# The effect of climate variability on the breeding behaviour of the Eastern Bluebird (*Siala sialis*) and the Mountain Bluebird (*Siala currucoides)* in different geographical areas throughout North America

Joren Bruggink

Toegepaste Biologie

12 November 2018 Almere

Floris Keizer

# The effect of climate variability on the breeding behaviour of the Eastern Bluebird (*Siala sialis*) and the Mountain Bluebird (*Siala currucoides)* in different geographical areas throughout North America

Joren Bruggink

Toegepaste Biologie

12 November 2018 Almere

Floris Keizer

# Preface

I am Joren Bruggink and a 4th year student from the study applied biology in Aeres University of Applied Sciences Almere. This is my thesis project for graduation.

I want to thank my supervisor from my last internship Gretchen Wagner for giving me advice, helping me with the analysis and for the feedback and help with the spelling. I also want to thank Floris Keizer and Maaike Cox for giving feedback on the research plan. Furthermore, I want to thank my afstudeerkring for the help and the useful discussion, in particular I want to thank Luca Versteege for giving feedback on the report. Lastly, I want to thank my parents Astrid Bijster and Henry Bruggink for checking the report for spelling and overall support.

# Content

## Summary

Climate change has great ecological consequences for animals. Furthermore, these changes can differ among different geographical areas. In birds it has been found that they can cause mismatches with their food supply as they do not respond to climate change at the same pace. By understanding more about these consequences on a full geographic range, more can be learned about the effects of climate change on birds.

In order to accomplish this, a dataset using citizen collected nest records from the eastern bluebird and the mountain bluebird over North-America were received from Nestwatch and analysed using linear regression models. Furthermore, models were created that interacted temperature and year with the breeding parameters in order to see how they progressed in the last twenty years over the geographic range and how they responded to change in temperature.

The geographic variation of the breeding parameters was mostly alike to what previous studies found: the clutch size increased from south to north and from coastal areas to more land-inwards. Other breeding parameters performed better in the western range for both species. This was the same for the interactions with year and temperature; the breeding parameters did better in the west in relation with year and temperature.

The mountain bluebird had an increase in clutch size at higher elevations, this is in contrast with previous studies. The mountain bluebird performed in other breeding parameters better as well at higher elevations, with more fledglings and hatch rate. The eastern bluebird, however, had no significant effect with altitude. The breeding performance across the altitude in the eastern bluebird was connected with year and temperature. The hatch rates and fledgling rates were positively affected by year in higher nests. Lower nests had larger clutch sizes during warm temperature as higher nests had.

This study showed that both bluebird species may be affected by climate change. Both performed worse at higher temperatures, even though eastern bluebirds did perform better over time. The geographic variation in breeding showed that populations performance differed significantly over different areas as well.

# Samenvatting

Klimaatverandering heeft grote ecologische consequenties op dieren. De veranderingen die dieren meemaken kunnen veel verschillen afhankelijk van de geografische locatie. Bij vogels is ontdekt dat klimaatverandering ervoor kan zorgen dat een 'mismatch' ontstaat tussen de vogels en hun voedselbron, omdat ze niet met dezelfde snelheid op de klimaatverandering reageren. Met het beter begrijpen van de consequenties van klimaatverandering over een volledige geografische reikwijdte, kan meer geleerd worden over de gevolgen van klimaatverandering op vogels.

Om dit te bereiken is een dataset gebruikt met nestdata van de roodkeelsialia en de bergsialia over heel Noord-Amerika verkregen van Nestwatch. Deze dataset is geanalyseerd met lineaire regressiemodellen. Verder zijn er modellen gemaakt waarin temperatuur en jaar met de broedparameters interacteren, zodat er gezien kan worden hoe het broeden vorderde in de laatste twintig jaar en hoe het broeden veranderd op verandering in temperatuur.

De geografische variatie binnen de broedparameters was over het algemeen in lijn met vorige studies: de nestgrootte werd groter van zuid naar noord en van kust tot meer landinwaarts. Andere broedparameters deden het beter in het westelijke verspreidingsgebied van beide soorten. Dit gold ook voor de interacties met jaar en temperatuur; de broed parameters deden het beter in het westen in relatie met jaar en temperatuur.

Er was een toename van nestgrootte bij de bergsialia op grotere hoogtes, dit was in contrast met eerdere studies. De andere broedparameters van de bergsialia deden het ook beter op grotere hoogtes. De roodkeelsialia, echter, had geen significant effect met de hoogteligging. Het broeden van de roodkeelsialia op verschillende hoogtes was wel afhankelijk van de jaar en temperatuur, met betere broed/uitvlieg ratio's in de laatste jaren in hooggelegen nesten en grotere nesten in relatie met temperatuur in lage nesten.

Deze studie laat zien dat beide sialia soorten effecten ondervonden van klimaatverandering. Beide soorten deden het slechter bij hogere temperaturen, ook al deed de roodkeelsialia het wel beter in de laatste jaren dan in de eerdere jaren. De mate van geografische variatie liet zien dat populaties in verschillende gebieden anders reageerden op klimaatverandering.

## 1. Introduction

The climate is changing, and this is likely anthropogenic, with more than half of the observed increase in temperature in the period between 1951 and 2010, probably caused by an increase in greenhouse gasses (IPCC, 2015). Climate change has strong ecological consequences on species (reviewed by McCarthy, 2001). Additionally, species may have different responses to climate change in different geographic areas, as was found in butterflies by Menzel et al. (2006). Another example found in birds was that great tits (*Parus major*) in the United Kingdom are seemingly adapted well to climate change (Charmantier et al., 2008), while great tits in the Netherlands are lagging behind (Nussey et al, 2005). For this reason, it is important to look at the responses of species in different areas to get a more complete picture of the consequences of climate change.

The effect of climate change is often studied in birds, because they are well studied and are relatively easy to observe (Møller & Fielder, 2010). The most established effect is that birds are generally advancing the timing of laying eggs (Crick et al., 1997; Both & Visser, 2005; Wright et al., 2009; Dunn & Winkler, 2010; Møller et al., 2010). When breeding, birds seem to adjust their laying date to ensure that hatching occurs during a food peak (Van Noordwijk et al, 1995; Both, 2010). One of the greater risks of climate change is that it might make it more difficult for birds to match their chicks' development to the food supply. This may result in an ecological mismatch, because different components of the food chain may shift their biological timing at different rates, in response to the change in climate (Visser et al., 1998; Visser et al., 2004; Both & Visser, 2005). In the study from Nussey et al. (2005), for example, caterpillars adapted more quickly to climate change than great tits did.

There is often geographical variation in breeding patterns within and across species. One of the most established effects is that clutch size increases with latitude in the northern hemisphere (reviewed by Sanz, 1998). In addition, Sanz (1998) found that the mean lay date (defined by the number of days that the first egg is laid after January the 1$^{st}$) increased with latitude. In both Europe and North America, clutch size was larger in eastern areas than in the west (reviewed by Klomp, 1970). Dhont et al. (2000) looked at the effect of latitude and longitude on the breeding biology in the eastern bluebird (*Siala sialis*) in the United States. They found a general effect of larger clutch size at higher latitudes, however they also found that the difference in breeding patterns in this instance made the relation somewhat complicated. In the south, clutch size peaked in the middle of the breeding season with relatively small clutch sizes in the beginning of the breeding season, while in the north clutch size was biggest early in the breeding season and then gradually declined.

The elevation at which birds live can also influence breeding performance. Multiple studies have found that clutch size decreased with increasing elevation (Badyaev, 1997; Sanz, 1998; Badyaev & Ghalambar, 2001). At higher elevations, birds provide more parental care, which is likely due to the more unpredictable environment (Badyaev & Ghalambar, 2001). This may point to a trade-off at high elevations, where birds produce fewer offspring but provide them with more parental care (Badyaev & Ghalambar, 2001).

To understand more about the impact of climate variability on birds over a wide geographical range, more needs to be learned about responses in different geographical areas. This study will focus on the effect of climate variability on the breeding behaviour of two bluebird species in North America: the eastern bluebird (*Siala sialis*) and the mountain bluebird (*Siala currucoides*), and how this effect varies across longitudes, latitudes and elevations. For both species, a large amount of data is available and given their relatedness they can be compared well to each other.

The eastern bluebird and the mountain bluebird mostly live in separate areas throughout North America. The mountain bluebird lives in the western part of North America, while the eastern bluebirds live in the eastern area of the country. Together these species occupy a large part of the United States and a small part of Canada and thereby stretch their breeding range over a large geographical range. The mountain bluebird on average lives in higher elevational areas than the eastern bluebird, hence this research will account for elevation as well. To determine the effect of climate change on these bird species, this study will analyse a database of nest records collected by citizens over the period between 1997 and 2017 in North America.

The main aim of this research is to determine effects of climate patterns on the breeding behaviour of the eastern bluebird and the mountain bluebird throughout different geographical ranges in North America within the period between 1997-2017. In addition, this research will investigate four sub questions with the aim to understand more specific aspects of the effects of climate patterns on breeding behaviour:

- What are the effects of temperature on the breeding behaviour of the eastern bluebird and the mountain bluebird?
- Is there geographical variation along latitudes and longitudes in the breeding behaviour of the eastern bluebird and the mountain bluebird?
- What is the effect of elevation on the breeding behaviour of the eastern bluebird and the mountain bluebird?
- What are the differences between the eastern bluebird and the mountain bluebirds in their overall breeding behaviour?

## 2. Methods

In this study a data set of the breeding biology of eastern and mountain bluebirds received from Nestwatch was used. The datasets span from 1997 to 2017 and cover a large part of their range in the United States and include a part of Canada as well. Nestwatch is a nationwide nest-monitoring program in North America, organized by the Cornell Lab of Ornithology (Cornell Lab of Ornithology, n.d). It is a citizen science project where volunteers collect numerous data from nests. Two separate datasets were created afterwards for each species in order to have separate files in the analysis. From those datasets, the clutch size (number of eggs in the nest), number of hatchlings (number of eggs that hatched), number of fledglings (number of chicks that leave the nest), laying date (number of days after January 1st, that the first egg is laid), hatching date (number of days after January 1st, that the first egg hatched) and the fledging date (number of days after January 1st, that the first chick has left the nest) were used. The altitude and geographic coordinates of the nests are used as well. Each individual nest was given a unique identification code. Any improbable data was removed from the dataset. This includes clutch sizes that are too big to be biologically probable or any data interactions that do not correspond with each other (for example: number of hatchlings that is larger than the clutch size).

The coordinates of all nests were added to an ArcGIS map. Grids with the size of one-degree of longitude and latitude were imposed on the map, with each cell representing a geographic population. Each cell with less than 10 nests per year and/or less than 10 years of data was removed from the dataset. In addition, because of time restraints, each eastern bluebird population with a sample size smaller than 500 was removed. The mountain bluebird populations were kept intact, as their overall sample size was already significantly smaller.

Climate data was obtained from the Daymet version 3 database (Thornton et al., 2018). The data consists of 1 km x 1 km gridded average daily maximum and minimum temperatures that was downloaded into the statistical program R (R Core Team, 2018). From the maximum and minimum temperature, an average daily temperature was calculated. The temperature data was added to the nest files in excel. With the R program climwin (Bailey & Van de Pol, 2016; Van de Pol et al., 2016) this climate data was used to predict the climate windows based on the lay date from each population. A climate window is defined in this study as a critical period where the weather is expected to have the strongest effect on the breeding performance. The climwin program gives a two numbers, a start date and an end date, both being different amount of days before the average lay date. The coefficient of variation of the temperature was then calculated by dividing the standard error of the temperature within the climate window by their mean and multiplying it by 100. The coefficient of variation shows the variation of temperature within the climate window and can indicate if the amount of stability in temperature affects the breeding performance.

The variables clutch size, the number of fledglings per nest, hatch rate (the proportion of eggs per clutch that hatched), hatching success (proportion of nests that had at least one egg that hatched), fledging rate (the proportion of nestlings per clutch that fledged), fledgling success (proportion of nests with at least one fledgling) were used as response variables. Linear mixed models then were used to assess effects on clutch size, laying date, hatching date, and fledging date of the eastern bluebird and the mountain bluebird, as these models are fit to analyse correlated data with random effects. For models dealing with a proportional response (i.e., hatch rate/success and fledging rate/success), generalized linear mixed models with a binominal distribution were used. The following fixed effects were tested in each model: year, temperature, variation of temperature, latitude, longitude and elevation. Using year as a fixed effect gave an opportunity to see the effect over time of each modelled factor in these 20 years. Year was included as a random effect as well, to control for any between-year differences in the overall pattern. To prevent multicollinearity, when factors influence each other, multiple models were tested and the ones with the lowest Akaike information criterion (a value that estimates the relative quality of statistical models with the lowest value having the best likelihood) were used. Additionally, $r^2$ values were calculated for each model using the MuMIn package in R. The MuMIn package uses Nakagawa & Schielzeth (2012) method to obtain $r^2$ values from general linear mixed models. The $r^2$ value indicates how much of the variety in the data can be explained by the statistical models

In order to determine the effect of year and temperature on each variable across the geographic factors, interactions between year/temperature and each geographic factor were made. Furthermore, were models created with temperature and year interactions with each variable to understand more about the difference between the species.

To get p-values for linear mixed models, null models were made that exclude the fixed effect that needs to be checked for significance. Afterwards, an ANOVA test was used to compare the fitted model and the null model to determine the significance of that specific fixed effect.

The R package ggplot2 was used for creating the graphs in R (Wickham, 2016). The graphs for the interaction models were made using the jtools package in R (Long, 2018).

## 3. Results

In this chapter the results of the study will be discussed.

### 3.1 Study area

This paragraph will shortly look into the study area of both species. The eastern bluebird nests are spread over a larger area and in more states as the mountain bluebird who are only around in a few states (figure 1).

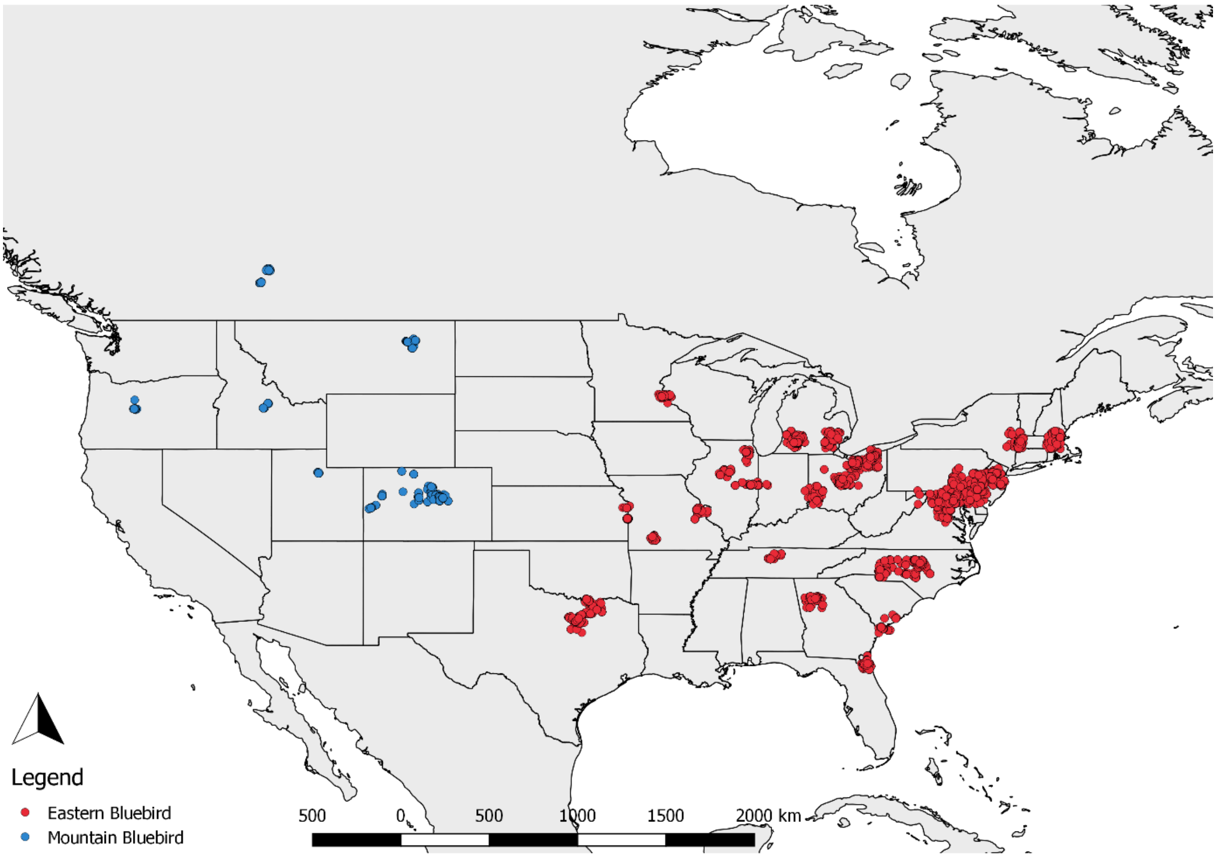


*Figure 1: the locations of the used bluebird nests. Eastern bluebird nests are shown with red points and the mountain bluebird nests are shown with blue points*

### 3.2 Climate windows

The climate windows were calculated with the climwin package on R and were used to determine the period where temperature is the most important in determining the lay date. The found climate windows were mostly a long time before the average laying date with an average starting time of 258 days before the mean laying date and closed 157 days before the mean laying date. A full table with all climate windows can be found in appendix I.

There were exceptions with smaller climate windows for three populations that started only 50 days before the mean laying date on average and ended directly at the mean laying date.

### 3.3 Overview climate

The climate progressed differently in the study areas of both species. In the eastern bluebird the expected temperature rise was found with a clear increase over the last twenty years (figure 2). In the study area of the mountain bluebird, however the temperature decreased in the last twenty year (figure 2).

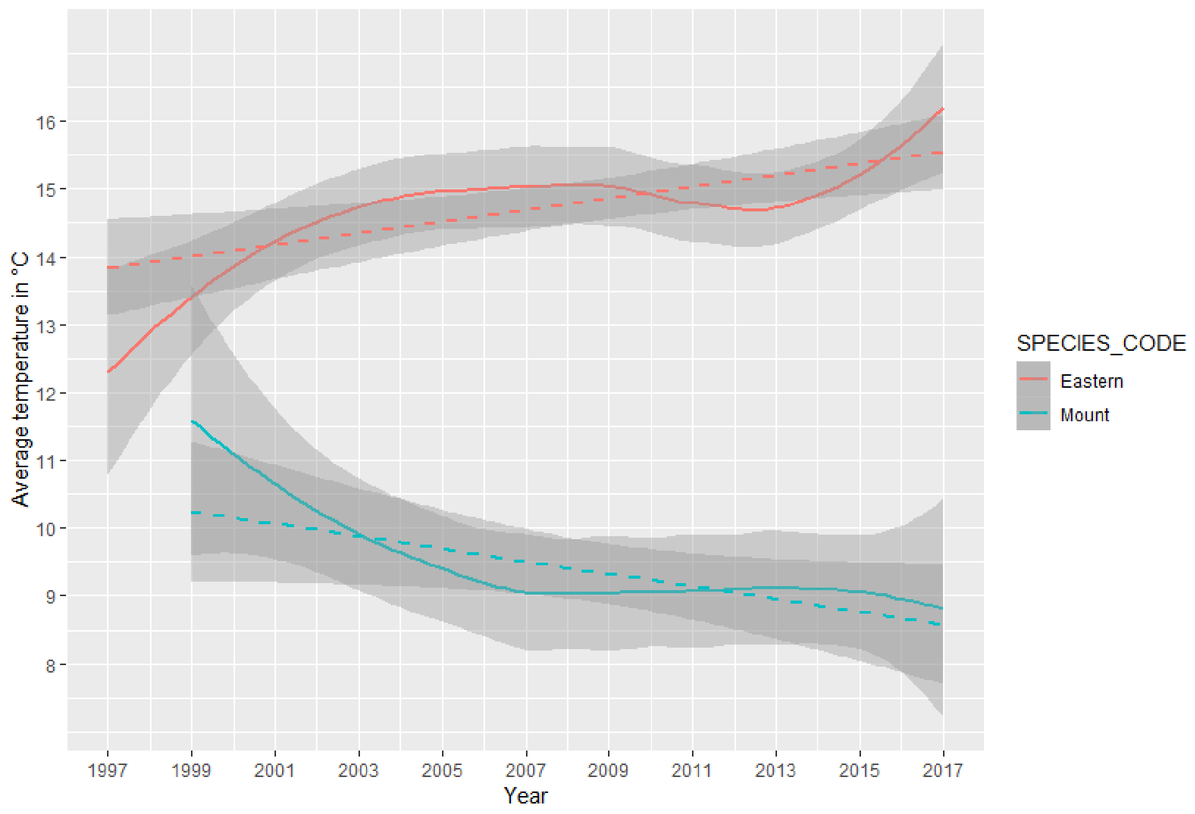


*Figure 2: overview of the average temperature in the last 20 years within the study areas. The eastern bluebird is shown in red and the mountain bluebird in blue. The x-axis shows the year and the y-axis shows the average temperature in °C. The grey field around the lines is the confidence interval. The dashed lines are the trendlines.*

The variation in temperature did not change in a clear pattern during the last twenty years. In the study areas from the eastern bluebird there was a slight negative trend, with a little less variation in the last years, however from 2001 to 2013 the coefficient of variation was more or less stable (figure 3). The coefficient of variation in the study areas of the mountain bluebird had a neutral trend (figure 3).

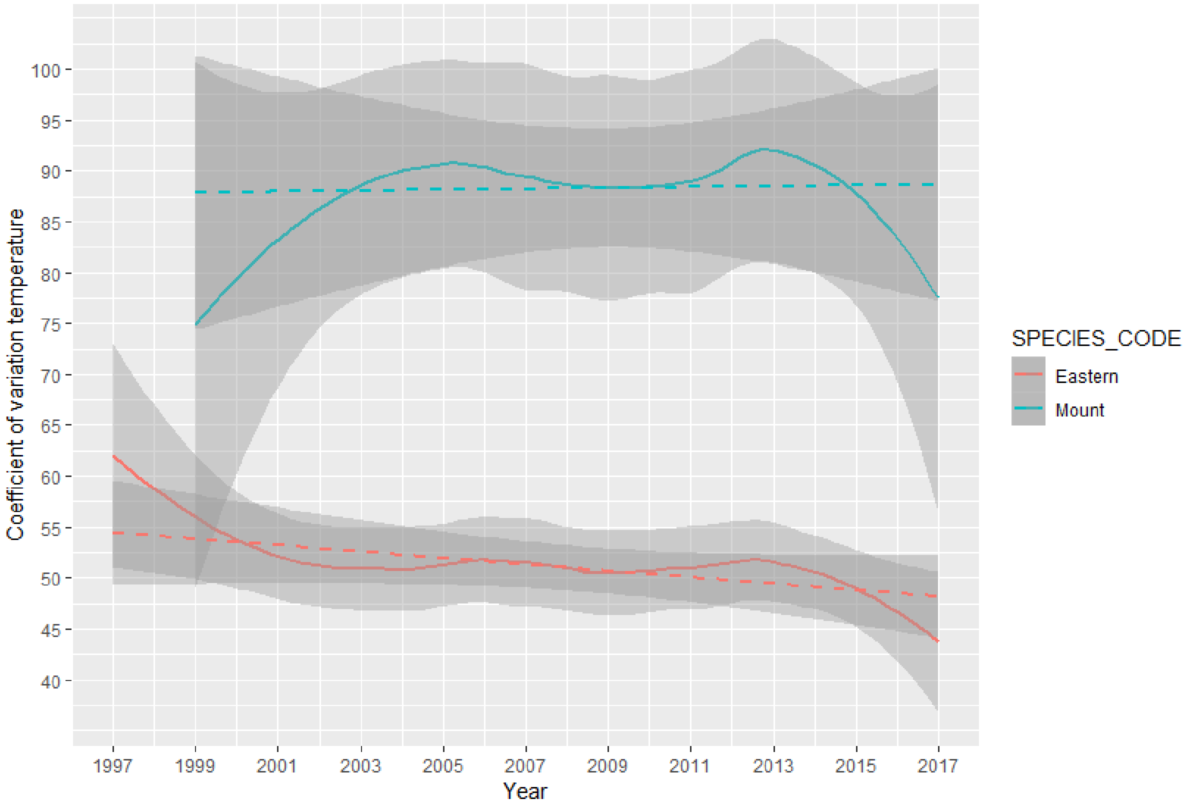


*Figure 3: overview of variation in temperature within the study areas. The eastern bluebird is shown in red and the mountain bluebird in blue. The x-axis shows the year and the y-axis the coefficient of variation in temperature. The grey field around the lines is the confidence interval. The dashed lines are the trendlines.*

## 3.4 Effect of climate variability on the breeding in the entire breeding range

This paragraph will examine the effect of climate variability on the breeding in the entire breeding range. First the effect of year is shown, which will illustrate how the breeding changed in the last twenty year. Lastly, is the effect of temperature on the breeding examined.

### *3.4.1 Year progression in the overall breeding range*

This section highlights the most relevant effects on year. The full model output can be found in appendix II.

The two species progressed in different manners throughout the year. The eastern bluebird progressed positively with more fledglings per nest on average (figure 4, $p=<0.001$ & $r^2= 0.039$) and better hatch rates (figure 5, $p<0.001$ & $r^2= 0.037$) and fledgling rates ($p<0.001$ & $r^2= 0.022$), while the mountain bluebird had less fledglings per nest on average in recent years (figure 4, $p=0.039$ & $r^2= 0.019$). The eastern bluebird had a positive trend in the fledgling rate with a steady increase. The mountain bluebird had a negative trend in the fledgling rate that fluctuated somewhat between years. The hatch rate (figure 5, $p=0.046$ & $r^2= 0.072$) and fledgling rate were smaller as well ($p=0.051$ & $r^2= 0.042$), however the fledgling rate was slightly not-significant. It should be noted though that the mountain bluebird does have more fledglings per nest overall (figure 4). The sample size of the mountain bluebird is relatively small in their first few years, which could explain the higher numbers in those years (figure 4 & figure 5), as individual successful nests have a stronger effect on the average.

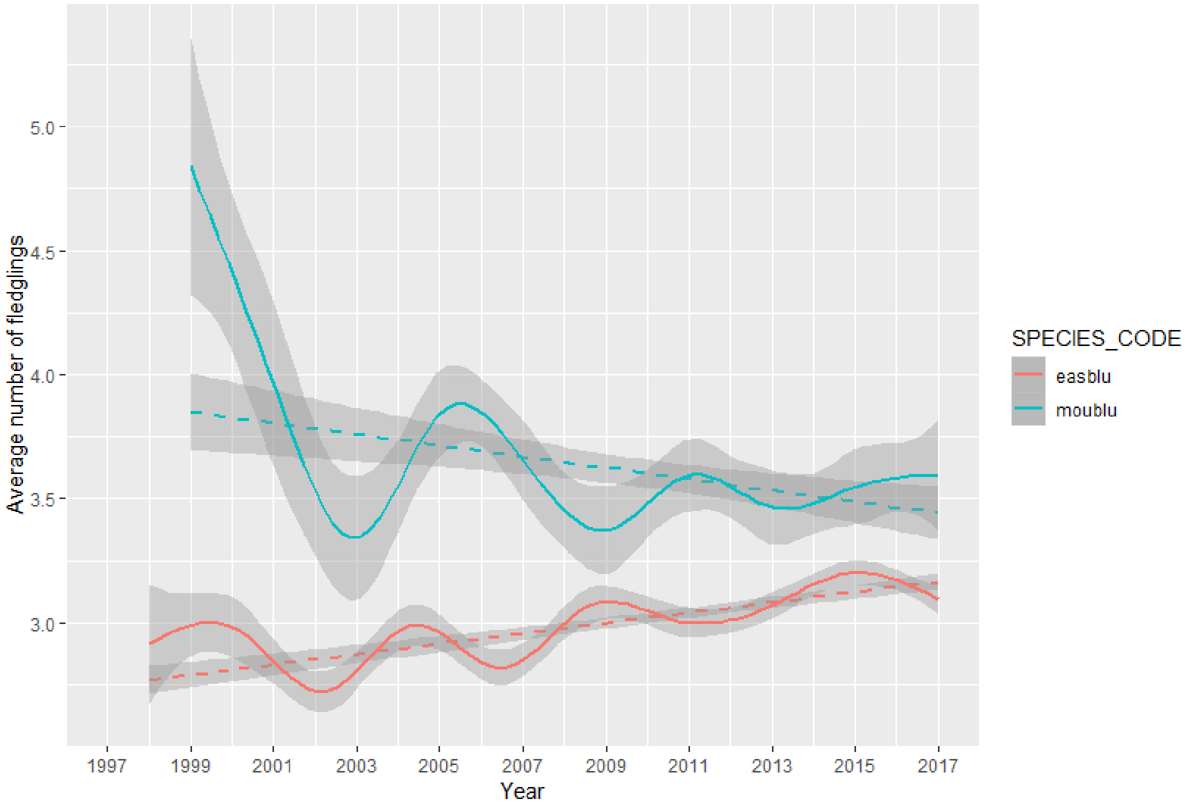


*Figure 4: Progression of the average numbers of fledglings throughout the years. In red the eastern bluebird (p<0.001 & $r^2$= 0.039) and in blue the mountain bluebird (p=0,039 & $r^2 = 0.019$). The grey field around the lines is the confidence interval. The dashed lines are the trendlines.*

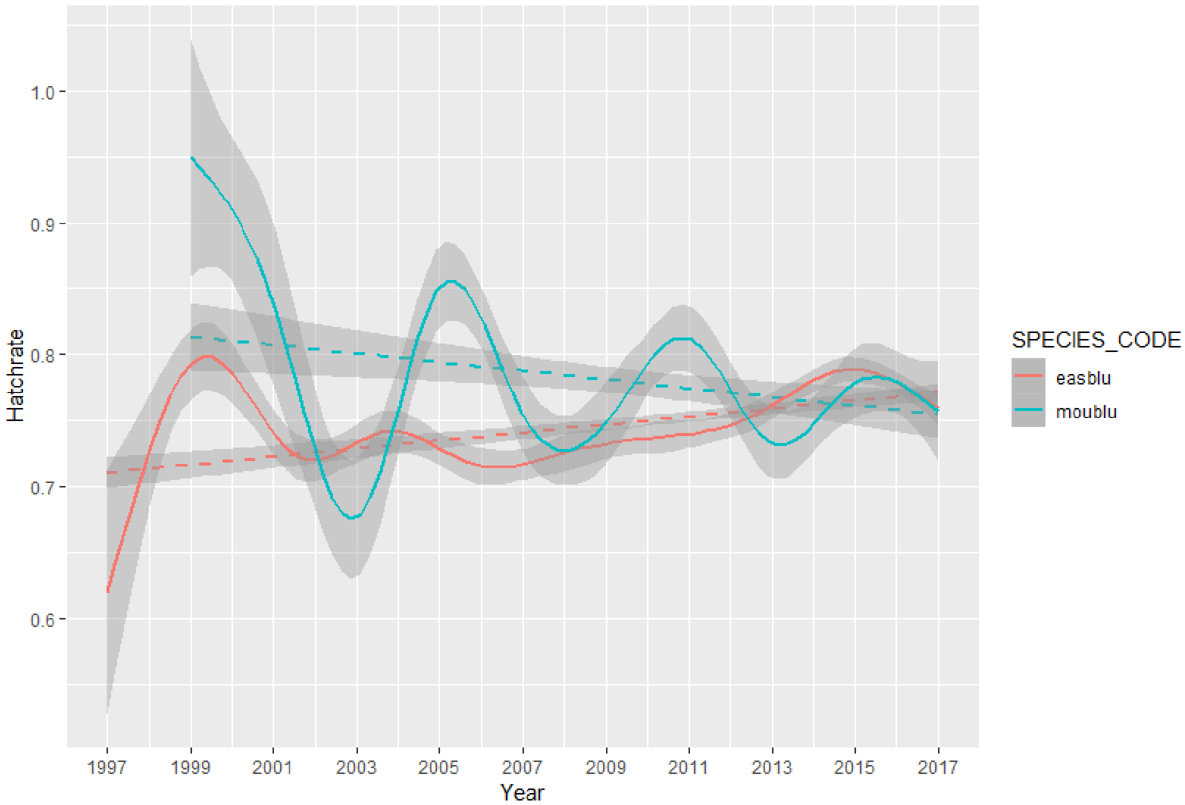


*Figure 5: Progression of the average hatch rate throughout the years. The eastern bluebird is shown in red (p<0.001 & $r^2$= 0.037) and the mountain bluebird in blue (p=0.046 & $r^2$= 0.072). The grey field around the lines is the confidence interval. The dashed lines are the trendlines.*

### *3.4.2 Effect of temperature on the overall breeding range*

The two-bluebird species had different responses to increasing temperature. The eastern bluebird had a positive interaction with temperature and had larger clutch sizes (figure 6, p<0.001 & $r^2$= 0.128), more fledglings (figure 7, <0.001 & $r^2$= 0.039) and a higher fledge rate (p=0.003 & $r^2$= 0.022) at higher temperatures. There were no instances of temperatures between 1 °C and 6 °C in the data of the eastern bluebird which explains the odd curve in that area of the graphs (figure 6 & figure 7). The mountain bluebird was less impacted, with mostly non-significant effects of increasing temperatures. It did have a negative relation with temperatures with the clutch size (figure 6, 0.031 & $r^2$= 0.119), with decreasing clutch sizes at increasing temperatures.

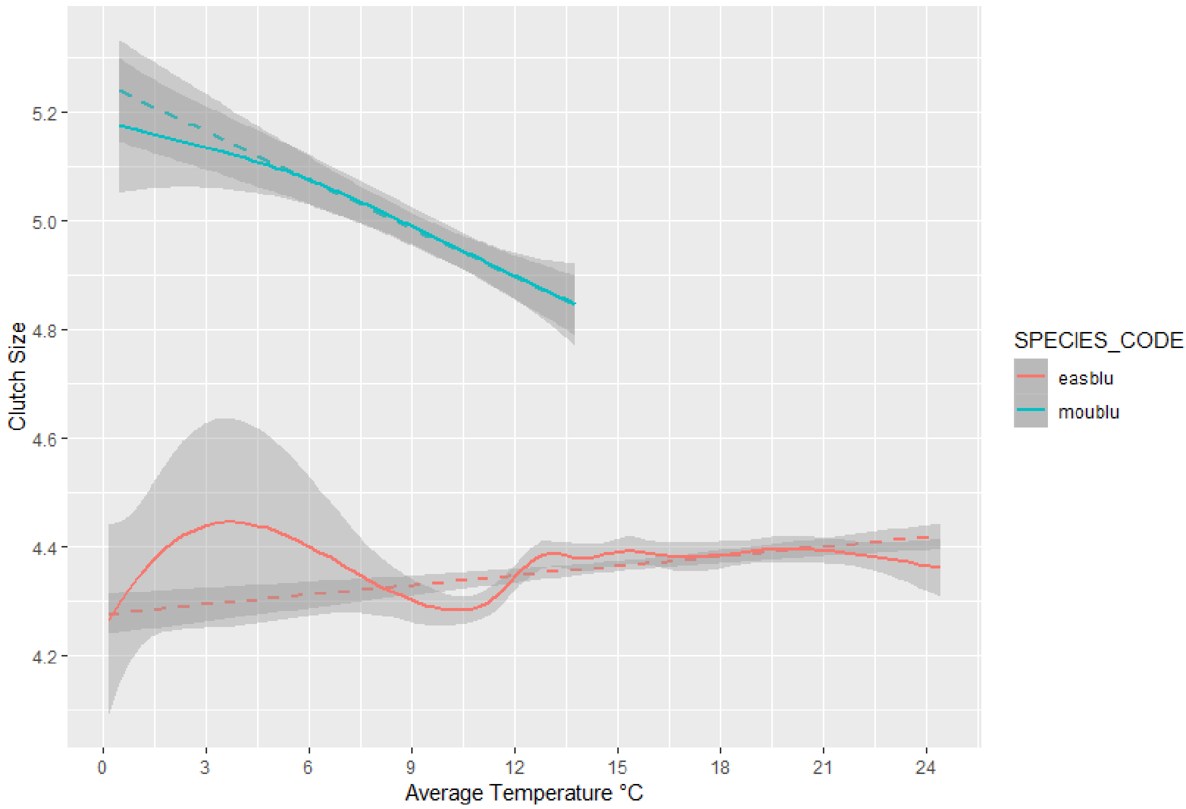


*Figure 6: The effect of average temperature on the clutch size. The eastern bluebird is in red (p>0.001 & $r^2$= 0.119). The mountain bluebird is in blue (p=0.031 & $r^2$= 0.128). The grey field around the lines is the confidence interval. The dashed lines are the trendlines.*

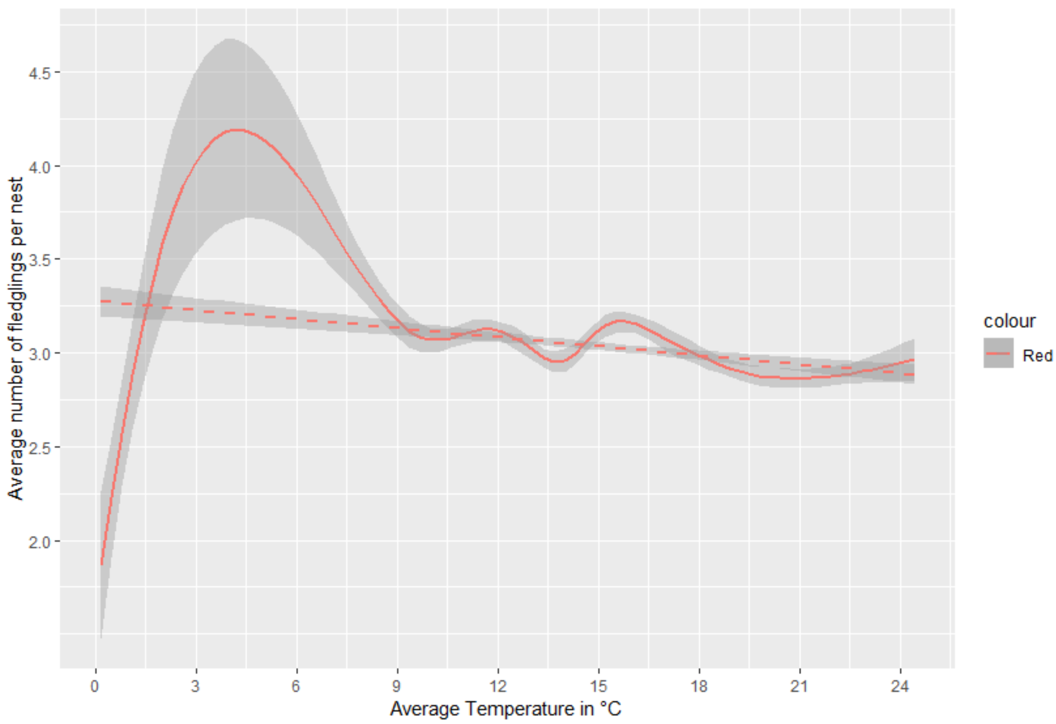


*Figure 7: The effect of temperature on the average number of fledglings per nest in the eastern bluebird (p<0.001 & $r^2$= 0.119). The grey field around the lines is the confidence interval. The dashed line is the trendline.*

The effect of coefficient of variation in temperature on the breeding was overall weaker. The eastern bluebird did not have a significant interaction with the variation of temperature at all. The mountain bluebird, however, did have a relation with the coefficient of variation in temperature. The hatch rate ($p=0.001$ & $r^2= 0.072$) and fledgling rate (figure 8, $p = 0.007$ & $r^2=0.042$) were negatively affected by increase of variation in temperature. The fledgling rate starts rather high at 0.7 (after a few low success nests at low CV temperatures). Afterwards there is a downward trend, with the lowest point at around the coefficient of 1000 and then goes up again, however the trend remains negative.

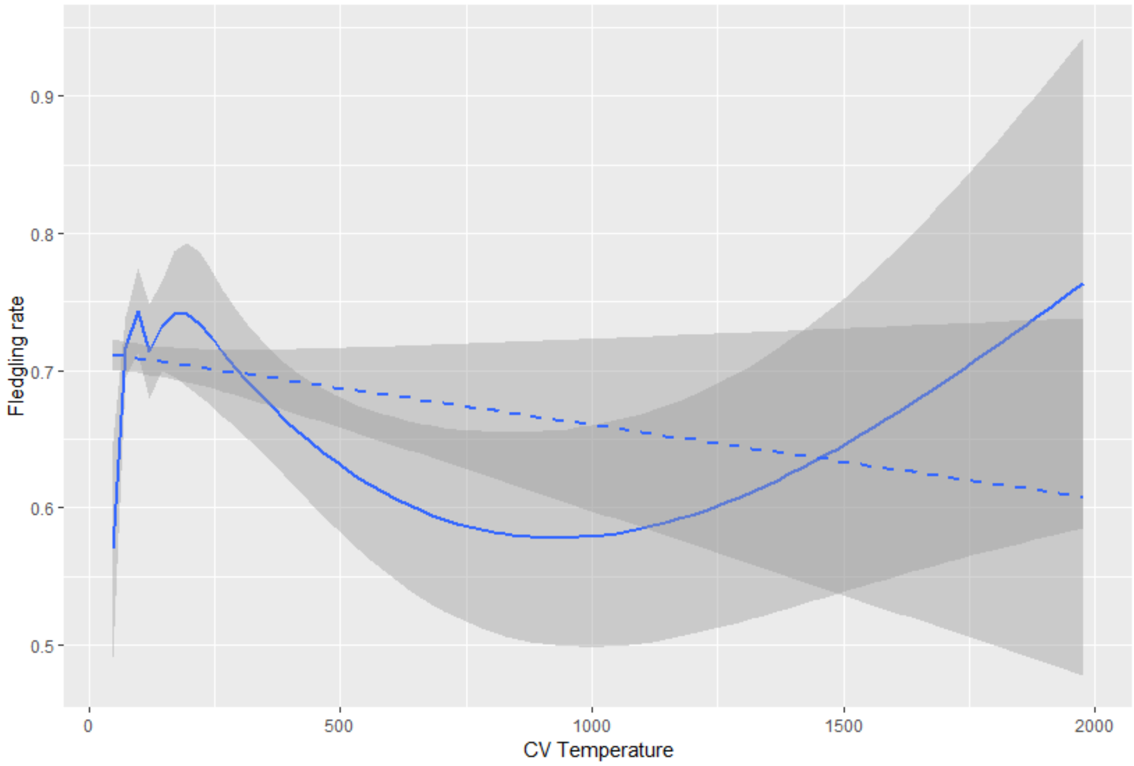


*Figure 8: The effect of coefficient of variation in temperature on the fledgling rate in the mountain bluebird ($p = 0.007$ & $r^2=0.042$). The general trend is shown in a trendline and is negative. The grey field around the lines is the confidence interval. The dashed line is the trendline.*

## 3.5 Effect of climate variability on the breeding across longitude

This paragraph will examine the effect of climate on the breeding across the longitudinal range. In the first sub-paragraph, a quick overview of the effects on the overall pattern is given. Afterwards is the relation of year on the breeding pattern across longitude examined to show how the breeding performance changed in the last twenty years. Lastly, is the relation of temperature on the breeding across longitude shown.

### *3.5.1 Overall pattern longitude*

The eastern bluebird had a negative relation with longitude. The clutch size ($p<0.001$ & $r^2= 0.128$) and the average number of fledglings ($p<0.001$ & $r^2=0.072$) were smaller at eastern longitudes. The same effect was found in the mountain bluebird, that had smaller fledgling rate ($p=0.002$ & $r^2=0.042$) and hatching rate ($p<0.001$ $r^2= 0.072$) in the east. The proportion of nests that are 'successful' (nests with at least one egg that hatched) was lower in the east as well ($p=0.002$ & $r^2=0.034$). The clutch size, in contrast, was larger in the east in the mountain bluebird, albeit not significantly (p=0.077 & $r^2$=0.119).

### *3.5.2 Effect of year on the breeding across longitude*

In this section the progression in the last twenty years of the breeding parameters is shown and how this progression differed among the longitude range. The higher values of longitude are in the east. The graphs in this section use standard deviations to illustrate western and eastern effects, these standard deviations are illustrated in a map in figure 9.

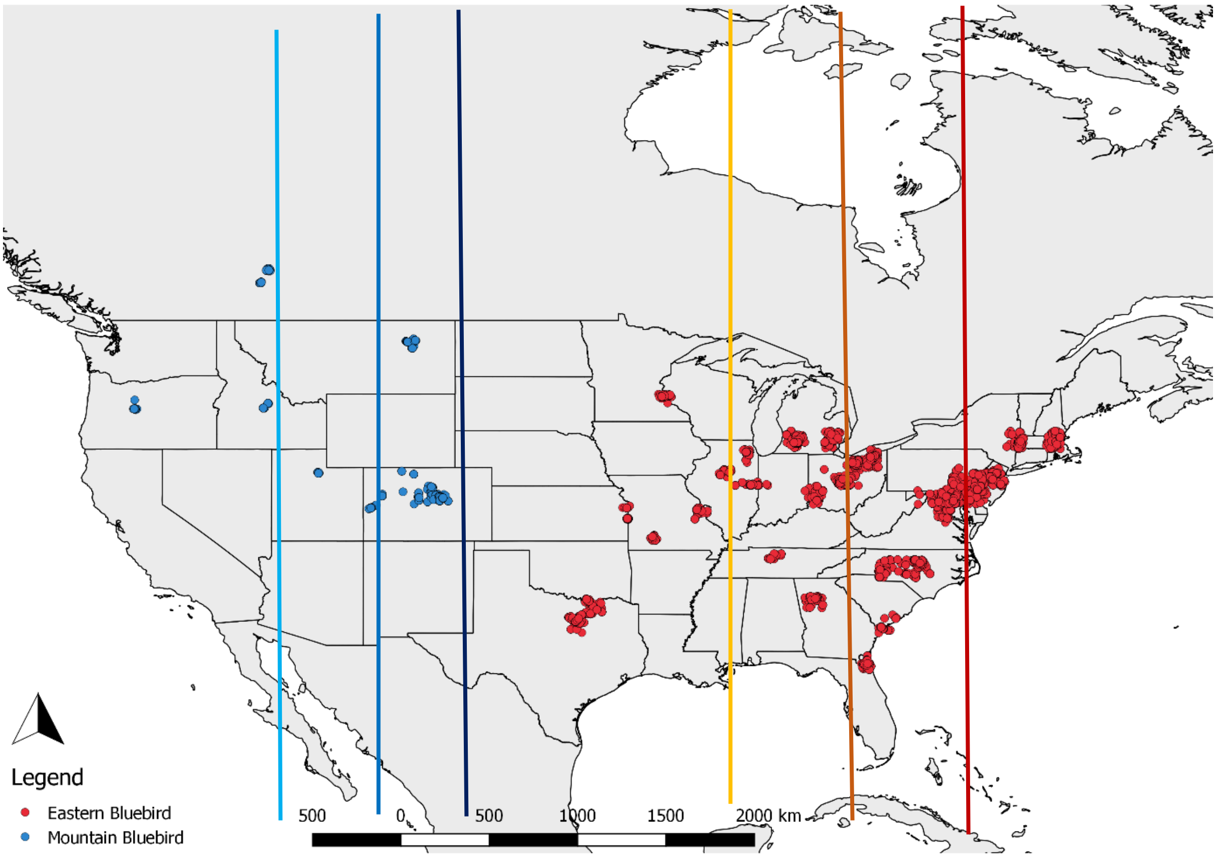


*Figure 9: map of the standard deviations of the average longitude for both the eastern and mountain bluebird. The dark blue line is the +1 SD longitude of the mountain bluebird (-103.832°W), the blue line shows the mean longitude of the mountain bluebird (- 107.708 °W) and the light blue line is de -1 SD longitude of the mountain bluebird (-111.584°W). The red line is de +1 SD longitude of the eastern bluebird (-74.465°W), the dark orange line is the mean longitude of the eastern bluebird (-81.813 °W) and the light orange line is de -1 SD longitude of the mountain bluebird (-89.163 °W).*

The only significant interactions were found in the mountain bluebird who had significantly better hatch rate (p=0.001 & $r^2$=0.085) and fledgling rates (p=0.002 & $r^2$=0.061) in the western range (figure 10 & 11). The populations in those areas were more affected in the last 20 years when it comes to the average number of fledglings and hatch rate than the populations in their eastern range did. The eastern longitudes suffered the most in the hatch rate and fledgling rate in recent years with a steep decline. The more western longitudes, however, were barely affected.

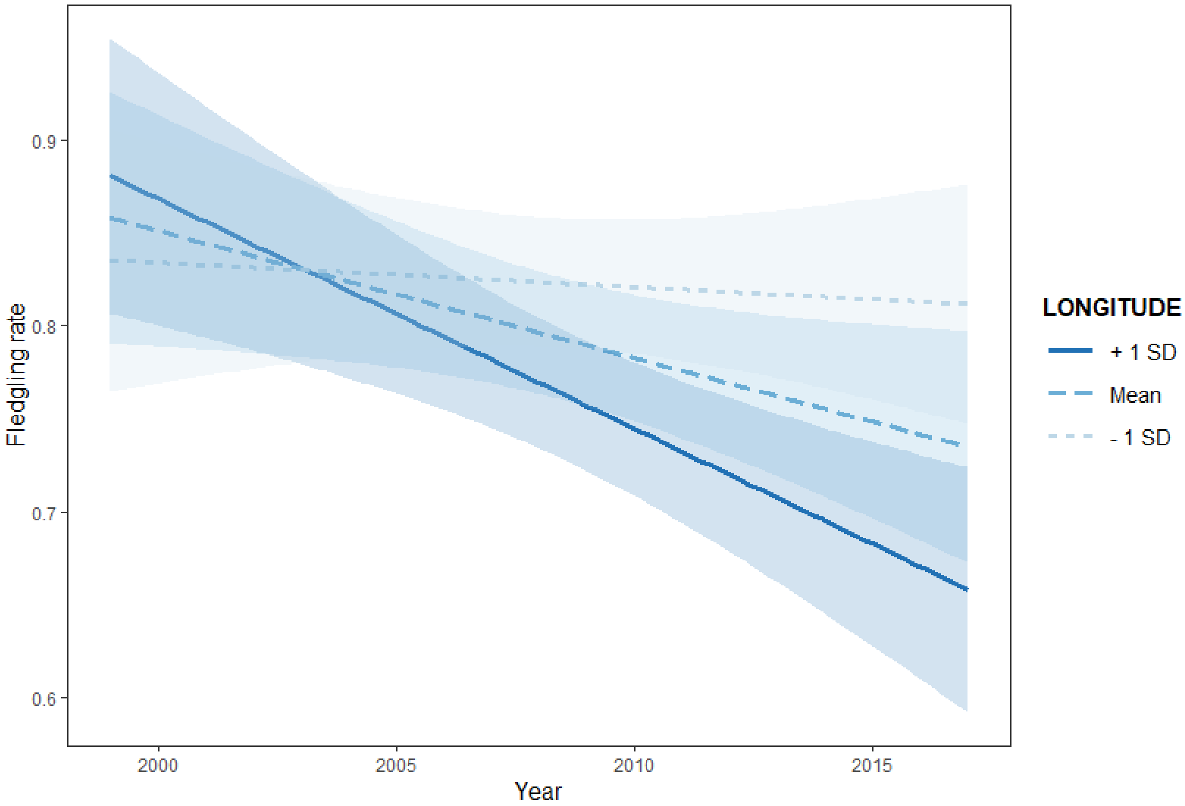


*Figure 10: Progression of the fledgling rate throughout the years at different longitudes (p=0.002 & $r^2$= 0.061). The x-axis is the year and y -axis the fledgling rate. The lines represent different standard deviation values of the longitude. The +1 SD is - -103.832°W, the mean is - 107.708 °W and the – SD is -111.584° W). These standard deviations are illustrated in a map in figure 9. The field around the lines is the confidence interval.*

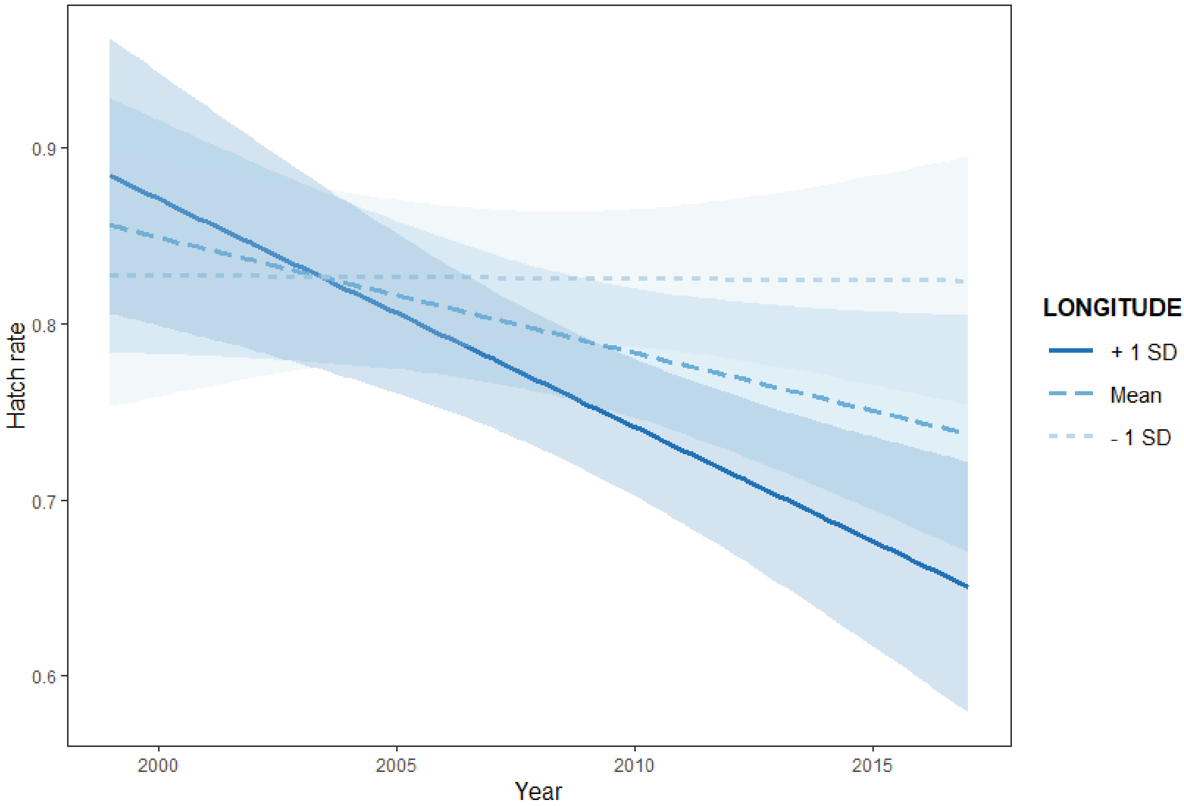


*Figure 11: Progression of the hatch rate throughout the years among longitude in the mountain bluebird ($p<0.001$ & $r^2=0.085$). The x-axis shows the year and the y-axis the hatch rate. The lines represent different standard deviation values of the longitude. The +1 SD is --103.832°W, the mean is - 107.708 °W and the – SD is -111.584° W. These standard deviations are illustrated in a map in figure 9. The field around the lines is the confidence interval.*

### *3.5.3 Effect of temperature on the breeding across longitude*

This section highlights the significant interactions of the breeding parameters with the temperature among the longitudinal range.

The only significant interaction was found with the mountain bluebird and hatch rate. While the hatch rate in the mountain bluebird had a negative relation with temperature in the east (figure 12, $p=0.004$ & $r^2=0.080$). Different longitudes showed opposite effects: the western nests had an increase in hatch rate when the temperature increased, while the eastern populations declined. The lines represent different standard deviation values of the longitude.

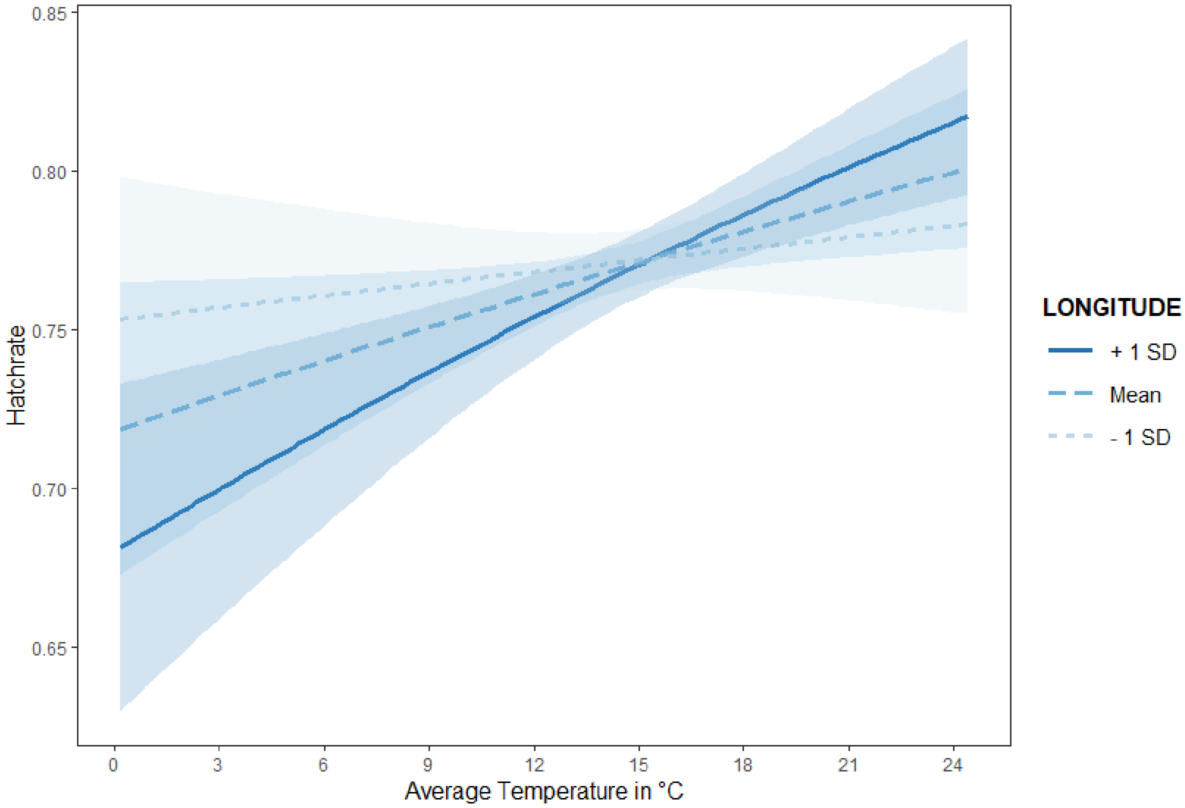


*Figure 12: effect of temperature on the hatch rate among longitude in the mountain bluebird (p=0.004). the x-axis is the average temperature in °C. and y-axis shows the hatch rate. The lines represent different standard deviation values of the longitude. The +1 SD is -103.832°W, the mean is - 107.708 °W and the – SD is -111.584° W. These standard deviations are illustrated in a map in figure 9. The field around the lines is the confidence interval.*

## 3.6 Effect of climate variability on the breeding among latitude

This paragraph will look into the effect of climate on the breeding across the latitudinal range. In this first section, the overall pattern is briefly examined. The second section will look into the relation of year on the breeding pattern across latitude and will show how the breeding changed the last twenty years. The third and last part looks into the effect of temperature on the breeding across latitude.

### *3.6.1 Overall pattern latitude*

The nests performed overall better at higher latitudes. Each breeding parameter performed better in the eastern bluebird in the north, with higher clutch sizes ($p$=0.001 & $r^2$= 0.128), more fledglings per nest ($p<0.001$ & $r^2$= 0.039) and better fledgling rates ($p<0.001$ & $r^2$=0.042) and hatch rates ($p<0.001$ & $r^2$= 0.072). The effects in the mountain bluebird were less strong, however they had higher clutch sizes ($p<0.001$ & $r^2$=0.119) and more fledglings ($p$=0.001 & $r^2$= 0.050) in the northern nests as well.

### *3.6.2 Effect of year on the breeding across latitude*

This paragraph will look into the significant interactions with the breeding parameters with year among the latitudinal range and will show how the breeding changed in different areas. The graphs in this section use standard deviations to illustrate northern and southern effects, these standard deviations are illustrated in a map in figure 13.

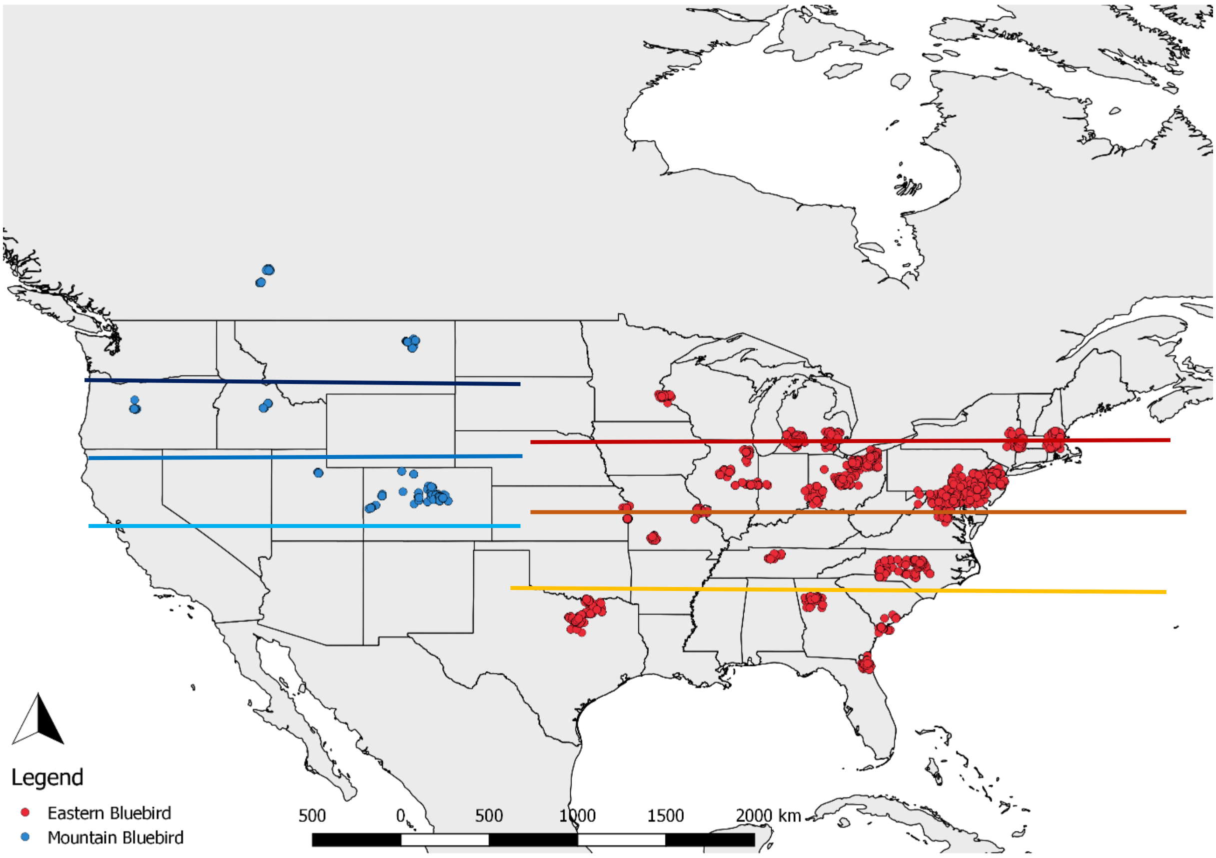


*Figure 13: map of the standard deviations of the average latitude for the eastern bluebird and the mountain bluebird. The dark blue line is the +1 SD latitude for the mountain bluebird (45.677 °N), the blue line is the mean latitude for the eastern bluebird (41.671 °N) and the light blue line is the -1 SD latitude for the mountain bluebird (37.576 °N). The red line is the +1 SD latitude for the eastern bluebird (42.121 °N), the dark orange line is the mean latitude for the eastern bluebird (38.285 °N) and the light orange line is the -1 SD latitude for the eastern bluebird (34.450 °N).*

All interactions were found in the eastern bluebird only. In both interactions the northern populations had a better relation with year than the southern populations did. Nests in the northern range had larger clutch sizes in recent years, while the clutch size in southern populations decreased in recent years (figure 14, $p<0.001$ & $r^2 = 0.129$). There was a clear difference between the latitudes. Higher latitudes had a positive relation with year, while southern latitudes had a negative relation. The lines represent different standard deviation values of the latitude. The northern populations had a better average number of fledglings as well in recent years. In this case, the southern populations still had a positive interaction, albeit smaller (figure 15, $p<0.001$ & $r^2 = 0.039$). In this case, there was a positive pattern all over the range in the last twenty years. In the northern populations however, this pattern was much stronger

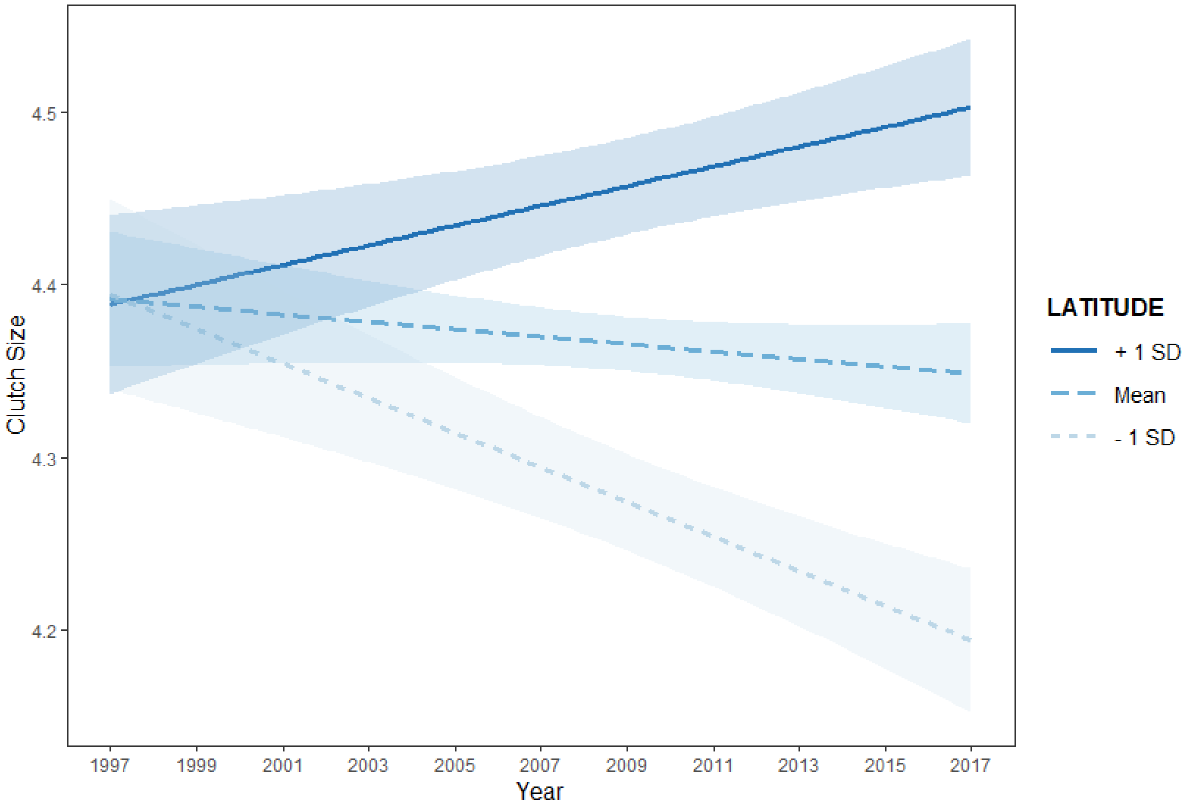


*Figure 14: the effect of year on clutch size at different latitudes in the eastern bluebird (p<0.001 & $r^2$= 0.129). The x-axis shows the year and the y-axis the clutch size. The bold blue line is +1 SD which is about 42.121 °N, the mean is about 38.285 °N. The lighter line is the -1 SD which is about 34.450 °N. These standard deviations are illustrated in a map in figure 13. The field around the lines is the confidence interval.*

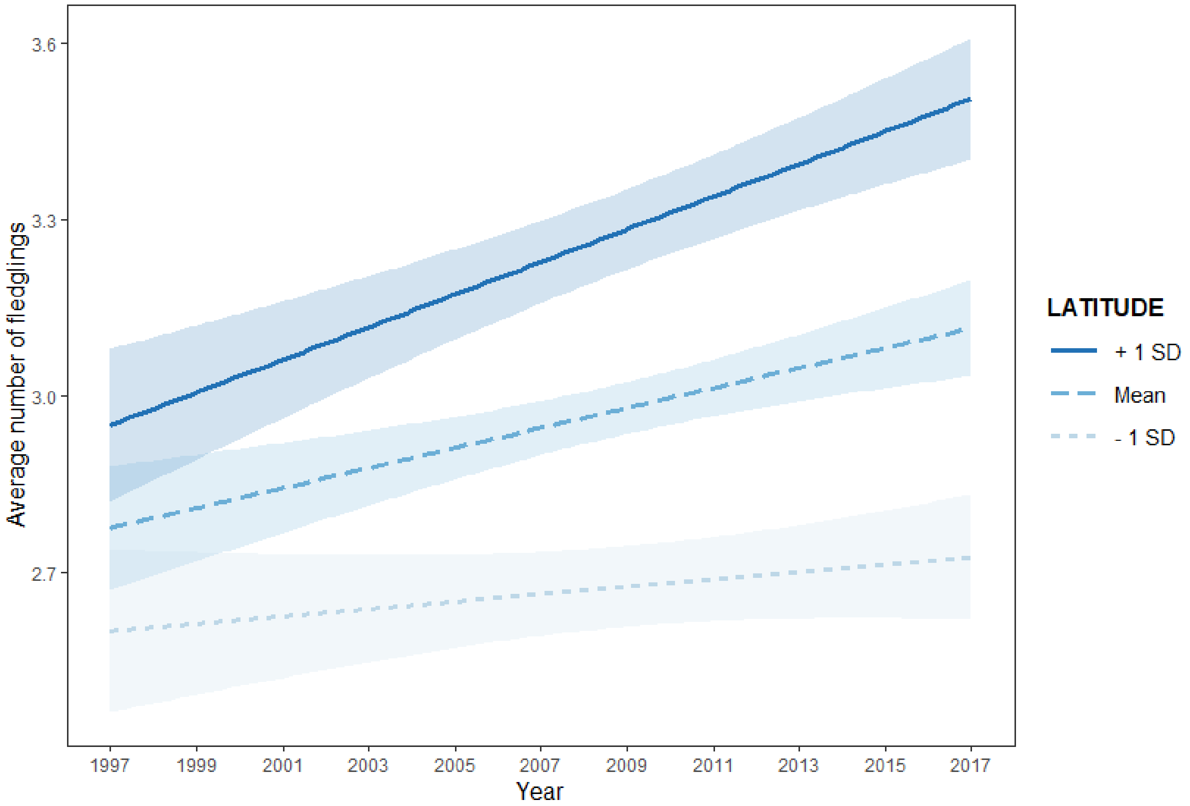


*Figure 15: the effect of year on the average number of fledglings in the eastern bluebird (p>0.001 & $r^2$= 0.039). The x-axis is the year and the y-axis the average number of fledglings. The bold blue line is +1 SD which is about 42.121 °N, the mean is about 38.285 °N. The lighter line is the -1 SD which is about 34.450 °N. These standard deviations are illustrated in a map in figure 13. The field around the lines is the confidence interval*

### 3.6.3 Effect of temperature on the breeding across latitude

This section highlights one significant interaction of temperature and latitude concerning clutch size in the eastern bluebird. The clutches in northern nests had a better relation with temperature than southern nests in the eastern bluebird (figure 16, p<0.001 & $r^2$= 0.128). At lower temperatures the southern nests performed better, however in contrast with the nests in the northern range, these nests were barely affected by temperature increase.

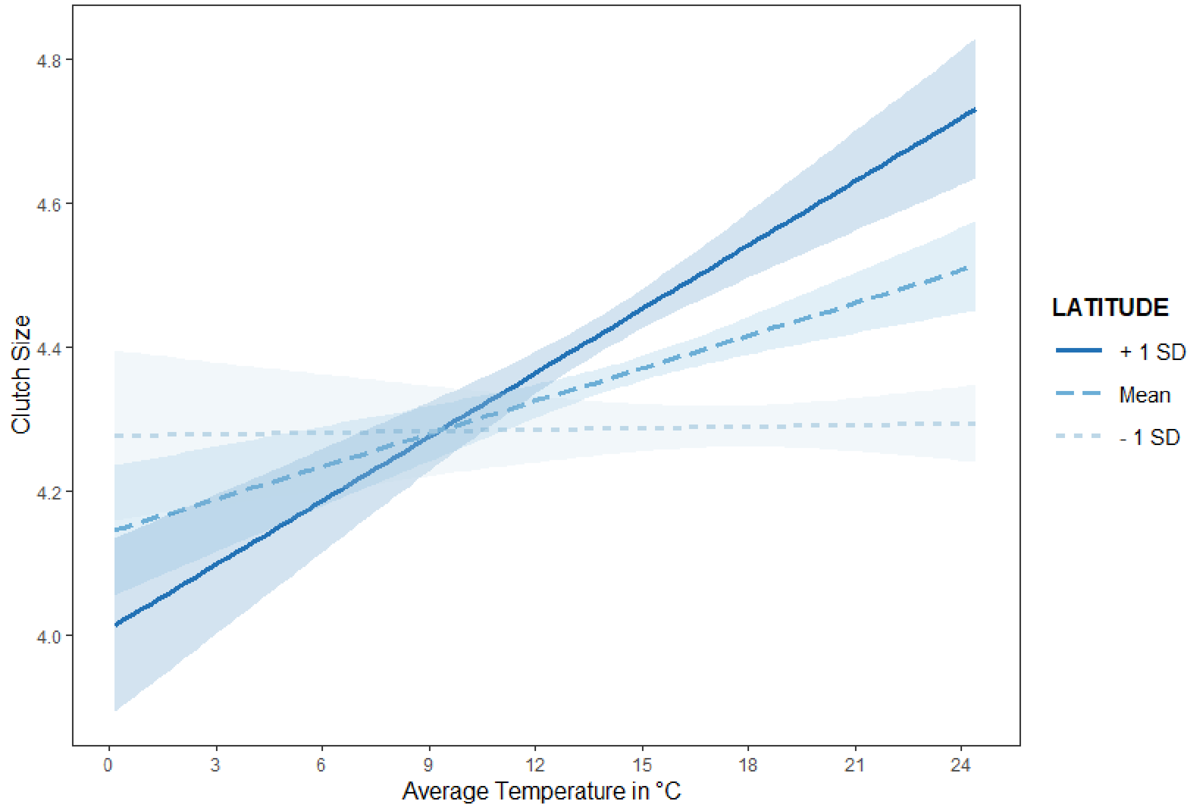


*Figure 16: effect of temperature on the clutch size among latitude in Eastern bluebird ($p<0.001$ & $r^2= 0.128$). the x-axis shows the average temperature in °C and the y-axis the clutch size. The bold blue line is +1 SD which is about 42.121 °N, the mean is about 38.285 °N. The lighter line is the -1 SD which is about 34.450 °N. These standard deviations are illustrated in a map in figure 13. The field around the lines is the confidence interval.*

## 3.7 Effect of climate variability on the breeding across altitude

This paragraph will examine the effect of climate on the breeding across altitude. In the first section, the overall pattern is shown. Afterwards the relation of year with breeding across altitude is examined. The relation of temperature with breeding across altitude is shown in the last section of this paragraph.

### *3.7.1 Overall pattern altitude*

There was a big difference in the response to increasing elevation between both species. The mountain bluebird was largely positively affected by increasing altitude, while the eastern bluebird was mostly negatively impacted. The mountain bluebird had a higher average number of fledglings per nest (figure 17, $p<0.001$ $r^2= 0.050$) and a better hatch rate ($p=0.001$ $r^2= 0.072$) and fledgling rate ($p=0.004$ & $r^2= 0.042$) at higher elevations, while the eastern bluebird performed worse in those areas (hatch rate: $p=0.292$ & $r^2= 0.037$/fledgling rate: $p=0.643$ & $r^2=0.022$), albeit not significantly.

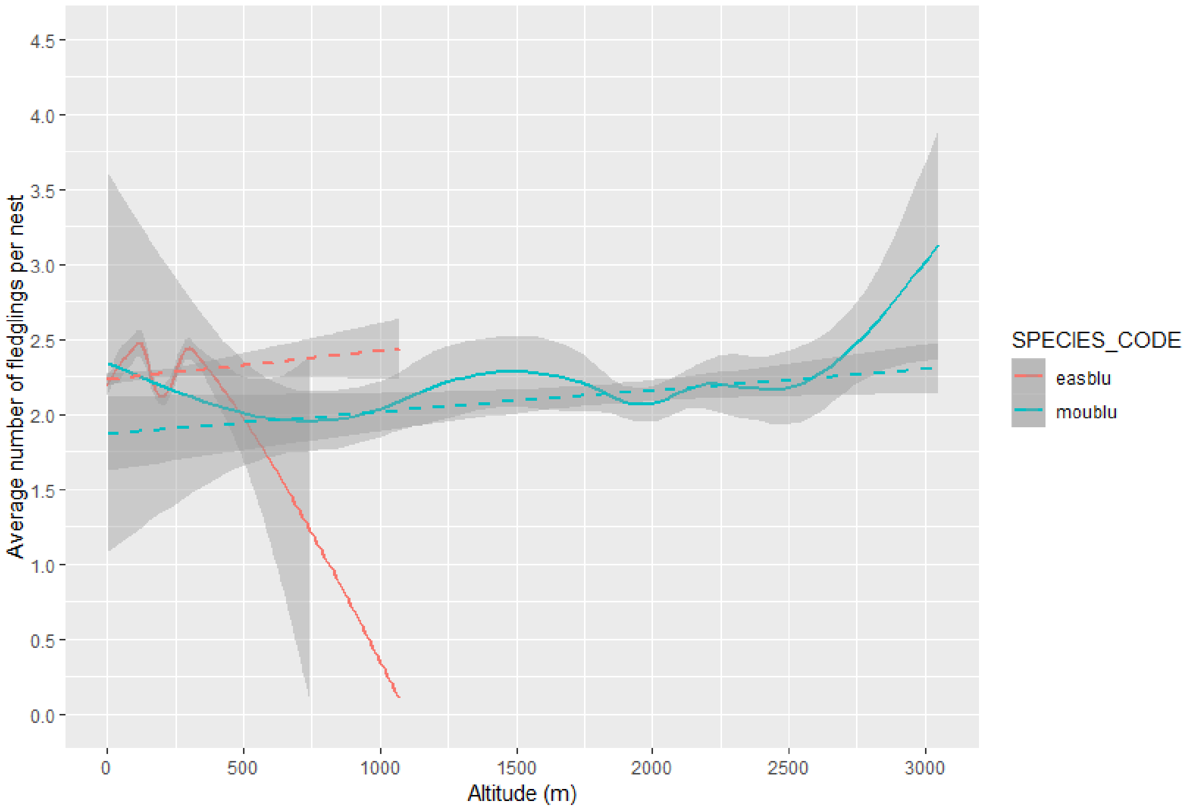


*Figure 17: effect of altitude on the average number of fledglings. The eastern bluebird is represented with a red line. (p=0.643 & $r^2$=0.039). The mountain bluebird is in blue (p=0.004 & $r^2$= 0.050). The field around the lines is the confidence interval. The dashed lines are the trendlines.*

### 3.7.2 Effect of year on the breeding across altitude

This section highlights the progression of the breeding parameters among the altitude in the last twenty years. Both significant interactions of altitude with year were in the eastern bluebird.

Higher nests did well in recent years for the eastern bluebird. These nests had an increase in hatch rate and fledgling rate in recent years (hatch rate: figure 18, p=0.007 & $r^2$= 0.039/ fledgling rate: figure 19, p=0.014 & $r^2$= 0.039). Nests on higher elevations had a stronger positive relation with year and hatch/fledging rate than lower nests. In the earlier years the higher nests performed worse than in recent years.

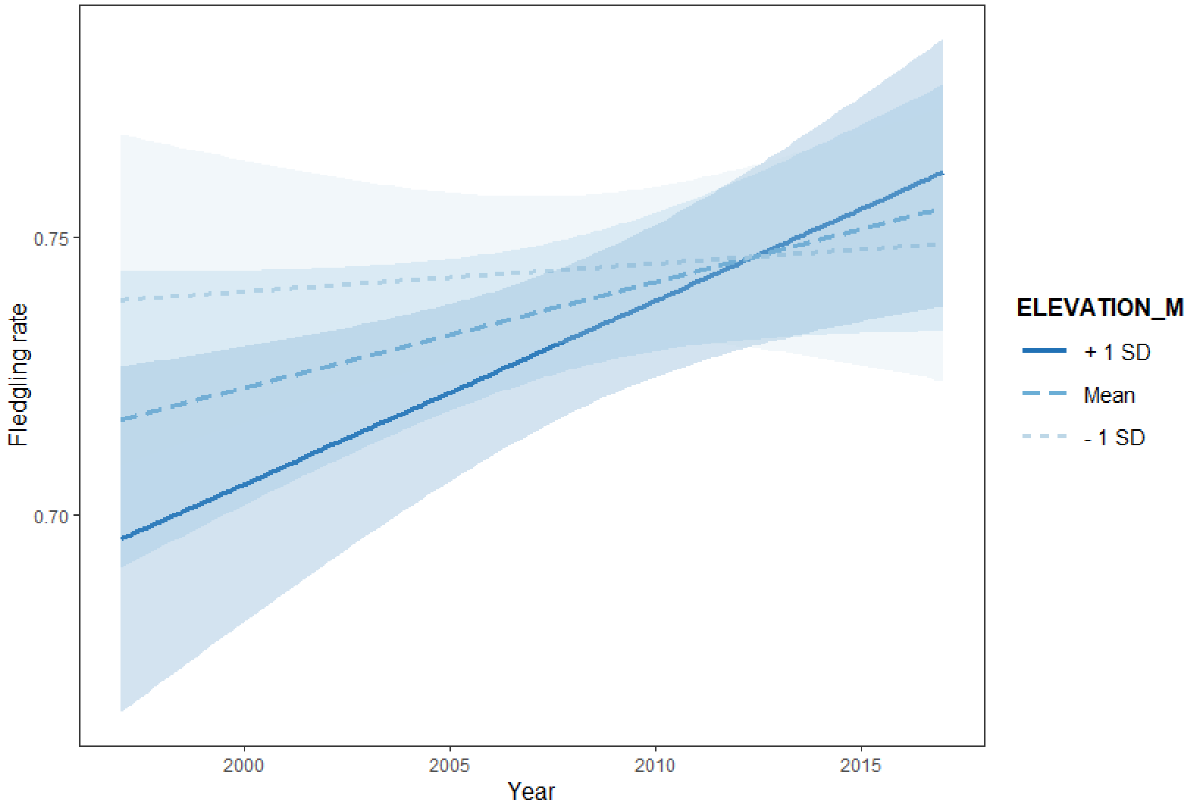


*Figure 18: Progression of fledgling rate throughout the years among altitude in the eastern bluebird (p=0.007 & $r^2$= 0.039). the x-axis shows the year and the y-axis the fledgling rate. The +1 SD is 277.58 m high, the mean is 115.546 m and the -1 SD is 46.48 m high. The field around the lines is the confidence interval.*

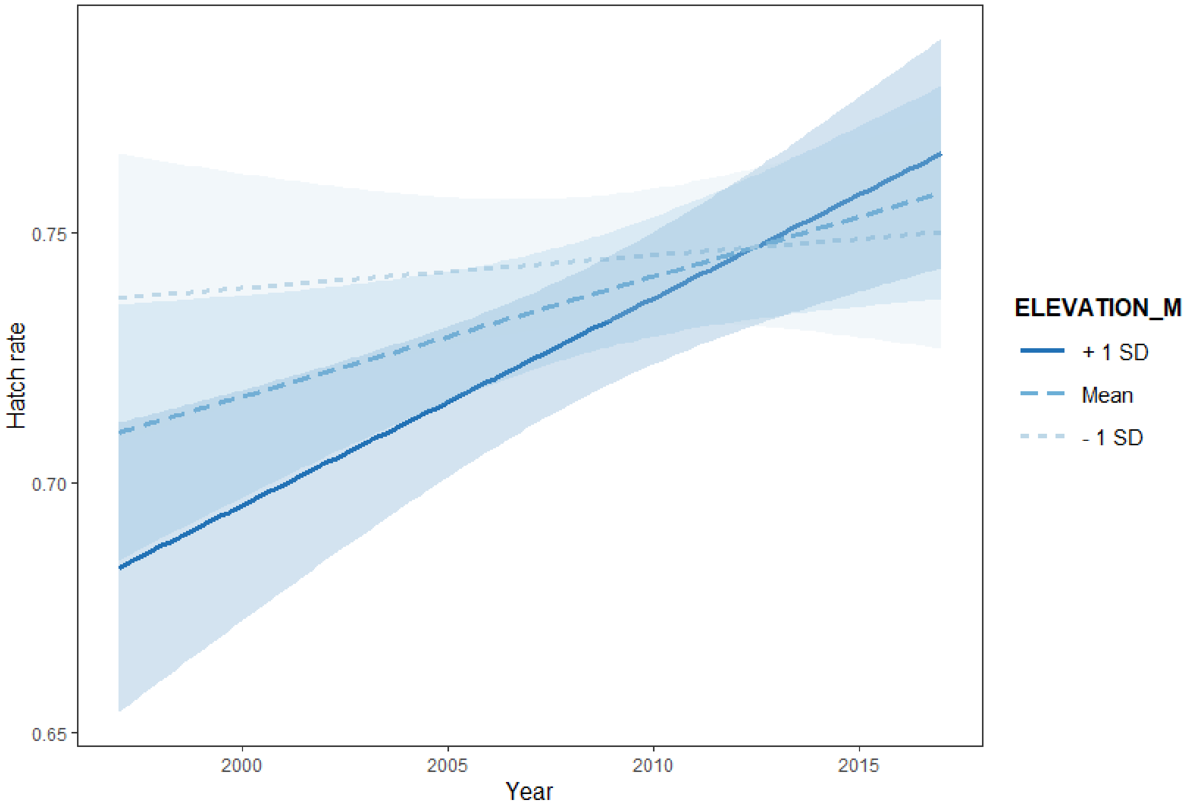


*Figure 19: Progression of hatch rate throughout the years among altitude in eastern bluebird (p=0.014 & $r^2$= 0.039). The y-axis is the year and the x-axis the hatch rate. The +1 SD is 277.58 m high, the mean is 115.546 m and the -1 SD is 46.48 m high.*

### *3.7.3 Effect of temperature on the breeding across altitude*

The clutch size differed in temperature reactions among the altitude in the eastern bluebird (figure 20, p<0.001 & $r^2$= 0.128). The higher nests performed better at lower temperatures, however only slightly improved with increasing temperature, while lower nests had a strong positive relation with temperature.

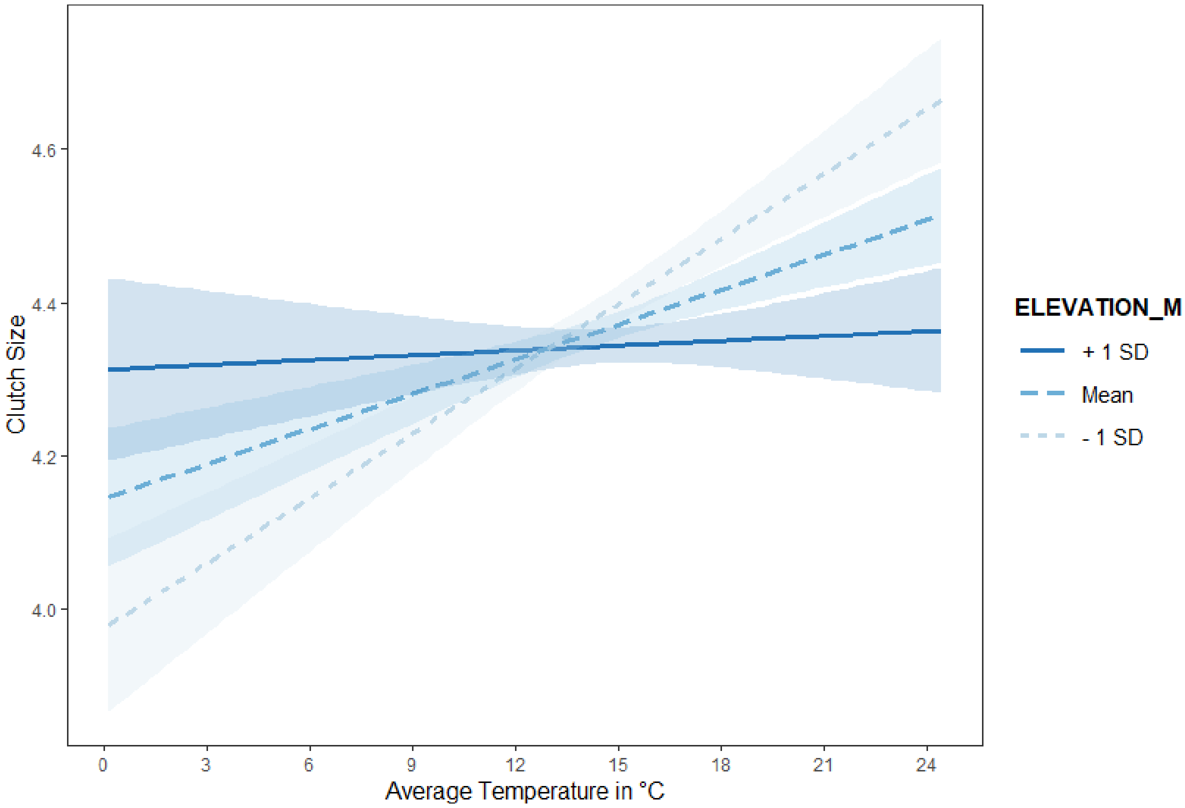


*Figure 20: Effect of temperature on clutch size among altitude in the eastern bluebird ($p<0.001$ & $r^2 = 0.128$). the x-axis shows the average temperature in °C and the y-axis the clutch size. The +1 SD is 277.58 m high, the mean is 115.546 m and the -1 SD is 46.48 m high.*

## 4. Discussion

All data was collected by citizens in this project. To ensure that the results stay reliable and that there are no obvious errors in the collected data, any nest with clear faults was removed from the dataset (this includes data that is biological improbable or obvious mistakes, including more fledglings as eggs in the clutch). With these measures the dataset can be used for reliable scientific analysis.

There was a large difference in sample size between the two species. The eastern bluebird had 33734 nests over 20 years, while the mountain bluebird had 5207. This should still be enough to perform reliable analysis; however, it could be possible that oddities emerged. Especially in the first few years of the dataset, the sample size from mountain bluebirds was relatively small.

Because of time restraints, several of the eastern bluebird population were removed (each population with a sample size <500). The process of obtaining the climate windows was very time consuming, hence it was decided to lower the sample size for the eastern bluebirds. Considering that the overall sample size of the eastern bluebird was already large, it should not have affected results too much. None of the mountain bluebird populations were removed as their sample size was already considerably lower.

There were two different kinds of climate windows found in the populations. One that started in about August a year before the average lay date and ended around December a year before the average lay date of that population. The other window started about two months before the birds laid and ended immediately after. The first climate window was somewhat unexpected as climate windows can be expected to be a period that starts just before the birds lay. In this case, however, it seems that the temperature from the previous year influences the timing of laying as well . These two windows suggest that there are two critical periods of temperature before the lay date and that different populations are affected more strongly by different periods.

There was a high degree of multicollinearity within the model results, which indicates that predictor values are affecting each other. This means that it's harder to predict whether the model results accurately present the true effects caused by the fixed effects. To limit this effect, multiple models were tested where predictor values were removed whenever they were strongly correlated to other predictor values and eventually the model with the lowest AIC value was used, which predicts the likelihoods of the models. Examples of predictor values that were often strongly correlated are temperature + latitude and temperature + elevation, with temperature decreasing with increasing latitude and increasing elevation.

Temperature and coefficient of variation are two other predictor values that were often correlated. This is likely connected to the climate in these regions: areas with low temperature have often more a temperate climate where the seasons are strong and where there is a high amount of variation in temperature, while areas with a high temperature are more subtropical and have less variability in seasons.

The $r^2$ values were generally very low, meaning that most of the variety in the data can not be explained by the statistical models. What could have caused this is the fact that most of the effects are quite small on an absolute scale (for example: the effect of temperature on the clutch size is strongly significant ($p<0.001$), however it lowers the clutch size by 0.041 in absolute numbers). These low numbers cannot account for all variety in the data.

## 4.1 Effect of temperature on the overall breeding performance

Temperature was positive for the fledglings in the eastern bluebird. Considering the hatch rate did not improve significantly, and thus this increase was likely not due to more hatched eggs, this indicates that the survival ability of the chicks improved under high temperatures. Greno et al. (2006) found that high temperatures have a negative effect on the post-fledgling survival in great tits. Perhaps increase in temperature has different effects on the survival ability of birds in different species.

The effect of temperature on the clutch size differed between species: a positive effect on the eastern bluebird and a negative effect on the mountain bluebird. However, temperature could still have negative impacts for the eastern bluebird: it was found that high temperatures affect the embryo health in eastern bluebird, with temperatures of 40.5°C causing mortality. Nests were found, however, to rarely get affected by these temperatures as eastern bluebirds avoid incubation during periods of excessive heat, which could explain that the negative impacts have not been found in eastern bluebirds yet (Cooper et al., 2006).

The effects of the coefficient of variation on the breeding performance was generally weaker. The eastern bluebird did not have a significant effect at all. The mountain bluebird did have interactions with the variation in temperature: more variation caused lower hatch rates and fledgling rates in the mountain bluebird. Unstable temperatures thus had a negative effect on the hatching and survival ability in the mountain bluebird.

The effect of temperature variation on breeding performance seems to be rather unexplored. This study showed that it can have an effect on the breeding. To my knowledge there have not been many studies that look at how the variation in temperature affects the breeding parameters that were presented in this study. It is recommended to further look at the effects that were found here to understand more how more unstable temperature can affect the breeding of birds.

## 4.2 Effect of climate variability on breeding across longitude

Western populations generally did better in both species. With the exception of clutch size in the mountain bluebird, which was higher in the east. Clutch size was overall better more land-inwards for both species. This is in line with previous studies (Sanz, 1998). Other breeding parameters performed better in the west for both species, regardless whether they were close to the coast or more land-inwards.

The mountain bluebird had interactions with the fledgling rate and hatch rate, in this case the populations more land-inward had a stronger negative trend than populations more in the west. It seems that in the case of the mountain bluebird the populations closer to the coast were more successful in breeding. This effect was not found in the eastern bluebird.

While the temperature had a negative effect across the entire longitude range of the eastern bluebird, the more western longitudes were affected more negatively when it comes to the average number of fledglings and the hatch rate. The mountain bluebird had an interaction with fledgling rate as well. In this case the more eastern populations more land-inwards performed worse at higher temperatures, while the more coastal populations did better.

It is curious that the western populations performed better in western areas for both species. It can be expected that the either populations closer to the coast or more land-inwards are doing better, however the trend only improves towards the west, regardless whether it is closer to the coast or not. The trends on breeding across needs to be examined further to understand more about this pattern and how it affects the survival of the species.

## 4.3 Effect of climate variability on latitude

The northern populations performed overall better in breeding for both species. This includes the clutch size, which was larger in the north. This pattern has been studied a lot (reviewed by Klomp, 1970) and this study affirms it. That the hatchability of eggs improved in the northern latitudes has been found before in the study of Koenig (1982). With the clutch size improving as well further up north, Koenig proposed that the higher hatchability caused selection for better fecundity. This study showed the same effect with higher hatch rates in the north.

The year and latitude interactions were weaker than the year interactions with longitude and only the interaction for clutch size in eastern bluebirds was significant. The northern populations had a positive interaction with year. The southern populations, in contrast, had smaller clutch sizes in recent years.

The northern populations had bigger clutch sizes during warmer periods. These populations generally live in more colder regions; hence it makes sense that they would respond better to increasing temperatures as it might bring the temperature closer to the optimum for hatching and survival. Southern populations were barely affected by temperature increase, possibly due to the climate there already being optimal for nesting and fledge survival.

## 4.4 Effect of climate variability on altitude

The mountain bluebird performed overall better in breeding at higher altitudes. This is in contrast with previous findings of Johnson et al (2006a) who found that the clutch sizes, albeit marginally insignificant, were somewhat lower at higher elevations in mountain bluebirds. Another study from Johnson et al (2006b) affirmed this. Badyaev & Ghalambar (2001) hypothesized a strategy that prefers parental care to producing a high number of offspring at higher elevations. This research may point to the mountain bluebird having a different strategy, however Johnson et al (2006b) in fact found that mountain bluebirds do give more parental care at higher elevations, especially in later stages. This study did not account for parental care; hence it is unknown what effect this has on the breeding behaviour at higher altitude within this study.

Higher nests had an increasing hatch rate and fledgling rate in the eastern bluebird. Apparently, the environment for success at higher elevations improved for the eastern bluebirds. Considering the temperature increase in the eastern bluebirds, it could be the case that heights that previously had a climate that was too harsh for the eastern bluebird to have successful nests, gained a better environment for the nests due to the temperature increase.

In eastern bluebirds an interaction with the clutch size was found. Nests at a high elevation had a strong negative effect with the temperature, while nests at a lower altitude reacted positively to the temperature rise. This is an interesting effect, considering the temperature is generally lower in higher regions, and it might be expected that colder regions improve under temperature increase.

## 4.5 Relevance

This study showed that both bluebird species were affected in their breeding performance over the last 20 years and that these effects differed throughout different geographical ranges. This information gives a broader perspective of the effects of temperature increase and more climate variability on the breeding of these species.

This information gives a better idea of how climate change can affect the breeding parameters of the eastern bluebird and the mountain bluebird. The increase in temperature caused two different responses between the species, which shows that the climate change does not necessarily cause the same responses in the bluebird species. This shows that it is important to look at the responses of multiple species to get a better idea how climate change affects species on a large scale.

In this study differences between geographical areas were found and gave indications on how climate variability affects bluebirds over their entire range and showed that populations fare differently in different areas. Populations from the eastern range performed worse in relation with both year and temperature. This pattern needs to examined further in order to understand what causes this pattern and how it affects the bluebird populations across the longitude.

## 5. Conclusion

This study showed that the bluebird species behaviour changed throughout the last 20 years and were affected by temperature increase and, in the case of mountain bluebird, increasing variability in temperature. The coefficient of variation had a negative effect on the hatch rate and fledgling rate in the mountain bluebird. These effects were not found in the eastern bluebirds.

Populations performed generally better in their western ranges. The eastern bluebird had more fledglings in the west and the mountain bluebird had better hatch rates and fledgling rates. The exception is the clutch size which was higher more land-inwards for both species (in the west for the eastern bluebird and in the east for the mountain bluebird. In line with previous studies, both species performed better in their northern range.

There was variability in how populations across different geographic ranges reacted to climate variability. In line with the overall pattern, populations in the eastern range of both species performed worse in relation with year and temperature. There was a negative trend in the hatch rate and fledgling rate in the eastern area of the mountain bluebird. The clutch size in the eastern bluebird was higher in the north in each situation. Besides being generally higher, the clutch size in these populations was better at higher temperatures and in relation with year as well.

The mountain bluebird performed better at higher elevations including bigger clutch sizes, which contradicts previous studies on that matter. Other breeding parameters performed better at higher altitudes as well. The mountain bluebird had no significant interaction with altitude and year and temperature. The eastern bluebird did, however, with better fledgling and hatching rates in higher elevations in recent years and smaller clutch sizes in high altitudes during warm temperatures.

This study shows that populations in different geographic areas have different responses to temperature increase. The importance of learning more about this kind of spatial variation and how climate variability cannot be understated. Understanding how the rise in temperature affects breeding performance in different areas will give a broad view on the effects of climate change on the breeding in birds and can pinpoint where populations are suffering the most in the breeding performance.

## Literature


Badyaev, A.V. (1997). Avian life history variation along altitudinal gradients: an example with cardueline finches. *Oecologica, 111*(3), 365-374.

Badyaev, A.V., Ghalambor, C.K. (2001). Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. *Ecology, 82*(10), 2948-2960.

Bailey, L.D. and Van de Pol, M. (2016). Climwin: An R Toolbox for Climate Window Analysis. *PLoS ONE* 11(12): e0167980<doi:10.1371/journal.pone.0167980>

Both, C., VIsser, M.E. (2005). The effect of climate change on the correlation between avian life-history traits. *Global Change Biology, 11*(10), 1606-1613.

Both, C (2010). Food availability, mistiming and climate change. In Moller, A.P., Fielder, W. Berthold, P. *Effects of Climate Change.* pp 129-149. Oxford University Press: New York.

Charlantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B., Sheldon, B.C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science, 320*(800), 800-803

Cooper, C.B., Hochachka, W.M., Phllips, T.B., Dhont, A.A. (2006). Geographical and seasonal gradients in hatching failure in Eastern Bluebirds Sialia sialis reinforce clutch size trends. *Iris, 148*(2)*,* 221-230.

Cornell Lab of Ornithology. (n.d). *About*. Used on 8 June 2017, taken from https://nestwatch.org/about/overview/

Crick, Q.H.P., Dudley, C., Glue, D.E. Thomson, D.L (1997). UK birds are laying earlier. *Nature, 388*(526), 526.

Dhondt, A. A., Kast, T. L. and Allen, P. E. 2000. Clutch-size Variation in Eastern Bluebirds. *Birdscope, Volume 14*(2), 3-5.

Dunn, P.O., Winkler, D.W. (2010). Effects of climate change on timing of breeding and reproductive success in birds. In Moller, A.P., Fielder, W. Berthold, P. *Effects of Climate Change.* pp 113-129. Oxford University Press: New York.

Greno, J.L., Belda, E.J., Barma, 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.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp assessment report of the intergovernmental panel on climate change.

Johnson, L.S., Ostlind, E., Brubaker, J.L., Balenger, S.L., Johnson, B.G.P., Golden, H. (2006). CHANGES IN EGG SIZE AND CLUTCH SIZE WITH ELEVATION IN A WYOMING POPULATION OF MOUNTAIN BLUEBIRDS. The Condor, 108(3), 591-600.

Johnson, L.S., Brubaker, J.L., Ostlind, E., Balenger, S.L. (2006). Effect of altitude on male parental expenditure in Mountain Bluebirds (*Sialia currucoides*): are higher-altitude males more attentive fathers? *Journal of Ornithology, 148*(16), 9-16

Klomp, H. (1970). The determination of clutch size in birds a review. *Ardea, 58*(1-2), 1-124.

Koenig, W.D (1982). Ecological and Societal Factors Affecting Hatchability of Eggs. *The Auk, 99*(3), 526-536.

McCarthy, J.P. (2002). Ecological consequences of recent climate change. *Conservation Biology, 15*(2), 320-331.

Menzel, A., Sparks, T.H., Estrella, N., Roy, D.B. (2006). Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography, 15*(5), 498-454.
Møller, A.P., Fielder, W. (2010). Long-term time series of ornithological data. In Moller, A.P., Fielder, W. Berthold, P. *Effects of Climate Change.* pp 33-38. Oxford University Press: New York.

Møller, A.P., Flensted-Jensen, E., Klarborg, K., Mardal, W., Nielsen, J.T. (2010). Climate change affects the duration of the reproductive season in birds. *Journal of Animal Ecology*, *79*(4), 777-784.

Nakaagawa, S., Schielzeth, H. (2012). A general and simple method for obtaining $R^2$ from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*(2), 133-142.

Nussey, D.H., Postma, E., Gienapp, P., Visser, M.E. (2005). Selection on heritable phenotypic plasticity in a wild bird population. *Science, 310*(5746), 304-306.

Sanz, J.J. (1998). Effects of Geographic Location and Habitat on Breeding Parameters of Great Tits. *The Auk, 115*(4), 1034-1051.

Thornton, P.E., M.M. Thornton, B.W. Mayer, Y. Wei, R. Devarakonda, R.S. Vose, and R.B. Cook. 2018. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 3. ORNL DAAC, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ORNLDAAC/1328

Tool, J.A. (2018). *jtools: Analysis and Presentation of Social Scientific Data.* R Package version 1.1.1.

Van de Pol, M., Bailey, L.D., McLean, N., Rijsdijk, L., Lawson, C.R., Brouwer, L. (2016). Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution 7:* 1246-1257<doi:10.1111/2041-210X.12590>

Visser, M. E., Both, C., & Lambrechts, M. M. (2004). Global Climate Change Leads to Mistimed Avian Reproduction. *Advances in Ecological Research*, 35, 89-110.

Visser, M.E., van Noordwijk, J., Tinbergen, J.M., Lessells, C.M. (1998). Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society, 265,* 1867-1870

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis.* Springer-Verlag: New York.

Winker, D.W., Dunn, P.O., McCulloch, C.E. (2002). Predicting the effects of climate change on avian life-history traits. *PNAS, 99*(22), 13595-13599.

Wright, L.J., Hoblyn, R.A., Green, R.E., Bowden, C.G.R., Mallord, J.W., Sutherland, W.J., Dolman, P.M. (2009). Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark Lullula arborea. *Journal of Animal Ecology, 78*(6), 1191-1202.

## Appendix I: table with climate windows

| Population code | Species | Open(days before the mean lay date) | Closed(days before the mean lay date) | p-value | Latitude midpoint | Longitude midpoint | State |
|---|---|---|---|---|---|---|---|
| AA52 | Mount | 295 | 158 | <0,001 | 38.5 | -108.5 | Colorado |
| AA66 | Eastern | 253 | 182 | <0,001 | 38.5 | -94.5 | Kansas |
| AA70 | Eastern | 281 | 141 | <0,001 | 38.5 | -90.5 | Missouri |
| AA83 | Eastern | 285 | 160 | <0,001 | 38.5 | -77.5 | Virginia |
| AA85 | Eastern | 259 | 177 | <0,001 | 38.5 | -75.5 | Delaware |
| AB67 | Eastern | 271 | 162 | <0,001 | 37.5 | -93.5 | Missouri |
| AC74 | Eastern | 261 | 159 | <0,001 | 36.5 | -86.5 | Tennessee |
| AD80 | Eastern | 266 | 169 | <0,001 | 35.5 | -80.5 | North Carolina |
| AD81 | Eastern | 247 | 185 | <0,001 | 35.5 | -79.5 | North Carolina |
| AD82 | Eastern | 274 | 157 | <0,001 | 35.5 | -78.5 | North Carolina |
| AF64 | Eastern | 243 | 151 | <0,001 | 33.5 | -96.5 | Texas |
| AF76 | Eastern | 260 | 163 | <0,001 | 33.5 | -84.5 | Georgia |
| AG63 | Eastern | 229 | 166 | <0,001 | 32.5 | -97.5 | Texas |
| AG80 | Eastern | 268 | 173 | <0,001 | 32.8 | -80.8 | South Carolina |
| AI79 | Eastern | 269 | 152 | <0,001 | 30.5 | -81.5 | Florida |
| N46 | Mount | 295 | 175 | <0,001 | 51.5 | -114.5 | Alberta |
| R54 | Mount | 292 | 153 | <0,001 | 47.5 | -106.5 | Montana |
| U39 | Mount | 307 | 173 | <0,001 | 44.5 | -121.5 | Oregon |
| U46 | Mount | 297 | 152 | <0,001 | 44.5 | -114.5 | Idaho |
| U68 | Eastern | 37 | 0 | <0,001 | 44.5 | -92.5 | Minnesota |
| W75 | Eastern | 272 | 163 | <0,001 | 42.5 | -85.5 | Michigan |
| W77 | Eastern | 275 | 163 | <0,001 | 42.5 | -83.5 | Massachusetts |
| W87 | Eastern | 271 | 189 | <0,001 | 42.5 | -73.5 | Massachusetts |
| W89 | Eastern | 263 | 184 | <0,001 | 42.5 | -71.5 | Illinois |
| X72 | Eastern | 47 | 0 | <0,001 | 41.5 | -88.5 | Ohio |
| X78 | Eastern | 266 | 170 | <0,001 | 41.5 | -82.5 | Ohio |
| X79 | Eastern | 265 | 170 | <0,001 | 41.5 | -81.5 | Ohio |
| Y49 | Mount | 299 | 160 | <0,001 | 40.5 | -111.4986 | Utah |
| Y54 | Mount | 283 | 189 | <0,001 | 40.5 | -106.5 | Colorado |
| Y71 | Eastern | 269 | 171 | <0,001 | 40.5 | -89.5 | Illinois |
| Y77 | Eastern | 277 | 155 | <0,001 | 40.5 | -83.5 | Ohio |
| Y78 | Eastern | 66 | 0 | <0,001 | 40.5 | -82.5 | Ohio |
| Y84 | Eastern | 266 | 167 | <0,001 | 40.5 | -76.5 | Pennsylvania |
| Y85 | Eastern | 271 | 182 | <0,001 | 40.5 | -75.5 | Pennsylvania |
| Y86 | Eastern | 268 | 187 | <0,001 | 40.5 | -74.5 | New Jersey |
| Z52 | Mount | 281 | 162 | <0,001 | 39.5 | -108.5 | Colorado |
| Z54 | Mount | 304 | 176 | <0,001 | 39.5 | -106.5 | Colorado |
| Z55 | Mount | 283 | 176 | <0,001 | 39.5 | -105.5 | Colorado |
| Z56 | Mount | 281 | 170 | <0,001 | 39.5 | -104.5 | Colorado |
| Z76 | Eastern | 281 | 173 | <0,001 | 39.5 | -84.5 | Ohio |
| Z82 | Eastern | 285 | 167 | <0,001 | 39.5 | -78.5 | West Virginia |
| Z83 | Eastern | 274 | 169 | <0,001 | 39.5 | -77.5 | Maryland |
| Z84 | Eastern | 263 | 183 | <0,001 | 39.5 | -76.5 | Maryland |
| Z85 | Eastern | 268 | 192 | <0,001 | 39.5 | -75.4 | New Jersey |

## Appendix II: tables with model output

*Table 1:Model output showing the how the fixed effects affected the clutch size. Estimates are the estimated absolute change that each predictor value had on the variable. Standard error is the standard deviation from the sampling mean. T/Z values are the measured value of the difference caused by the predictor values, relative to the variation in the data.*

| Clutch size | Eastern Bluebird | | | | Mountain Bluebird | | | |
|---|---|---|---|---|---|---|---|---|
| | *Estimate* | *Std. Error* | *T/Z-value* | *p-value* | *Estimate* | *Std. Error* | *T/Z-value* | *p-value* |
| Year | -0.007 | 0.007 | -0.915 | 0.362 | -0.020 | 0.021 | -0.906 | 0.366 |
| Temperature | 0.041 | 0.011 | 3.745 | <0.001 | 0.042 | 0.020 | 2.167 | 0.031 |
| CV Temperature | 0.001 | 0.009 | 0.062 | 0.951 | -0.002 | 0.019 | -0.116 | 0.908 |
| Longitude | -0.053 | 0.007 | -7.98 | <0.001 | 0.049 | 0.019 | 2.592 | 0,01 |
| Latitude | 0.092 | 0.012 | 7.97 | <0.001 | 0.232 | 0.032 | 7.227 | <0.001 |
| Altitude | -0.014 | 0.008 | -1.817 | 0.069 | 0.109 | 0.029 | 3.732 | <0.001 |
| Lay date | -0.321 | 0.001 | -58.736 | <0.001 | -0.325 | 0.014 | -22.792 | <0.001 |
| Year*Long | -0.010 | 0.006 | -1.811 | 0.095 | 0.034 | 0.020 | 1.742 | 0.082 |
| Year*Lat | -0.039 | 0.006 | 6.777 | <0.001 | 0.018 | 0.029 | 0.602 | 0.550 |
| Year*Alt | 0.009 | 0.008 | 1.194 | 0.235 | -0.046 | 0.026 | -1.742 | 0.081 |
| Temp*Long | -0.040 | 0.009 | -4.476 | <0.001 | -0.006 | 0.026 | -0.22 | 0.832 |
| Temp*Lat | 0.058 | 0.010 | 5.914 | <0.001 | -0.048 | 0.037 | -1.307 | 0.192 |
| Temp*Alt | -0.053 | 0.010 | -5.115 | <0.001 | 0.047 | 0.030 | 1.578 | 0.116 |

Table2: Model output showing the how the fixed effects affected the average number of fledglings. Estimates are the estimated absolute change that each predictor value had on the variable. Standard error is the standard deviation from the sampling mean. T/Z values are the measured value of the difference caused by the predictor values, relative to the e variation in the data.

| Fledglings | Eastern Bluebird | | | | Mountain Bluebird | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | T/Z-value | p-value | Estimate | Std. Error | T/Z-value | p-value |
| Year | 0.091 | 0.020 | 4.429 | <0.001 | -0.175 | 0.082 | -2.139 | 0.039 |
| Temperature | 0.110 | 0.025 | 4.363 | <0.001 | 0.029 | 0.051 | 0.578 | 0.565 |
| CV Temperature | 0.008 | 0.021 | 0.384 | 0.702 | -0.053 | 0.039 | -1.369 | 0.171 |
| Longitude | 0.054 | 0.015 | -3.622 | <0.001 | -0.070 | 0.039 | -1.77 | 0.077 |
| Latitude | 0.303 | 0.026 | 11.606 | <0.001 | 0.195 | 0.070 | 2.789 | 0.001 |
| Altitude | -0.019 | 0.018 | -1.056 | 0.292 | 0.251 | 0.064 | 3.913 | <0.001 |
| Lay date | -0.324 | 0.012 | -26.535 | <0.001 | -0.158 | 0.029 | -5.384 | <0.001 |
| Year*Long | -0.022 | 0.012 | -1.749 | 0.082 | -0.182 | 0.041 | -4.453 | <0.001 |
| Year*Lat | 0.053 | 0.013 | 4.053 | <0.001 | 0.090 | 0.061 | 1.47 | 0.143 |
| Year*Alt | 0.021 | 0.017 | 1.253 | 0.231 | 0.037 | 0.055 | 0.675 | 0.503 |
| Temp*Long | 0.022 | 0.018 | 1.215 | 0.224 | <-0.001 | 0.054 | -0.007 | 0.123 |
| Temp*Lat | 0.010 | 0.020 | 0.522 | 0.6 | 0.003 | 0.070 | 0.043 | 0.965 |
| Temp*Alt | -0.004 | 0.023 | -0.183 | 0.857 | 0.030 | 0.060 | 0.049 | 0.623 |

Table 3: Model output showing the how the fixed effects affected the hatch rate. Estimates are the estimated absolute change that each predictor value had on the variable. Standard error is the standard deviation from the sampling mean. T/Z values are the measured value of the difference caused by the predictor values, relative to the variation in the data.

| Hatch rate | Eastern Bluebird | | | | Mountain Bluebird | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | T/Z-value | p-value | Estimate | Std. Error | T/Z-value | p-value |
| Year | 0.094 | 0.016 | 5.853 | <0.001 | -0.180 | 0.090 | -1.993 | 0.046 |
| Temperature | 0.035 | 0.028 | 1.229 | 0.219 | -0.021 | 0.065 | -0.328 | 0.743 |
| CV Temperature | 0.048 | 0.028 | 1.712 | 0.087 | -1.108 | 0.039 | -2.784 | 0.001 |
| Longitude | 0.006 | 0.021 | 0.269 | 0.788 | -0.309 | 0.048 | -6.418 | <0.001 |
| Latitude | 0.302 | 0.034 | 8.859 | <0.001 | -0.035 | 0.092 | -0.375 | 0.708 |
| Altitude | -0.033 | 0.023 | -1.431 | 0.153 | -0.254 | 0.043 | 5.911 | <0.001 |
| Lay date | -0.259 | 0.015 | -16.976 | <0.001 | -0.004 | 0.038 | -0.102 | 0.918 |
| Year*Long | 0.014 | 0.019 | 0.736 | 0.462 | -0.250 | 0.041 | -5.981 | <0.001 |
| Year*Lat | 0.015 | 0.020 | 0.765 | 0.444 | 0.002 | 0.082 | 0.026 | 0.979 |
| Year*Alt | 0.042 | 0.015 | 2.717 | 0.007 | 0.014 | 0.071 | 0.2 | 0.842 |
| Temp*Long | 0.024 | 0.022 | 1.086 | 0.277 | -0.183 | 0.064 | -2.86 | 0.004 |
| Temp*Lat | 0.051 | 0.018 | 2.849 | 0.005 | -2.243 | 0.141 | -1.719 | 0.086 |
| Temp*Alt | 0.009 | 0.029 | 0.325 | 0.746 | -0.126 | 0.086 | -1.469 | 0.142 |

Table 4: Model output showing the how the fixed effects affected the hatch success. Estimates are the estimated absolute change that each predictor value had on the variable. Standard error is the standard deviation from the sampling mean. T/Z values are the measured value of the difference caused by the predictor values, relative to the variation in the data. The year/temperature interactions were not done for this variable.

| Hatch success | Eastern Bluebird | | | | Mountain Bluebird | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | T/Z-value | p-value | Estimate | Std. Error | T/Z-value | p-value |
| Year | 0.038 | 0.025 | 1.502 | 0.133 | -0.069 | 0.076 | -0.906 | 0.365 |
| Temperature | -0.022 | 0.045 | -0.494 | 0.621 | -0.023 | 0.114 | -0.2 | 0.841 |
| CV Temperature | 0.063 | 0.052 | 1.237 | 0.216 | -0.041 | 0.092 | -0.444 | 0.657 |
| Longitude | 0.034 | 0.033 | 1.033 | 0.302 | -0.239 | 0.079 | -3.029 | 0.002 |
| Latitude | 0.536 | 0.036 | 14.889 | <0.001 | -0.202 | 0.155 | -0.14 | 0.889 |
| Altitude | -0.027 | 0.039 | -0.694 | 0.494 | 0.326 | 0.066 | 4.993 | <0.001 |
| Lay date | -0.338 | 0.025 | -13.518 | <0.001 | -0.096 | 0.070 | -1.379 | 0.168 |

Table 5: Model output showing the how the fixed effects affected the fledgling rate. Estimates are the estimated absolute change that each predictor value had on the variable. Standard error is the standard deviation from the sampling mean. T/Z values are the measured value of the difference caused by the predictor values, relative to the variation in the data.

| Fledgling rate | Eastern Bluebird | | | | Mountain Bluebird | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | T/Z-value | p-value | Estimate | Std. Error | T/Z-value | p-value |
| Year | 0.133 | 0.015 | 7.608 | <0.001 | -0.149 | 0.076 | -1.952 | 0.051 |
| Temperature | 0.078 | 0.027 | 2.927 | 0.003 | 0.073 | 0.057 | -1.473 | 0.141 |
| CV Temperature | 0.030 | 0.025 | 1.195 | 0.232 | -0.091 | 0.033 | -2.709 | 0.007 |
| Longitude | -0.003 | 0.018 | -0.154 | 0.877 | -0.149 | 0.047 | -3.18 | 0.002 |
| Latitude | 0.278 | 0.029 | 9.62 | <0.001 | -0.007 | 0.066 | -0.11 | 0.912 |
| Altitude | -0.010 | 0.021 | -0.463 | 0.643 | 0.168 | 0.058 | -2.909 | 0.004 |
| Lay date | -0.175 | 0.014 | -12.353 | <0.001 | 0.039 | 0.034 | 1.137 | 0.256 |
| Year*Long | 0.014 | 0.019 | 0.736 | 0.462 | -0.223 | 0.040 | -5.573 | <0.001 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Year*Lat | 0.026 | 0.018 | 1.444 | 0.149 | 0.002 | 0.082 | 0.026 | 0.979 |
| Year*Alt | 0.041 | 0.018 | 2.292 | 0.022 | 0.014 | 0.071 | 0.2 | 0.842 |
| Temp*Long | 0.027 | 0.018 | 1.508 | 0.131 | -0.032 | 0.037 | -0.86 | 0.390 |
| Temp*Lat | -0.020 | 0.023 | -0,833 | 0.405 | -0.048 | 0.123 | -0.387 | 0.699 |
| Temp*Alt | 0.023 | 0.027 | 0.872 | 0.383 | -0.029 | 0.050 | -0.575 | 0.566 |

Table 6: Model output showing the how the fixed effects affected the fledgling success. Estimates are the estimated absolute change that each predictor value had on the variable. Standard error is the standard deviation from the sampling mean. T/Z values are the measured value of the difference caused by the predictor values, relative to the variation in the data. The year/temperature interactions were not done for this variable.

| Fledgling success | Eastern Bluebird | | | | Mountain Bluebird | | | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Std. Error | T/Z-value | p-value | Estimate | Std. Error | T/Z-value | p-value |
| Year | 0.051 | 0.025 | 2.063 | 0.039 | -0.023 | 0.068 | -0.335 | 0.738 |
| Temperature | 0.041 | 0.041 | 1.005 | 0.315 | 0.021 | 0.107 | 0.198 | 0.843 |
| CV Temperature | 0.083 | 0.049 | 1.699 | 0.089 | 0.075 | 0.083 | 0.91 | 0.363 |
| Longitude | 0.065 | 0.034 | 1.919 | 0.055 | -0.120 | 0.088 | -1.377 | 0.169 |
| Latitude | 0.411 | 0.031 | 13.366 | <0.001 | -0.077 | 0.141 | -0.546 | 0.585 |
| Altitude | 0.009 | 0.031 | 0.292 | 0.77 | 0.223 | 0.058 | 3.825 | <0.001 |
| Lay date | -0.267 | 0.025 | -10.844 | <0.001 | -0.090 | 0.063 | -1.426 | 0.154 |

*Table 7: coefficient of determination ($r^2$) of each model. $r^2$ m is the marginal coefficient of determination that is explained by the fixed effect and $r^2$ c is the coefficient of determination explained by the full model. For models that deal with a binominal distribution, a theorized value is given.*

| Model | $r^2$ m | $r^2$ c |
|---|---|---|
| Clutch size Eastern | 0.127 | 0.127 |
| Clutch size Mountain | 0.113 | 0.119 |
| Fledglings Eastern | 0.037 | 0.039 |
| Fledglings Mountain | 0.014 | 0.050 |
| Hatch rate Eastern (theorized) | 0.037 | 0.037 |
| Hatch rate Mountain (theorized) | 0.028 | 0.072 |
| Hatch success Eastern (theorized) | 0.091 | 0.091 |
| Hatch success Mountain (theorized) | 0.034 | 0.034 |
| Fledgling rate Eastern (theorized) | 0.022 | 0.022 |
| Fledgling rate Mountain (theorized) | 0.013 | 0.042 |
| Fledgling success Eastern (theorized) | 0.060 | 0.060 |
| Fledgling success Mountain (theorized) | 0.019 | 0.019 |
| Clutch size year int Eastern | 0.128 | 0.129 |
| Clutch size year int Mountain | 0.116 | 0.122 |
| Fledglings year int Eastern | 0.038 | 0.039 |
| Fledglings year int Mountain | 0.025 | 0.061 |
| Hatch rate year int Eastern (theorized) | 0.039 | 0.039 |
| Hatch rate year int Mountain (theorized) | 0.041 | 0.085 |
| Fledge rate year int Eastern (theorized) | 0.039 | 0.039 |
| Fledge rate year int Mountain (theorized) | 0.041 | 0.092 |
| Clutch size temp int Eastern (theorized) | 0.128 | 0.128 |
| Clutch size temp int Mountain (theorized) | 0.118 | 0.127 |
| Fledglings temp int Eastern (theorized) | 0.037 | 0.039 |

| | | |
|---|---|---|
| Fledglings temp int Mountain (theorized) | 0.015 | 0.051 |
| Hatch rate temp int Eastern (theorized) | 0.036 | 0.036 |
| Hatch rate temp int Mountain (theorized) | 0.034 | 0.080 |
| Fledge rate temp int Eastern (theorized) | 0.022 | 0.022 |
| Fledge rate temp int Mountain (theorized) | 0.013 | 0.041 |