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Effects of Long-Term Variation in Temperature on Reproductive Phenology in a Population of Eastern Bluebirds (*Sialia sialis*)

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Effects of Long-Term Variation in Temperature on Reproductive Phenology in a Population of
Eastern Bluebirds (*Sialia sialis*)

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Biology

by

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Bachelor of Science in Environmental and Sustainable Science, 2014

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This thesis is approved for recommendation to the Graduate Council.

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ABSTRACT

This study investigates the relationship between multiple temperature variables, to include annual and pre-lay date temperatures with first-egg and mean first-egg lay dates of the eastern bluebird at the Warner Parks in Nashville, Tennessee, USA. Data is collected by citizen scientists for the Eastern Bluebird Nesting Box Project while visiting artificial nest boxes throughout the park and recording observations made during the breeding season. Temperature data is retrieved from the Northwest Alliance for Computational Science and Engineering's Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group, based at Oregon State University. The analyses showed no correlation between annual or pre-lay date temperatures and first-egg and mean first-egg lay dates, despite observable trends. With the results of this study, I conclude that annual and pre-lay date temperatures do not advance first-egg or mean first-egg lay date in the eastern bluebird at this study site.

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DEDICATION

I dedicate my thesis to Dr. Kimberly G. Smith, Amelia Laskey, and to the staff of The Warner Parks. Dr. Smith was more than a major professor. He was friend, a member of my family, and a role model. His contribution to science, whether through research or mentorship to his students, will always be worthy of recognition. You will forever be missed.

I also dedicate this to Amelia Laskey. If she had not started the Eastern Bluebird Nest Box Project (EBNP) at The Warner Parks in 1936, this dataset may have never existed. Thanks to her dedication to ornithological research, I was able to produce this thesis for my degree.

Lastly, without the Warner Parks' staff's continued commitment to the EBNBP, this project may have never lived on. Thanks to The Warner Parks' staff for allowing me to be a part of their team over the years, and especially for granting me permission to utilize their data for my own research.

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Effects of Long-Term Variation in Temperature on Reproductive Phenology in a Population of Eastern Bluebirds (*Sialia Sialis*)

INTRODUCTION

Climate change on Earth is a natural phenomenon that occurs in cycles. The Croll-Milankovitch theory suggests that long-term climate cycles can be explained by small changes in Earth's position to the sun, which results in varying amounts of solar energy reaching our planet's surface (Elias, 1997; Williams, 1998). In part, increases in solar energy reaching Earth's surface causes warming, while decreases in energy result in cooling. The cycle between glacial and interglacial periods result from changes in summer insolation (Kawamura et al., 2007).

We are currently in the Quaternary Period of the Cenozoic Era, and during this period, numerous advancements and retreating's of ice sheets have occurred since its beginning roughly 2.4 million years ago (Hewitt, 2000). In the first 1.5 million years of the Quaternary Period, the Arctic ice cap's ice sheets would advance and recede approximately every 41,000 years, while they have occurred approximately every 100,000 years in the last 0.9 million years (Hewitt, 2000).

Greenhouse gases are gases trapped within our atmosphere. The five greenhouse gases mainly contributing to the current rapid climate changes are carbon dioxide (CO₂), methane (CH₄), nitrous oxide (N₂O), Water vapor (H₂O), and fluorinated gases. One of the most abundant and detrimental greenhouse gases is CO₂, and as of August 2020, mean concentrations measured at Mauna Loa Observatory, Hawaii were 412.55 parts per million (ppm) (NOAA, 2020). That is a 47 % increase from the pre-1700 annual average of 280 ppm (EPA, 2020). The drastic increase in greenhouse gas emissions are primarily due to anthropogenic activities such as industrial processes, livestock and agriculture practices, the combustion of fossil fuels, as well as the decay of fossil fuels and other organic materials (IPCC, 2014).

The effects climate change has on our environment extend beyond just warmer and cooler temperatures. What is novel is that global warming is occurring at an unprecedented rate. In the last 1,400 year, 1983 to 2012 is likely to be the warmest period on record and is even more likely the warmest three consecutive decades of the last 800 years (IPCC, 2014). The worst-case scenario for the year 2100, with no emission control, would be a mean rise in global surface temperature from 1990 of 2.3°C (Webster et al., 2001). This warming, better known as global warming, is having dramatic effects on our planet. Indeed, global warming has already affected our environment in many ways, including the melting of sea ice, which has had a significant impact on rising sea levels during the twentieth century (Douglas, Kearney, & Leatherman, 2001). Sea levels rise due to sea ice melting, which occurs by the ocean absorbing most of the solar energy contained by greenhouse gases in our atmosphere. This oceanic warming ultimately changes the distribution, anatomy, and diversity of marine life (Brander, 2007; Harley et al., 2006). The effects of global warming go beyond the atmosphere and ocean, though, with changes evident in terrestrial ecosystems as well.

Major terrestrial communities responses to global warming through shifts in the ranges and phenology of their constituent species (Barry, Baxter, Sagarin, & Gilman, 2017; Julia, 2014; Parmesan & Yohe, 2003; Thackeray et al., 2010). One review observed an average change in range of 6.1 km per decade among 99 species of birds, butterflies, and alpine herbs (Parmesan & Yohe, 2003). As for phenology, plants and animals have shown a multitude of reactions to climate change. Plants have responded to climate change with earlier budding, earlier fruit-setting, and longer growing seasons (Parmesan, 2006; Parmesan & Yohe, 2003). Due to animals' physiological and behavioral characteristics, their phenological responses to climate change are different from those of plants; however, many species have advanced their phenology

significantly since 1950 by 2.88 days per decade (Cohen, Lajeunesse, & Rohr, 2018). Although precipitation is a predictor of phenological advancements in amphibians in temperate zones, temperature seems to be a better predictor of these advancements (Cohen et al., 2018). Mammals have shown a strong reaction to shifting growing seasons due to temperature changes in polar regions with reduced body mass, earlier termination of hibernation, earlier onset of reproduction, and possibly higher metabolic rates (Forrest & Miller-Rushing, 2010; Lovegrove, 2000; Teplitsky & Millien, 2014; Yom-Tov & Yom-Tov, 2004). The most evident changes in phenology among vertebrates are seen within the birds, where the timing of reproduction has changed for many species (Peterson, 2011).

The breeding season for birds is an annual event triggered by several physiological and environmental factors. These cues cause birds' testes and ovaries to increase in size and with their growth comes the production of sperm and ova, a physiological response to the time of year, day length, and temperature. In addition to these physiological responses, as the breeding season approaches, birds attempt to align raising their progeny with food abundance (Lack, 1950; Martin, 1987), so breeding and food abundance match in time. A plethora of evidence suggests climate change has led to changes in many species' phenology (Blaustein et al., 2017; Brown, Li, & Bhagabati, 1999; Dudley, Glue, & Thomson, 1997). Birds migrate earlier due largely to increasing mean global temperatures (Cotton, 2003; Hüppop & Hüppop, 2003; Marra, Francis, Mulvihill, & Moore, 2005; Mills, 2005). This study focuses on shifts in reproductive phenology, specifically lay date, of eastern bluebirds using thirty years of nesting data from birds using approximately 45-50 nest boxes located at the Warner Parks, Nashville, Tennessee, USA.

Effects of Long-Term Variation in Temperature on Reproductive Phenology in a Population of Eastern Bluebirds (*Sialia Sialis*)

INTRODUCTION

Recent rapid changes in our climate can be explained by anthropogenic activities (IPCC, 2014). Some continents have experienced more changes than others in the last five centuries, with the Northern Hemisphere showing a greater increase in surface temperatures than the Southern Hemisphere (Huang, Pollack, & Shen, 2000). From 1880 to 2012, an average increase of 0.85 °C in global land and ocean surface temperatures was identified, with the Northern Hemisphere's warmest 30 years in 1,400 years likely being between 1983 and 2012 (IPCC, 2014). Shrinking glaciers, sea level rise, increased frequency and severity of natural disasters, and heat waves are all changes observed as a result of climate change. These same changes in our climate have also already affected the geographic distributions, phenology, and life-history traits of many plant and animal species.

Many organisms have responded to global warming, with plants flowering earlier and many bird populations advancing egg-laying (Crick & Sparks, 1999; Dunn & Dunn, 2019; Parmesan & Yohe, 2003), especially in response to ambient temperatures in the weeks prior to egg laying (Both et al., 2004; Crick & Sparks, 1999; Visser et al., 2003). These shifts are more pronounced north of 50°, where temperatures have warmed rapidly in the last 50 years (Root et al., 2003). Most studies of the effects of global warming on bird phenology have occurred in Europe, where some of the most significant warming trends are observed (Julia, 2014; Parmesan & Yohe, 2003). Consequently, studies in other regions are needed to better understand the geographic extent of these trends. However, documenting these trends requires long-term studies, which are often difficult to obtain.

Whether organized and operated by scientists or citizen scientists, nest box trails provide an excellent opportunity for researchers to study long-term trends in bird populations. Because of the sheer amount of nesting data submitted by researchers and volunteers, large-scale studies can help determine the effects of temperature on egg-laying. One study analyzed approximately 92,000 nesting records from 36 bird species in the UK and found that 72% of species advanced egg-laying in response to warmer pre-laying temperatures among at least two breeding seasons and 58% of these species showed long-term trends of laying eggs earlier in response to temperature (Crick & Sparks, 1999). Migrant and resident birds have been shown to respond differently to temperature where they breed, with larger magnitude response among resident species (Berthold, Fiedler, Schlenker, & Querner, 1998) and migrants travelling the furthest being the least responsive to warming temperatures (Usui, Butchart, & Phillimore, 2017). Resident birds are hypothesized to exhibit greater flexibility in their ability to adjust their laying date in response to temperature because unlike migratory species, their arrival to the breeding area does not constrain timing of reproduction (Both & Visser, 2001). Although the number of studies investigating changes in breeding bird phenology have increased rapidly over the past several years, additional studies are valuable for understanding how robust observed trends are.

In this study, relationships between climate variables (annual mean temperature, annual mean maximum temperature, annual mean minimum temperature, pre-lay date mean temperature, pre-lay date mean maximum temperature, and pre-lay date mean minimum temperature) and reproductive phenology (first-egg lay date and mean first-egg lay date) of an understudied species on the topic are investigated at a metropolitan park in Nashville, Tennessee, USA. The study species is the eastern bluebird (*Sialia sialis*) (hereafter referred to as “bluebird”), a secondary cavity-nesting bird. Bluebirds are a small thrush species with sexual dichromatism,

where the male has more vibrant colors than the female. Their preferred habitat is of open fields and meadows with little to no understory, allowing the capture of their food to be done so more efficiently. A bluebird's diet is primarily insectivorous, but small fleshy fruits are added in late summer and into winter. Breeding pairs in Tennessee form from November to the end of January (Laskey, 1939) and have multiple broods each breeding season. They are known to be either resident or short-distance migrants that readily accept artificial nest boxes. Nest boxes are often easily located, easy to access, and cavity nesting birds are commonly researched to study changes in reproductive phenology (Sockman and Courter, 2018). These factors make bluebirds an ideal species to study. The Nashville Basin has suitable topography throughout, with like-vegetation and climate, presumably supporting bluebird reproduction, making it a good location for studying the effects of climate on lay date in this species. The data presented in this study is likely representative of other bluebird populations in Central Tennessee.

Here, the relationship between various temperature variables and lay date within and among years are investigated. It is hypothesized that first-egg lay dates and mean first-egg lay dates would correlate negatively with annual mean, annual mean maximum, and annual mean minimum temperatures over the length of this study's time period. The effect pre-lay date temperatures might have on first-egg lay date and mean first-egg lay date are also examined. Here, it is hypothesized that first-egg lay date and mean first-egg lay date would have a negative correlation with pre-lay date mean, pre-lay date mean maximum, and pre-lay date mean minimum temperatures

METHODS

Study site and data collection

The study site is located at Edwin and Percy Warner Parks (hereafter, “The Warner Parks”) (36°03’N, 86°54’W) in the suburbs of Nashville, Tennessee, USA. At more than 1,254 ha, the Warner Parks, which opened in 1927, are collectively one of the largest municipally run parks in the state and are managed by the Metro Nashville Parks and Recreation Department. The parks are comprised of second growth forest, regenerated since logging and farming, comprised primarily of sassafras (*Sassafras albidum*), American beech (*Fagus grandifolia*), black walnut (*Juglans nigra*), and tulip poplar (*Liriodendron tulipifera*). Fields and meadows in the park, where the nest boxes are located, are the result of human disturbance and are dominated by exotic grasses and forbs. The Eastern Bluebird Nest Box Project (EBNBP) is the longest operating project at the park and is one of the longest operating bluebird trails in existence today (1936 – present). The EBNBP was created by amateur ornithologist, Amelia Laskey.

Egg-lay dates were obtained from over 1,600 nest records submitted by citizen scientists to the EBNBP at the study site from 1985 to 2014. Nest records prior 1985 were recorded on index cards and were too numerous and disorganized to retrieve data in a timely manner. A typical nest record contained box number, dates, and number of eggs from each nest box observation. Over the 84 years in which the EBNBP has been active, approximately 10-50 nest boxes have been monitored throughout the parks in a given year, with 90-95% of 45-50 nest boxes monitored since 1985.

In an effort to estimate egg-lay dates as accurately as possible, only nest attempt records with observed dates were used to approximate lay dates (i.e., first egg date, date clutch was complete, date eggs hatched, and date nestlings fledged). If the first egg was observed on the

date it was laid, first-egg lay date was recorded. The bluebird is known to lay one egg per day (Hartshorne, 1962). Thus, the number of eggs present once the clutch was completed was used to determine the lay date by counting back the same number of days as there are eggs. Although the duration of incubation in the bluebird is quite variable (Peakall, 1970), the typical incubation period of 14 days (Gowaty & Plissner, 2020) was used to estimate the date a clutch was completed, by subtracting 14 days from the date in which the eggs hatched. Nestlings in parts of the southern regions of the United States fledge in 17.6 days (Gowaty & Plissner, 2020) on average. By counting back 17.6 days from the date the young fledged, the hatch date was estimated. Mean first-egg lay dates were determined by averaging all recorded first-egg lay dates that fell within the 30 days that followed the first-egg lay date of each year. All records with insufficient date data were excluded from analyses.

Temperature Data

Temperature data was obtained from the Northwest Alliance for Computational Science and Engineering's Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group, based at Oregon State University on 3 March 2020. PRISM processes National Oceanic and Atmospheric Administration's (NOAA) data, and many other (non-NOAA) data sources through the PRISM system to generate its datasets for the entire continental United States from 1895 to present.

Annual mean temperature was generated by averaging the mean monthly temperatures of each year. Annual mean maximum and annual mean minimum temperatures were calculated in the same manner, by averaging their respective monthly mean temperatures. Pre-lay dates were comprised of the 30-day window before the mean first-egg lay date for each year (e.g., if the

mean first-egg lay date for a given year is 10 April, then the 30-day window is 11 March to 9 April). Using daily mean temperature data from the pre-lay date window, an average for the 30-day window were calculated. Pre-lay date mean daily minimum and mean maximum temperatures were calculated in the same manner; the only difference being that mean daily minimum and mean maximum temperatures were averaged instead of mean temperatures. Because the parks' location exists within four grids of PRISM's data explorer map, these temperature variables were averaged using data from all four grids.

Statistical Analysis

Linear regressions were used to see if any trends were present over the span of this study for annual mean, annual mean maximum, and annual mean minimum temperatures. Long-term trends for first-egg lay date and mean first-egg lay date were analyzed using linear regressions. Analysis of year was conducted to see if any trends existed over time, which may have indicated a driving force worth exploring. To test the prediction that first-egg date and mean first-egg date would negatively correlate with annual mean temperature, annual mean maximum temperature, annual mean minimum temperature, pre-lay date mean temperature and pre-lay date mean maximum temperature, and pre-lay date mean minimum temperature, a linear regression model was used for first-egg lay date and a weighted linear regression model was used for mean first-egg lay date; the number of first nests per year was used as the weighting factor. All analyses were conducted using R (R Core Team, 2020).

RESULTS

Summary of nesting data

From 1985 to 2014, 1,453 nest records exist, of which 37% did not provide sufficient date data to use in phenology analyses. Therefore, 63% (n=909) of nest attempts were considered for this study. Out of the 909 nest attempts examined, the number that met the criteria for inclusion (n = 412) varied among years (Table 1). On average, each year consisted of 13.73 nest attempts with a standard deviation of 5.13 nests.

Associations of temperature measures with time

Although annual mean temperatures have increased since 1985, there is considerable variation from year to year, and this trend is not statistically significant ($p = 0.47$, Figure 1a). The lowest and highest recorded annual mean temperature observed in the 30-year period of the study were 13.5 °C in 1989 and 15.65 °C in 2012, respectively. Annual mean maximum temperatures were highly variable between 1985 and 2014 and were not related to year ($p = 0.95$, Figure 1b). The highest annual mean maximum temperature was 22.4 °C in 2007. Annual mean minimum temperatures have risen slightly in the 30-year period of the study, but again this result was not statistically significant ($p = 0.08$, Figure 1c). The lowest recorded annual mean minimum temperature from 1985 to 2014 was 6.7 °C in 1988.

Associations of lay dates with time

First-egg lay dates varied from 1985 to 2014, with a trend for the first egg of the breeding season to advance through time ($p = 0.06$, Figure 2a). Mean first-egg lay dates were much more variable but also unrelated to year ($p = 0.37$, Figure 2b).

Associations of temperature measures with first egg lay dates

First-egg lay dates show a trend for the first egg of the breeding season to advance with annual mean ($p = 0.16$, Figure 3a), annual mean maximum ($p = 0.33$, Figure 3b), or annual mean minimum temperatures ($p = 0.06$, Figure 3c) over the study period.

The trend for first-egg dates of the breeding season delay with pre-lay date mean temperatures ($p = 0.26$, Figure 3d), pre-lay mean maximum temperatures ($p = 0.30$, Figure 3e) or pre-lay mean minimum temperatures ($p = 0.27$, Figure 3f).

Associations of temperature measures with mean first-egg lay dates

Mean first-egg lay dates also varied from 1985 to 2014, with a trend for the mean first egg of the breeding season advancing with annual mean ($p = 0.21$, Figure 4a), annual mean maximum ($p = 0.22$, Figure 4b), and annual mean minimum temperatures ($p = 0.29$, Figure 4c).

Mean first-egg lay date is delayed over the span of the study period with pre-lay date mean temperatures ($p = 0.32$, Figure 4d), pre-lay mean maximum temperatures ($p = 0.54$, Figure 4e), and pre-lay mean minimum temperatures ($p = 0.14$, Figure 4f).

DISCUSSION

Overall, the results did not support the hypotheses. The predictions that the bluebird would advance its first-egg lay date and mean first-egg lay date to warmer annual mean, annual mean maximum, annual mean minimum, pre-lay date mean, pre-lay date mean maximum, and pre-lay date mean minimum temperatures were not supported by these results. Below, these results are discussed in more detail placing them within the broader context of studies investigating how climate change has and has not affected species breeding phenology.

Over the past 30 years, annual mean and annual mean minimum temperatures have increased at the study site, with a strong positive trend for increased annual mean minimum temperature. Annual mean maximum temperatures have remained fairly constant but do show a very weak negative trend for decreased temperature with time. These trends are consistent with the annual mean and annual mean minimum temperature warming observed at the global scale (Folland et al., 2002; IPCC, 2014). The lack of change in annual mean maximum temperatures might be explained by locational climate variability (Mahlstein et al., 2011), but few studies exist that focus on temperature variations at this level (Stott et al., 2000; Stott, 2003; Gillett et al., 2008; Zhang et al., 2006).

A strong negative trend is observed for first-egg lay date over time and with annual mean minimum temperature for this study, while a weak negative trend is present with annual mean and annual mean maximum temperatures. An opposite and weak positive trend was present among first-egg lay date and pre-lay date mean, pre-lay date mean maximum, and pre-lay date mean minimum temperatures. However, no significant advancement or delay is evident. One study in North America showed the bluebird advanced their lay date to the average of March, April, and May temperatures across the bluebird's breeding range, over a 50-year period (Torti and Dunn, 2005), while another study in Ohio showed advancement related to March and April temperatures (Sockman and Courter, 2018). Neither study specified whether their bluebird populations were migratory or resident birds, which made comparisons difficult. Similar patterns with advanced lay dates were expected with this population of bluebirds, but variances within species do occur. The same study from Ohio, showed bluebirds lay date varied differently in response to temperature based on their location in the state (Sockman and Courter, 2018). European pied flycatchers (*Ficedula hypoleuca*) throughout most of the species' breeding range

were shown to advance their lay date over time to spring temperature, while pied flycatchers in parts of Russia, Wales, and Spain did not (Both et. al, 2004). The same trends were observed among two populations of collared flycatchers (*Ficedula albicollis*), where one population advanced and the other did not (Both et. al, 2004).

Similar negative trends were observed with mean first-egg lay date over time, and with annual mean, annual mean maximum, and annual mean minimum temperatures as it did with first-egg lay date, but all trends appeared to be weak. Weak positive trends were observed with mean first-egg lay date and pre-lay date mean, pre-lay date mean maximum, and pre-lay date mean minimum temperatures. As discussed earlier, trends may be observed in one species or population in a specific location, while they may not be observed in others. This applies to migratory versus resident species as well. One study in northern Italy showed earlier trends toward egg-laying dates among two migratory species, the barn swallow (*Hirundo rustica*) and the common swift (*Apus apus*) (Rubolini et. al, 2007). However, no long-term trends were observed in two resident birds, the European starling (*Sturnus vulgaris*) and the Italian sparrow (*Passer italiae*) (Rubolini et. al, 2007). It is also important to note that while the European starling did not respond to mean temperatures from February to April in the study from northern Italy, it did strongly vary its lay date in response to mid-winter temperatures in British Columbia, Canada (Williams et al., 2015).

The temperature and lay date variables in this study have potential limitations. Sample size varied greatly from 1985 to 2014 and is likely not representative of the bluebird population at the Warner Parks, where only four lay dates are analyzed in 1995, with 23 in 2009. In one study of 36 species, the only five populations that did not show a response to temperature were with a relatively small annual sample size (Crick and Sparks, 1999). The smaller sample size of

this study may have made it difficult to identify significant relationships between the timing of reproduction and temperature. Another point to consider is that the data was collected by citizen scientists that may have lacked scientific data collecting experience, a common design flaw with many citizen science projects (Lukyanenko et al., 2016). This limitation may have created possible inconsistencies with the record keeping process, potentially recording inaccurate lay dates. Other limiting factors that possibly interfered with finding significant results were the temperature variables used in this study. Various temperature windows, like spring, winter, and pre-lay date temperatures were used to investigate their effect on lay date in multiple studies. Modeling this study using said research proved difficult, due to these windows not always being clearly defined. For example, spring temperature in two studies lacked a specific timeline and are simply defined as spring (Dudley et al., 1997; Crick and Sparks, 1999). Lacking clear definition for seasons in the literature, pre-lay date temperatures for this study are modeled using mean, mean maximum, and mean minimum from the 30-day window prior to the mean first-egg lay dates for each year. This decision is based on other studies using similar methods (Visser et al., 2003; Both et al., 2004; Williams et al., 2015). While bluebirds at the Warner Parks are considered to be residents, there is no evidence to verify these assumptions, which is important because temperature can affect the phenology of migrant and resident birds differently (Rubolini et. al, 2007).

Future research to consider using this dataset would be to investigate the relationships between mid-winter temperatures and lay date, where like a population of resident European starlings, advancement of lay dates is possible (Williams et al., 2015). Other research to consider is whether bluebirds align their lay date so that hatch date coincides with food abundance, a relationship this study did not consider. To do this it would be important to verify emergence

dates for staple prey species to see if bluebirds do in fact align lay date with food availability. This would possibly provide a different 30-day window to investigate, rather than the 30-day window of this study. Although not discussed in this study, other data exists from this data set (e.g. band numbers, clutch size, hatch date, number of nestlings, and fledge date). Temperature's effect on clutch size is worth exploring, although not many studies show any cause and effect. Another consideration is whether there is a relationship with lay date and fledging success. These ideas are premised on other research investigating these particular variables.

CONCLUSIONS

This study highlights the effect of temperature across different timeframes on avian reproductive phenology. As it compares to other studies, this study shows bluebirds' response to temperature varies to a mentionable degree by location. The results of this study compared with results of similar studies may emphasize the variable effects of temperature on avian reproductive phenology between migrant and resident species and are consistent with the differences observed in other species, showing not all populations of the same species advance their lay date to temperature. It also shows the importance of determining whether a study population is a migrant or resident species, because there may be a different response between the two among bluebirds. The results and considerations of this study, coupled with further research, are important in determining breeding success of the bluebird.

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Tables and Figures

Table 1. Observed Nest Attempts

Year	Total Clutches	First Egg Clutches
1985	23	6
1986	25	13
1987	22	10
1988	16	6
1989	26	11
1990	25	10
1991	22	13
1992	22	14
1993	20	10
1994	22	12
1995	11	4
1996	16	10
1997	16	8
1998	23	8
1999	20	9
2000	33	14
2001	50	21
2002	50	19
2003	42	11
2004	43	15
2005	38	17
2006	38	16
2007	38	20
2008	43	19
2009	46	23
2010	35	17
2011	36	22
2012	29	17
2013	36	18
2014	43	19

Notes: Table shows the total number of eastern bluebird clutches observed each year at the Warner Parks, Nashville, Tennessee USA and those first-egg clutches within the 30-day window following the first-egg lay date of each year.

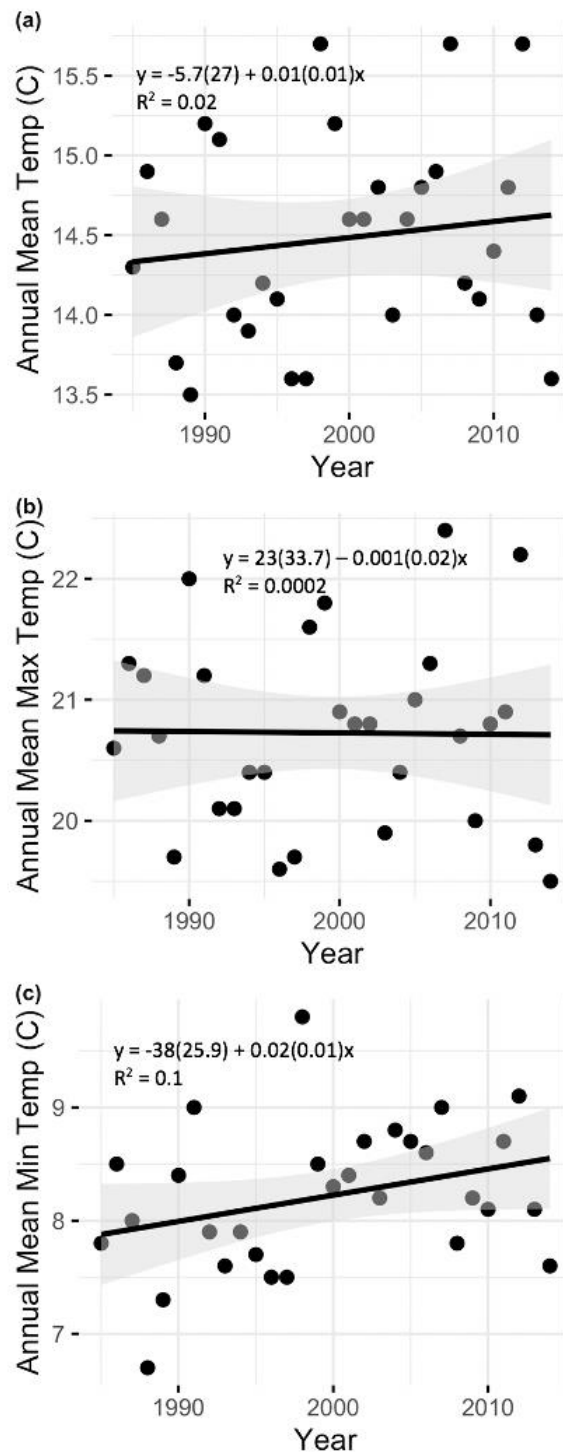


Figure 1. Associations of annual mean temperature, annual mean maximum temperature, and annual mean minimum temperature with year over a 30-year span at the Warner Park, Nashville, Tennessee, USA. Trend lines represent linear regressions, which showed no statistically significant (all $P > 0.05$) long-term trends in temperature. The gray band represents the 95% confidence interval of the regression.

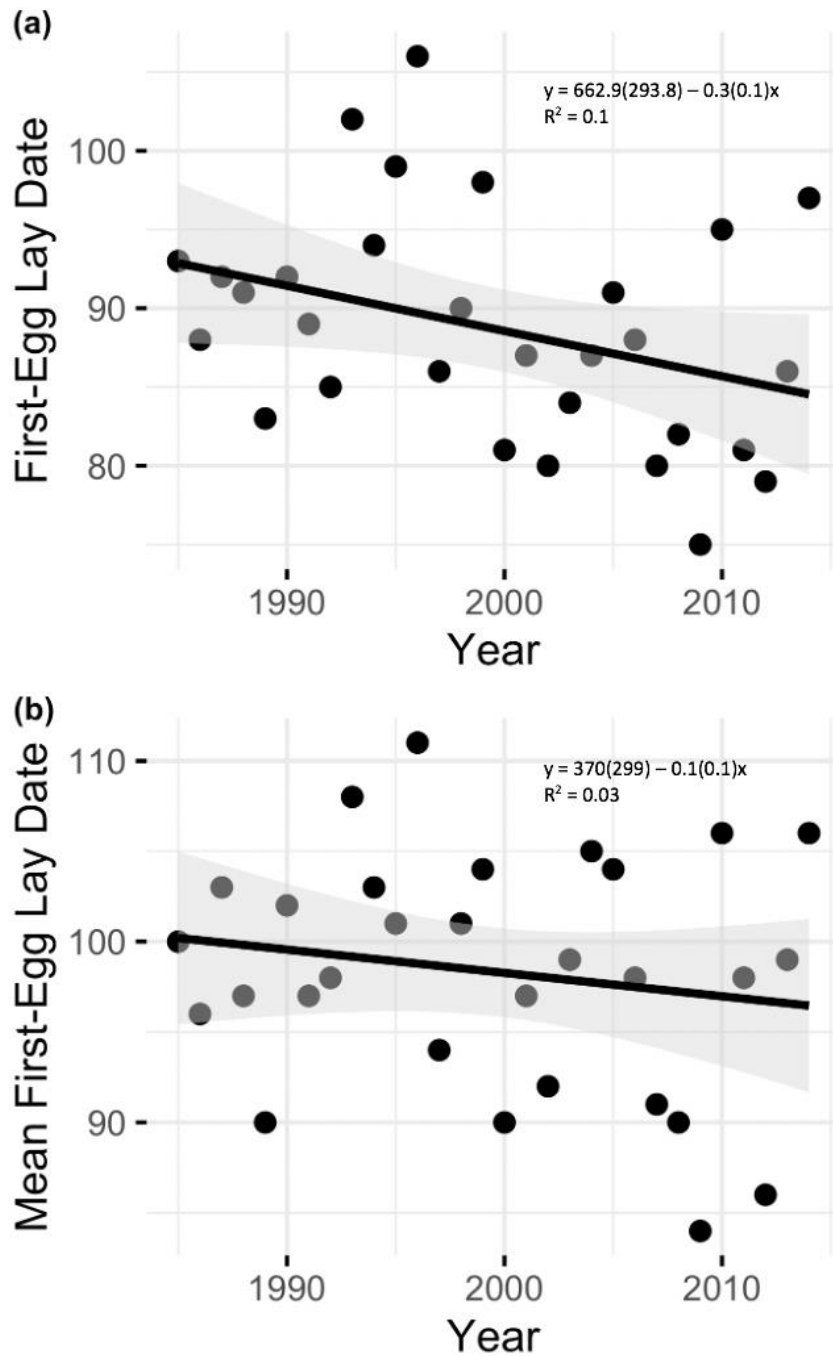


Figure 2. Linear regressions of first-egg lay date and mean first-egg lay date in relation to year over a 30-year span. Lay date values are day of year since 1 January = 0. Points show first recorded observation of an egg laid each year (a), and the mean first-egg laid each year (b). Lines are linear regressions, which showed no statistically significant long-term change in first-egg lay date and mean first-egg lay date ($p > 0.05$). The gray bands represents the 95% confidence interval of the regression.

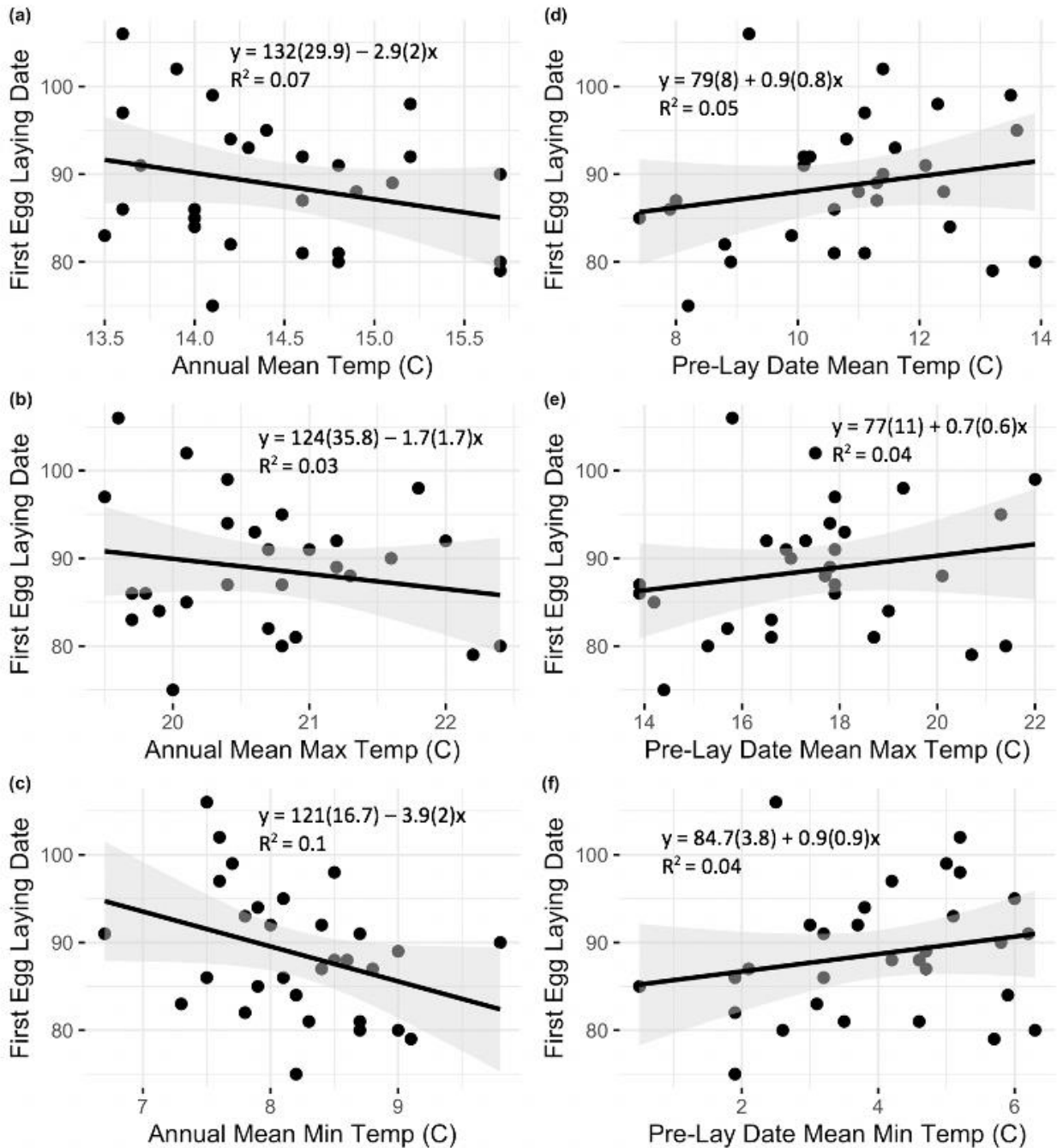


Figure 3. Linear regressions of first-egg lay date in relation to annual mean temperature, annual mean maximum temperature, annual mean minimum temperature, pre-lay date mean temperature, pre-lay date mean maximum temperature, and pre-lay date mean minimum temperature over a 30-year span. Lay date values are day of year since 1 January = 0. Points show first recorded observation of an egg laid each year. Lines are linear regressions, which showed no statistically significant changes in first-egg lay date in response to annual temperatures (a, b, and c), and pre-lay date temperatures (d, e, and f). The gray bands represent the 95% confidence interval of the regression.

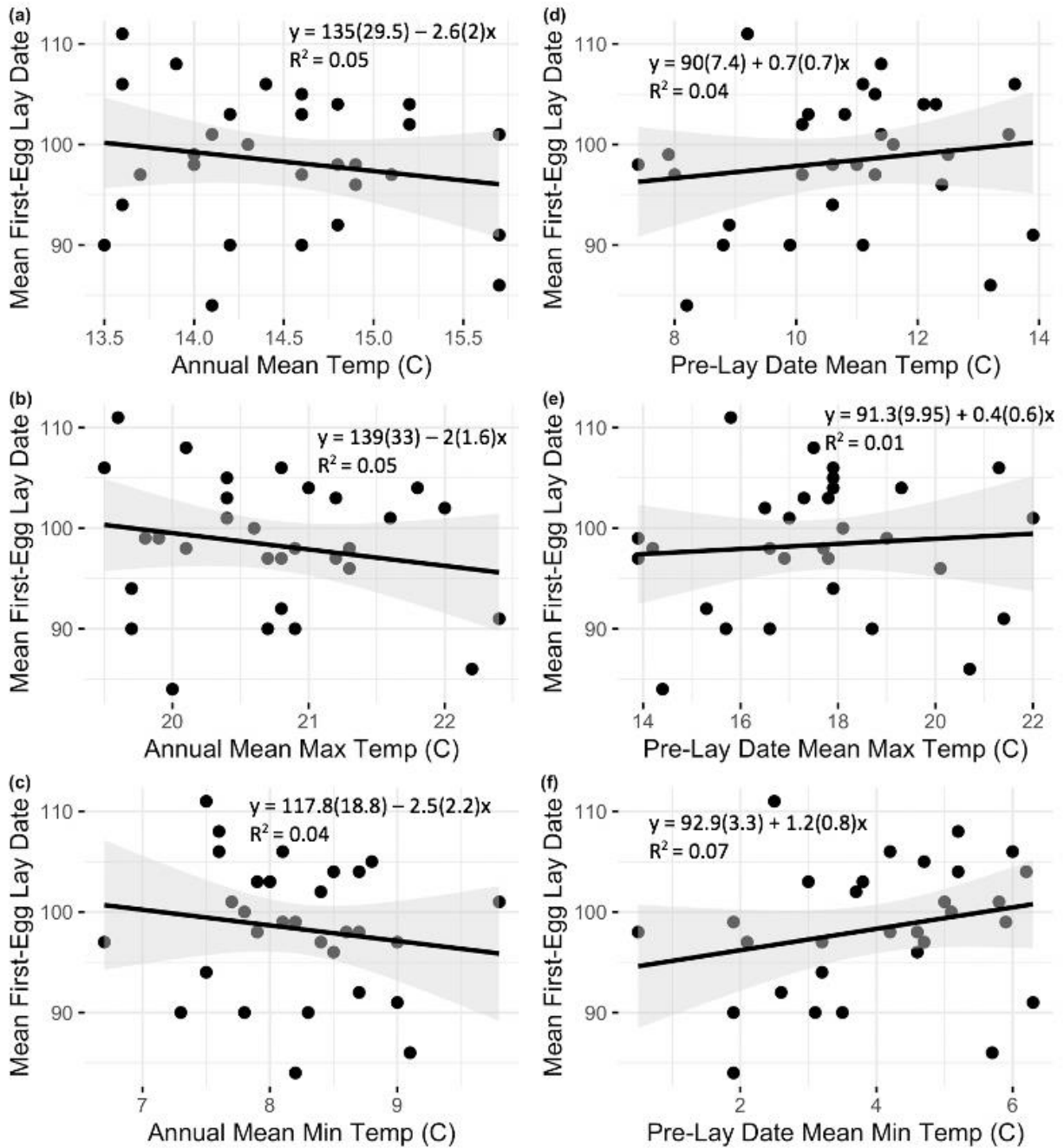


Figure 4. Linear regressions of mean first-egg lay date in relation to annual mean temperature, annual mean maximum temperature, annual mean minimum temperature, pre-lay date mean temperature, pre-lay date mean maximum temperature, and pre-lay date mean minimum temperature over a 30-year span. Lay date values are day of year since 1 January = 0. Points show the mean first recorded observations of eggs laid each year. Lines are linear regressions, which showed no statistically significant changes in mean first-egg lay date in response to annual temperatures (a, b, and c), and pre-lay date temperatures (d, e, and f). The gray bands represent the 95% confidence interval of the regression.