Abstract

Recent trends show that species are undergoing a widespread shift in the timing of life history events in accordance with climate change. Butterflies typify this effect because they are ectothermic and therefore sensitive to changes in temperature. Multiple studies have examined the relationship between spring appearance dates in butterflies and rising temperatures, but the trends vary widely geographically. The southeast US is one such region where phenological shift in butterflies is not well known. In this study, we use an extensive citizen science dataset to examine changes in the flight dates of 40 butterfly species in North Carolina between 1993 and 2020. We also explore whether species-specific traits – voltinism and overwintering stage – play a role in phenological shifts. We found that... (effect of temp, not year. Effect of voltinism but not overwinter). These results point to possible further shifts in butterfly arrival date as temperatures are projected to rise in the southeastern US and the potential for using citizen science data to observe widespread phenological shifts.

Introduction

Mounting evidence indicates that species are undergoing significant changes in seasonal timing and distribution on a global scale in response to climatic change (Walther et al. 2002, Parmesan and Yohe 2003). While species can have varied responses to changing temperatures due to variation in physiology and range, distinct patterns have emerged. Firstly, species have generally shifted their ranges both towards the poles and upwards in elevation (Parmesan et al. 1999). Secondly, spring events have advanced, largely occurring earlier over time (Parmesan and Yohe 2003). These patterns have repercussions for individual fitness, community interactions, and the continued persistence of certain species (reviewed in Parmesan 2006, Møller et al. 2008). Therefore, as global temperatures rise, it is increasingly crucial to study the consequences of changes in temperature on seasonal timing and biological processes.

Spring phenology is an informative measure for examining how species respond to changing temperatures and is consequently used in numerous reports of climate change response (IPCC 2007, Parmesan 2007). Butterflies are a useful model organism for studying changes in spring phenology because they have predictable and readily observable life events (Roy et al. 2001). Additionally, butterflies have long been a popular subject for naturalists and hobbyists, which has allowed for the persistence of long-term datasets of butterfly observations and museum specimens (Thomas 2005, Eskildsen et al. 2015). As ectotherms, they are also sensitive to changes in temperature (Pollard et al. 1993). As temperatures increase, the date of spring emergence has advanced in many butterfly species, as observed in California (Forister and Shapiro 2003), the Mediterranean Basin (Stefanescu et al. 2003), England (Diamond et al. 2011; Roy and Sparks 2000), and Ohio (Diamond et al. 2014).

While there have been multiple studies of changes in butterfly spring phenology from around the globe (Roy and Sparks 2000, Forister and Shapiro 2003, Stefanescu et al. 2003, Diamond et al. 2011, Diamond et al. 2014), our understanding of this phenomenon in the southeastern United States is unclear. This region is noteworthy because it has not experienced the same clear upwards trend in temperature observed on a global scale. Rather, the southeastern US experienced a slight cooling trend over the 20th century (Portmann et al. 2009). This designates the southeastern US as a climatically unique region with the potential to shed light on how species interactions may be altered in this region as temperatures are projected to rise (US Global Change Research Program 2014). More discussion on the practicality of looking at year vs. temperature effects when making inferences about phenological change.

Paragraph about the pros of and cons/potential of using incidental observation databases.

In this study, we use a database of butterfly observations collected opportunistically throughout North Carolina by citizen scientists to determine whether butterflies have shifted their spring appearance dates between 1993 - 2020 and whether temperature plays a role in these shifts. We also explore how species-specific traits relate to changes in first appearance dates in North Carolina butterflies, focusing on voltinism, overwintering stage, diet breadth, and diet composition. When examining voltinism, we expected species with higher voltinism to experience a greater advancement in early flight date in warm years because warming has been shown to be associated with an increase in the number of generations per year in butterflies (Altermatt 2010b). We hypothesize that species which overwinter as adults will experience a greater advance because the adults are more mobile and may more readily respond to temperature changes.

Methods

*Study system and dataset*

We used observational butterfly sighting data from the *Butterflies of North Carolina* (29th Approximation, LeGrand and Howard 2021). The database was first created in 1993 and covers North Carolina’s 177 known butterfly species. It is updated yearly and included 232,779 records from 1899 to 2020. The data is collected opportunistically, wherein participants may submit sightings from any time or location. It covers all North Carolina counties. Each entry lists the common name, date, observer name, number of individual butterflies observed, and the county of sighting.

We selected observations from the NC Triangle region, which comprises Durham, Orange, and Wake Counties. These counties had the highest number of records and occur in the Piedmont ecoregion. We also selected records collected between 1993 and 2020, because there are few records prior to this interval. From this interval, we selected species that had least 10 years with at least 10 unique observer dates. We also excluded species migratory that are in the Piedmont ecoregion from our analyses, resulting in 40 focal species (Supplemental Table 1). We used R (v 4.1.1) for all analyses.

*Early date estimate*

To account for effort variability, each unique observer-date-county-species combination was considered a single record. For example, suppose a total of two independent observers recorded at least one common buckeye (*Junonia coenia*) on the same date in the same county. We treated this as two records for *J. coenia*, regardless of how many individuals of this species each observer reported.

Since first record of appearance is heavily subject to outliers (van Strien et al. 2008), we instead defined early date as the date on which 10% of records had been collected for each unique species-year.

*Temperature proxy*

Mean monthly temperature data was obtained from the PRISM Climate Group (Oregon State University). We used the raster (Hijmans 2022) and rgdal (Bivand 2022) packages in R to to rasterize and subset the Triangle region. For a given year, we defined the spring temperature as the mean monthly temperature for the Triangle region averaged over a static 4-month window (March to June). We selected this window because spring temperatures strongly dictate the variation in the timing of insect emergence (Forister and Shapiro 2003, Dell et al. 2005).

*Phenological change*

* Removed outliers based on CooksD
* Summarized slopes and standard deviations. Slope is response, inversely weighted by standard devation of earlydate so highly variable species are penalized in the model
* library(lme4) #for constructing mixed models
* library(lmerTest) #for displaying p-values
* library (car) #for Anova function
* mod7 <- lm(year.slope~voltinism\*mean.year.earlydate, data=dat, weights=(1/dat$sd.year.earlydate))
* mod9 <- lm(temp.slope~voltinism\*mean.temp.earlydate, data=dat, weights=(1/dat$sd.temp.earlydate))
* mod11 <- lm(year.slope~voltinism\*mean.year.earlydate+overwinter, data=dat, weights=(1/dat$sd.temp.earlydate))
* mod12 <- lm(temp.slope~voltinism\*mean.temp.earlydate+overwinter, data=dat, weights=(1/dat$sd.temp.earlydate))

Results

Diagram

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**Figure 1.** Violin plots illustrating the distribution of slope values by species traits. Red dots indicate the mean, and error bars indicate the standard deviation. A) Distribution of earlydate versus temperature slopes and year slopes. B) Distribution of earlydate versus temperature slopes and year slopes by voltinism. The slopes for species with 3.5 and 5 voltinism are not displayed because there is a single value for each. C) Distribution of earlydate versus temperature and year by overwintering stage.

Chart

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Chart

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**Supplemental Figure 1.** A) A map of North Carolina counties, with NC Counties indicated in light green and Triangle counties (Durham, Orange, Wake) indicated in purple. B) Non-cumulative number of Triangle butterfly observations records per year and yearly fluctuations in mean temperature from March to June between 1990 and 2020. Map compiled using ArcGIS Version 10.6.1. County shapefile obtained from the US Census Bureau. Temperature data obtained from PRISM Climate Group (Oregon State University 2022).

Chart, histogram

Description automatically generated

**Supplemental Table 1.** Summary of species and species traits included in analysis.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Family | Species | Voltinism | Overwintering stage | Reference |
| Hesperiidae | *Ancyloxypha numitor* | 3 | larvae | LeGrand and Howard 2022 |
| Hesperiidae | *Atalopedes campestris* | 3 | larvae | LeGrand and Howard 2022, NABA North Jersey Chapter 2017 |
| Hesperiidae | *Epargyreus clarus* | 2 | pupae | LeGrand and Howard 2022, Hall 2008 |
| Hesperiidae | *Erynnis* spp. | 3 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Hesperiidae | *Euphyes vestris* | 2 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Hesperiidae | *Lerema accius* | 1 | pupae | LeGrand and Howard 2022, Burgess 2018 |
| Hesperiidae | *Nastra lherminier* | 2 | larvae | LeGrand and Howard 2022, NABA North Jersey Chapter 2017 |
| Hesperiidae | *Polites origenes* | 2 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Hesperiidae | *Pompeius verna* | 2 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022. Note possible main change |
| Hesperiidae | *Pyrgus communis* | 3 | larvae | LeGrand and Howard 2022, BAMONA 2022. Note possible name change |
| Hesperiidae | *Thorybes bathyllus* | 2 | larvae | LeGrand and Howard 2022, BAMONA 2022. Note possible name change |
| Hesperiidae | *Wallengrenia otho* | 2 | larvae | LeGrand and Howard 2022, Burgess 2018. Note name change |
| Lycaenidae | *Calycopis cecrops* | 2 | larvae | LeGrand and Howard 2022, Hall and Butler 2019 |
| Lycaenidae | *Celastrina* spp. | 3 | pupae | LeGrand and Howard 2022, BAMONA 2022, Alabama Butterfly Atlas 2022 |
| Lycaenidae | *Cupido comyntas* | 4.5 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Lycaenidae | *Strymon melinus* | 3 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Nymphalidae | *Asterocampa celtis* | 2 | larvae | LeGrand and Howard 2022, Hall and Butler 2021 |
| Nymphalidae | *Chlosyne nycteis* | 3 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Nymphalidae | *Cyllopsis gemma* | 3 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Nymphalidae | *Hermeuptychia sosybius* | 3 | larvae | LeGrand and Howard 2022, Tan and Lucky 2016 |
| Nymphalidae | *Lethe anthedon* | 2 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022 |
| Nymphalidae | *Lethe appalachia* | 2 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022 |
| Nymphalidae | *Libytheana carinenta* | 2 | adults | LeGrand and Howard 2022, Hall and Butler 2021 |
| Nymphalidae | *Limenitis archippus* | 3 | larvae | LeGrand and Howard 2022, Wisconsin Pollinators |
| Nymphalidae | *Limenitis arthemis astyanax* | 3 | larvae | LeGrand and Howard 2022, Hall and Butler 2019 |
| Nymphalidae | *Megisto cymela* | 1 | larvae | LeGrand and Howard 2022, BAMONA 2022 |
| Nymphalidae | *Phyciodes tharos* | 4.5 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022 |
| Nymphalidae | *Polygonia comma* | 2 | adults | LeGrand and Howard 2022 |
| Nymphalidae | *Polygonia interrogationis* | 2 | adults | LeGrand and Howard 2022 |
| Nymphalidae | *Speyeria cybele* | 1 | larvae | LeGrand and Howard 2022, Alabama Butterfly Atlas 2022. Note possible name change |
| Nymphalidae | *Vanessa virginiensis* | 3.5 | adults | LeGrand and Howard 2022, Hall 2021 |
| Papilionidae | *Battus philenor* | 3 | pupae | LeGrand and Howard 2022, Illinois Department of Natural Resources 2017 |
| Papilionidae | *Eurytides marcellus* | 3 | pupae | LeGrand and Howard 2022, Hall and Butler 2020 |
| Papilionidae | *Papilio glaucus* | 2 | pupae | LeGrand and Howard 2022, BAMONA 2022. Note name change |
| Papilionidae | *Papilio polyxenes* | 3 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Papilionidae | *Papilio troilus* | 2 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Pieridae | *Abaeis nicippe* | 3 | adults | LeGrand and Howard 2022, Florida Museum 2021 |
| Pieridae | *Anthocharis midea* | 1 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Pieridae | *Colias eurytheme* | 4.5 | pupae | LeGrand and Howard 2022, BAMONA 2022 |
| Pieridae | *Pieris rapae* | 5 | pupae | LeGrand and Howard 2022, BAMONA 2022 |

**Results (below is 2016 results)**

***Phenology analysis***

Between 1990 and 2016, 14 out of the 56 species tested experienced a significant correlation between early flight date and year. Of those 14 species, 2 had a positive correlation between early flight date and year, and the remaining 12 had a negative correlation (Figure 3a, Table 3). Overall there were 40 negative and 16 positive slopes, a much higher proportion of negative slopes than the expected equality (binomial test, *p*<0.0001). Across all species, there was an average advance of 0.51 days for every year.

Using temperature as the predictor variable, 5 out of the 56 species tested experienced a significant correlation between early flight date and temperature. Of those 5 species, 4 had a negative relationship and 1 had a positive relationship (Fig. 3b, Table 3). Out of the 56 species, there were 35 negative slopes and 21 positive slopes, which was again a much higher proportion of negative slopes than expected (binomial test, *p*<0.05). Across all species, there was an average advance of 1.62 days for every 1°C increase in mean temperature.

Of the 56 species tested, there were no species for which both year and temperature were significant predictors of early flight date. However, there were 23 species for which both year and temperature had a non-significant negative relationship with early date.

***Phenology analysis- regions***

For the effect of year on early flight date, 11 of the 50 species had a significantly different slope when comparing the mountains to the Piedmont, all of which had a smaller or more negative slope in the mountains (ANCOVA). When comparing the Coastal Plain to the Piedmont, 6 species had a significantly different slope, 5 of which were smaller or more negative in the Coastal Plain. When comparing the Coastal Plain to the mountains, 8 species had a significantly different slope, 7 of which were smaller or more negative in the Mountains. In all three regions, the majority of species had negative slopes for early flight date versus year (Table 4).

For the effect of temperature on early flight date, 3 species had a significantly different slope when comparing the mountains to the Piedmont, all of which were more negative in the mountains (ANCOVA). When comparing the Coastal Plain to the mountains, only *Lerema accius* had a significantly more negative slope in the mountains. No species were significantly different between the Piedmont and the Coastal Plain. Again, in all three regions the majority of species had negative slopes for early flight date versus temperature (Table 5).

***Species Traits***

From an ANOVA on the full linear model, early flight date varied strongly by diet type (F2,37=7.7313, p=0.0016, Figure 4, Table 2) and voltinism (F5,37=6.4586, p=0.0002, Figure 4, Table 2).

Using model averaging on the full model, voltinism was an important predictor of early flight date in 103 of the 106 models tested (97%). Diet type was an important predictor in 89 of the 106 (84%) of the models tested.

**Discussion**

The results of the state-wide phenology analyses are consistent with trends in advancement of early flight date in butterflies, as demonstrated by previous studies of long-term butterfly data (Diamond et al. 2011; Roy and Sparks 2000, Forister and Shapiro 2003, Stefanescu et al. 2003), and with a well-established trend of the influence of temperature on insect spring phenology (Forister and Shapiro 2003, Dell et al. 2005). However, it is noteworthy that none of 56 species tested shared both year and temperature as a strong predictor of early flight date. It is also notable that more of species experienced a strong negative correlation when year was used as covariant than when temperature was used. This is unusual because the relationship between higher temperatures and earlier flight dates is well-established, and it would be expected that temperature would have a significant effect on early flight date.

For those species for which temperature was not a strong predictor of early flight date, it is likely that an environmental variable besides mean temperature may be important. For example, photoperiod is a more effective predictor of phenology for some insects (Bale et al. 2002, Valtonen et al. 2011). In California, winter precipitation was also found to be an effective predictor for phenology (Forister and Shapiro 2003). Butterflies are varied in their life history traits, so they are likely to be affected differently by different seasonal cues. Insects in seasonal environments in particular benefit from having life history events which are synchronous with their specific host plants, which in turn have evolved to respond to different cues (van Asch et al. 2007). Indeed, in an analysis of the effect of species traits on early flight date we found that diet type was important in 89/106 (84%) of the models tested, pointing to the potential importance of host plant type in shaping phenology.

Another potential reason that temperature was not a widely effective predictor of phenology is that North Carolina is part of a climatically unique region which has experienced an atypical warming pattern compared to the rest of the world. This region- sometimes termed the “warming hole”- describes a region of the southeast where changes in temperature have not risen as consistently as they have globally (Folland et al. 2002, Portmann et al. 2009). This may have repercussions on the strength of the correlation between early flight date and year parameters in this analysis, as butterflies in North Carolina have not experienced a warming trend for as long as most other regions. We found no significant correlation between mean temperature and year for the 26-year interval used in this study.

In the regional data, only a very small proportion of the species tested experienced significantly different changes in early flight date between the three regions. However, when comparing the mountains to the other two regions, there were 23 instances in which species’ slopes differed significantly, 22 of which were more steeply negative in the mountains. The reason for this is unclear. Butterflies may be adapted to local climate at different elevational gradients, which may allow species in this region to better track seasonal changes.

There are many potential biases from working with data generated by citizen science. For example, sampling effort was highly variable between species, years, and regions. Although the proxy analysis sought to minimize the effect of sampling bias, there may have been an effect between regions, where sampling effort tended to be greater in the Piedmont than in either the Coastal Plain or the Mountains. In addition, it is possible that observers were more likely to go out to observe butterflies when temperatures were warmer, possibly influencing when butterflies were first sighted in a year. Despite these limitations, this dataset demonstrates the usefulness of citizen science data in phenological studies, which often require tracking diverse species over a wide geographical area over many years.

Average temperatures in the southeastern US are projected to climb (US Global Change Research Program 2014). This analysis therefore points to the potential for continued changes in early flight date as temperatures continue to warm. This could have repercussions for survival at both the individual and species level (reviewed in Parmesan 2006, Møller et al. 2008). For a more cohesive model of predicting phenological change in butterflies, additional analyses should account for climatic variables such as precipitation and photoperiod in addition to temperature.

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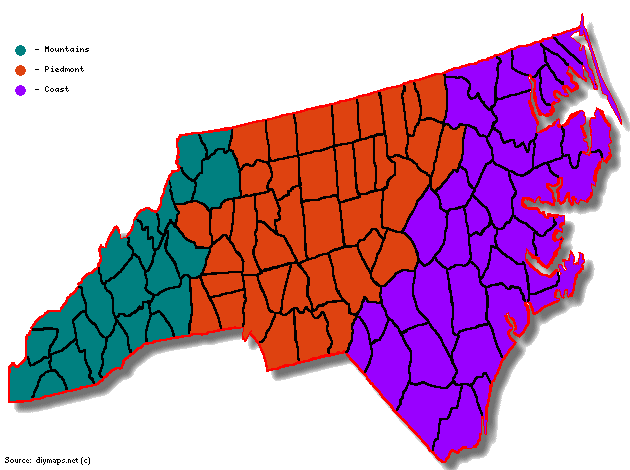
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**Tables and Figures**

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**Figure 1:** Calculated flight dates using hypothetical subsample of data and different proxies of early flight date.



**Figure 2.** The three regions used for analysis. From left to right: Mountains, Piedmont, and Coastal Plain.

(a)

**Chart, histogram

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(b)

Chart, histogram

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**Figure 3.** Histograms of the distribution of values of the slopes for all 56 species in a linear regression analysis. Red vertical lines indicate the average slope. (a) Distribution of slope values for early flight date vs. year. The average slope is an advance of 0.51 days for every one year. (b) Distribution of slope values for early flight date vs. temperature. The average slope is an advance of 1.62 days for every 1°C rise in temperature.