experienced by the tree swallows. Ideally, localized thermometers or rain gauges would have been used to get more precise measurements. Additionally, maximum rainfall and total rainfall were highly variable with coefficients of variation (*C.V.*) of 0.524 and 0.621. This could mean that using these variables for predictions could lead to inconsistencies. Minimum temperatures had a better *C.V.* at 0.137, and maximum temperatures held a *C.V.* of 0.035. In terms of predictability, the temperature components have smaller variations, and may be a better predictor than the rainfall components.

Future research could identify more variables that may or may not impact tree swallow chick fledging times. Such variables could be other weather components such as wind, or other non-weather factors such as brood size and recording if the chick was a part of a first or second brood. Further research can also try to isolate or simulate weather variables used in this study to see how they more directly impact the time it takes for tree swallows to fledge. Additionally, it would be beneficial to compare my models to other data sets to see if trends remain the same. For instance, waiting 5 years before requesting more Nestwatch data and seeing if the best model continues to be significant and account for similar levels of variation would be an insight into the strength of my model. It would also be interesting to compare my model to species with a similar natural history to see if my model can be used for more than just tree swallows.

Tree swallows are accruing detrimental effects in the face of climate change. As temperature extremes are becoming more prevalent, and rainfall variation is becoming increasingly unpredictable, I show that tree swallow fledging times may be increasing. This



could have important implications on tree swallow population decline, and perhaps the decline of other aerial insectivore species as the climate changes.

## REFERENCES

- Andreasson, F., Nord, A., & Nilsson, J.-Å. (2018). Experimentally increased nest temperature affects body temperature, growth and apparent survival in blue tit nestlings. *Journal of Avian Biology*, 49(2), jav-01620.
- Barras, A. G., Niffenegger, C. A., Candolfi, I., Hunziker, Y. A., & Arlettaz, R. (2021). Nestling diet and parental food provisioning in a declining mountain passerine reveal high sensitivity to climate change. *Journal of Avian Biology*, 52(2). <https://doi.org/10.1111/jav.02649>
- Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.
- Bourne, A. R., Cunningham, S. J., Spottiswoode, C. N., & Ridley, A. R. (2020). High temperatures drive offspring mortality in a cooperatively breeding bird. *Proceedings of the Royal Society. B, Biological sciences*, 287(1931), 20201140. <https://doi.org/10.1098/rspb.2020.1140>
- Ceballos, G., P.R. Ehrlich, and P.H. Raven. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *PNAS* 117:13596-13602. [doi.org/10.1073/pnas.1922686117](https://doi.org/10.1073/pnas.1922686117)
- Conradie, S. R., Woodborne, S. M., Cunningham, S. J., & McKechnie, A. E. (2019). Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proceedings of the National Academy of Sciences - PNAS*, 116(28), 14065-14070. <https://doi.org/10.1073/pnas.1821312116>
- Cox, A. R., Robertson, R. J., Lendvai, Á. Z., Everitt, K., & Bonier, F. (2019). Rainy springs linked to poor nestling growth in a declining avian aerial insectivore ( Tachycineta bicolor). *Proceedings of the Royal Society. B, Biological sciences*, 286(1898), 20190018. <https://doi.org/10.1098/rspb.2019.0018>
- Crick, H. Q. P. (2004). The impact of climate change on birds. *Ibis (London, England)*, 146(s1), 48-56. <https://doi.org/10.1111/j.1474-919X.2004.00327.x>
- Dawson, R. D. (2008). Timing of breeding and environmental factors as determinants of reproductive performance of tree swallows. *Canadian journal of zoology*, 86(8), 843-850. <https://doi.org/10.1139/Z08-065>

- Dawson, R. D., & Bortolotti, G. R. (2000). Reproductive Success of American Kestrels: The Role of Prey Abundance and Weather. *The Condor (Los Angeles, Calif.)*, 102(4), 814-822. <https://doi.org/10.1093/condor/102.4.814>
- Dawson, R. D., Lawrie, C. C., & O'Brien, E. L. (2005). importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia*, 144(3), 499-507. <https://doi.org/10.1007/s00442-005-0075-7>
- de Zwaan, D. R., Camfield, A. F., MacDonald, E. C., Martin, K., & Sandercock, B. (2019). Variation in offspring development is driven more by weather and maternal condition than predation risk. *Functional ecology*, 33(3), 447-456. <https://doi.org/10.1111/1365-2435.13273>
- Dunn, P. O., & Winkler, D. W. (1999). Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society. B, Biological sciences*, 266(1437), 2487-2490. <https://doi.org/10.1098/rspb.1999.0950>
- English, P. A., Nocera, J. J., Pond, B. A., & Green, D. J. (2017). Habitat and food supply across multiple spatial scales influence the distribution and abundance of a nocturnal aerial insectivore. *Landscape ecology*, 32(2), 343-359. <https://doi.org/10.1007/s10980-016-0454-y>
- Garrett, D. R., Pelletier, F., Garant, D., & Bélisle, M. (2022). Interacting effects of cold snaps, rain, and agriculture on the fledging success of a declining aerial insectivore. *Ecological applications*, 32(7), e2645-n/a. <https://doi.org/10.1002/eap.2645>
- Greño, J. L., Belda, E. J., & Barba, E. (2008). Influence of temperatures during the nestling period on post-fledging survival of great tit *Parus major* in a Mediterranean habitat. *Journal of avian biology*, 39(1), 41-49. <https://doi.org/10.1111/j.0908-8857.2008.04120.x>
- Grüebler, M. U., Morand, M., & Naef-Daenzer, B. (2008). A predictive model of the density of airborne insects in agricultural environments. *Agriculture, ecosystems & environment*, 123(1-3), 75-80.
- IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.
- Kukal, M. S., & Irmak, S. (2018). US Agro-Climate in 20th Century: Growing Degree Days, First and Last Frost, Growing Season Length, and Impacts on Crop Yields. *Scientific reports*, 8(1), 1-14. <https://doi.org/10.1038/s41598-018-25212-2>

- Martin, K., Wilson, S., MacDonald, E. C., Camfield, A. F., Martin, M., & Trefry, S. A. (2017). Effects of severe weather on reproduction for sympatric songbirds in an alpine environment: Interactions of climate extremes influence nesting success. *The Auk: Ornithological Advances*, 134(3), 696-709.
- McCarty, J. P., & Winkler, D. W. (1999). Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. *Ibis (London, England)*, 141(2), 286-296. <https://doi.org/10.1111/j.1474-919X.1999.tb07551.x>
- Morrison, S. A., & Bolger, D. T. (2002). Variation in a Sparrow's Reproductive Success with Rainfall: Food and Predator-Mediated Processes. *Oecologia*, 133(3), 315-324. <https://doi.org/10.1007/s00442-002-1040-3>
- Naef-Daenzer, B., Widmer, F., & Nuber, M. (2001). Differential Post-Fledging Survival of Great and Coal Tits in Relation to Their Condition and Fledging Date. *The Journal of animal ecology*, 70(5), 730-738. <https://doi.org/10.1046/j.0021-8790.2001.00533.x>
- Öberg, M., Arlt, D., Pärt, T., Laugen, A. T., Eggers, S., & Low, M. (2015). Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecology and evolution*, 5(2), 345-356. <https://doi.org/10.1002/ece3.1345>
- Pérez, J. H., Ardia, D. R., Chad, E. K., & Clotfelter, E. D. (2008). Experimental heating reveals nest temperature affects nestling condition in tree swallows (*Tachycineta bicolor*). *Biology letters (2005)*, 4(5), 468-471. <https://doi.org/10.1098/rsbl.2008.0266>
- Radford, A., McCleery, R., Woodburn, R., & Morecroft, M. (2001). Activity patterns of parent Great Tits *Parus major* feeding their young during rainfall. *Bird Study*, 48(2), 214-220.
- Radford, A. N., & Du Plessis, M. A. (2003). The importance of rainfall to a cavity-nesting species. *Ibis (London, England)*, 145(4), 692-694. <https://doi.org/10.1046/j.1474-919X.2003.00198.x>
- R Core Team (2023). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. URL <https://www.R-project.org/>.
- Rahmstorf, S., & Coumou, D. (2011). Increase of extreme events in a warming world. *Proceedings of the National Academy of Sciences - PNAS*, 108(44), 17905-17909. <https://doi.org/10.1073/pnas.1101766108>
- Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology (Durham)*, 86(10), 2805-2814. <https://doi.org/10.1890/05-0074>

- Riggio, J., Engilis, A., Cook, H., de Greef, E., Karp, D. S., & Truan, M. L. (2023). Long-term monitoring reveals the impact of changing climate and habitat on the fitness of cavity-nesting songbirds. *Biological conservation*, 278, 109885. <https://doi.org/10.1016/j.biocon.2022.109885>
- Robinson, B. G., Franke, A., & Derocher, A. E. (2017). Weather-mediated decline in prey delivery rates causes food-limitation in a top avian predator. *Journal of avian biology*, 48(5), 748-758. <https://doi.org/10.1111/jav.01130>
- Rosenberg, K.V., A.M. Dokter, P.J. Blancher, J.R. Sauer, A.C. Smith, P.A. Smith, J.C. Stanton, A. Panjabi, L. Helft, M. Parr, and P.P. Marra. (2019). Decline of the North American avifauna. *Science*, 366:120-124.
- Schou, M. F., Bonato, M., Engelbrecht, A., Brand, Z., Svensson, E., Melgar, J., Muvhali, P. T., Cloete, S. W. P., & Cornwallis, C. K. (2021). Extreme temperatures compromise male and female fertility in a large desert bird. *Nature communications*, 12(1), 666-610. <https://doi.org/10.1038/s41467-021-20937-7>
- Shrestha, S. (2019). Effects of climate change in agricultural insect pest. *Acta Sci. Agric*, 3(12), 74-80.
- Quinney E.T., D. J. T. H., TM C. Davison Ankney (1986). Sources of variation in growth of Tree Swallows. *The Auk*, 103(2), 389-400.
- Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M., & Speakman, J. R. (2001). Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, 291(5513), 2598-2600.
- Visser, M. E., Noordwijk, A. J. V., Tinbergen, J. M., & Lessells, C. M. (1998). Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1408), 1867-1870. <https://doi.org/10.1098/rspb.1998.0514>
- Visser, M. E., Both, C., & Lambrechts, M. M. (2004). Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research*(35), 89-110.
- Wheelwright, N. T., Freeman-Gallant, C. R., & Mauck, R. A. (2022). Nestling Savannah Sparrows and Tree Swallows differ in their sensitivity to weather. *Ornithology*, 139(4), 1-14. <https://doi.org/10.1093/ornithology/ukac032>
- Winkler, D. W., Luo, M. K., & Rakhimberdiev, E. (2013). Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). *Oecologia*, 173(1), 129-138. <https://doi.org/10.1007/s00442-013-2605-z>

Wuebbles, D. J., Kunkel, K., Wehner, M., & Zobel, Z. (2014). Severe Weather in United States Under a Changing Climate. *Eos (Washington, D.C.)*, 95(18), 149-150.  
<https://doi.org/10.1002/2014EO180001>

APPENDIX A  
R Model Code and Output

Table 1. The following table shows the model abbreviations, the full names, and the code to show how each model was created. Models with the word “Base” are all multi-linear regression type models. All other models with a “Y” in them are mixed-effects models accounting the year an observation took place as a random effect.

Model Abb	Full Name	R Code
ABase	Additive Base	lm(Days ~ MinTemp + MaxTemp + AvgTemp + MaxRain + AvgRain, data=Data)
RBase1	Reduced Base 1	lm(Days ~ MinTemp + MaxTemp + MaxRain + AvgRain, data=Data)
RBase2	Reduced Base 2	lm(Days ~ MinTemp + MaxTemp + AvgRain, data=Data)
RBase3	Reduced Base 3	lm(Days ~ MinTemp + MaxTemp + MaxRain, data=Data)
RBase4	Reduced Base 4	lm(Days ~ MinTemp + AvgRain + MaxRain, data=Data)
RBase5	Reduced Base 5	lm(Days ~ MaxTemp + AvgRain + MaxRain, data=Data)
RBase6	Reduced Base 6	lm(Days ~ MinTemp + AvgRain, data=Data)
RBase7	Reduced Base 7	lm(Days ~ MinTemp + MaxRain, data=Data)
RBase8	Reduced Base 8	lm(Days ~ MaxTemp + AvgRain, data=Data)
RBase9	Reduced Base 9	lm(Days ~ MaxTemp + MaxRain, data=Data)
RBase10	Reduced Base 10	lm(Days ~ MaxRain + AvgRain, data=Data)
RBase11	Reduced Base 11	lm(Days ~ MinTemp + MaxTemp, data=Data)



Table 1 continued.

Model Abb	Full Name	R Code
YAM	Yearly Additive Model	<code>lmer(Days ~ MinTemp + MaxTemp + AvgTemp + MaxRain + AvgRain + (1   Year), data=Data)</code>
RYAM1	Reduced Yearly Additive Model 1	<code>lmer(Days ~ MinTemp + MaxTemp + MaxRain + AvgRain + (1   Year), data=Data)</code>
RYAM2	Reduced Yearly Additive Model 2	<code>lmer(Days ~ MinTemp + MaxTemp + AvgRain + (1   Year), data=Data)</code>
RYAM3	Reduced Yearly Additive Model 3	<code>lmer(Days ~ MinTemp + MaxTemp + MaxRain + (1   Year) , data=Data)</code>
RYAM4	Reduced Yearly Additive Model 4	<code>lmer(Days ~ MinTemp + AvgRain + MaxRain + (1   Year), data=Data)</code>
RYAM5	Reduced Yearly Additive Model 5	<code>lmer(Days ~ MaxTemp + AvgRain + MaxRain+ (1   Year), data=Data)</code>
RYAM6	Reduced Yearly Additive Model 6	<code>lmer(Days ~ MinTemp + AvgRain+ (1   Year), data=Data)</code>
RYAM7	Reduced Yearly Additive Model 7	<code>lmer(Days ~ MinTemp + MaxRain+ (1   Year), data=Data)</code>
RYAM8	Reduced Yearly Additive Model 8	<code>lmer(Days ~ MaxTemp + AvgRain+ (1   Year), data=Data)</code>
RYAM9	Reduced Yearly Additive Model 9	<code>lmer(Days ~ MaxTemp + MaxRain+ (1   Year), data=Data)</code>
RYAM10	Reduced Yearly Additive Model 10	<code>lmer(Days ~ MaxRain + AvgRain+ (1   Year), data=Data)</code>
RYAM11	Reduced Yearly Additive Model 11	<code>lmer(Days ~ MinTemp + MaxTemp+ (1   Year), data=Data)</code>

Table 2. The following table shows the model abbreviations as well as the corresponding AIC score. The table is ordered from lowest to highest AIC score to show the relative significance of each model. The left table shows the lowest half of the models based on AIC, the right table shows the upper half.

Model	AIC
RYAM1	2591.855
RBase1	2593.825
YAM	2595.357
ABase	2595.429
RBase3	2604.958
RYAM3	2612.632
RBase11	2631.024
RBase2	2631.84
RYAM2	2631.893
RYAM11	2633.425
RYAM4	2639.601
RBase4	2640.097
RYAM5	2641.415
RYAM10	2642.56
RBase5	2643.839
RBase10	2648.06
RBase7	2671.806
RYAM7	2678.375
RBase6	2684.654
RBase9	2684.985
RYAM6	2685.44
RYAM9	2689.483
RYAM8	2692.467
RBase8	2693.995

Table 3. This table includes p-values for the fixed effects of the model RYAM1. This table also shows estimates and their corresponding confidence intervals (CI). The marginal and conditional r-squared values are also included.

<u>Table 3</u>				
<i>RYAM1</i>	<i>Estimates</i>	<i>CI</i>		<i>p</i>
Intercept	-22.247	-28.024	— -16.469	0.000135
MinTemp	-0.242	-0.273	— -0.211	7.81E-14
MaxTemp	0.551	0.478	— 0.624	2.58E-13
MaxRain	2.934	2.490	— 3.378	1.05E-10
AvgRain	-13.191	-16.182	— -10.200	1.28E-05
Marginal r-squared		0.237		
Conditional r-squared		0.280		
Observations	485			

## VITA

Caleb Gruber was born in Cleveland, Tennessee where he spent most of his childhood. He graduated from Walker Valley High School, then went to the local university Lee University for his undergraduate experience. Caleb spent 5 years at Lee University, gaining a Bachelor's of Science degree in Biology with a minor in Humanities in May of 2021. In August of 2021, Caleb began to pursue a Master's degree in Environmental Science at the University of Tennessee at Chattanooga. Here, Caleb accepted a graduate teaching assistant role, where he taught Biology labs as he pursued his education.