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Tracking climate impacts on the migratory monarch butterfly

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Abstract

Understanding the impacts of climate on migratory species is complicated by the fact that these species travel through several climates that may be changing in diverse ways throughout their complete migratory cycle. Most studies are not designed to tease out the direct and indirect effects of climate at various stages along the migration route. We assess the impacts of spring and summer climate conditions on breeding monarch butterflies, a species that completes its annual migration cycle over several generations. No single, broad-scale climate metric can explain summer breeding phenology or the substantial year-to-year fluctuations observed in population abundances. As such, we built a Poisson regression model to help explain annual arrival times and abundances in the Midwestern United States. We incorporated the climate conditions experienced both during a spring migration/breeding phase in Texas as well as during subsequent arrival and breeding during the main recruitment period in Ohio. Using data from a state-wide butterfly monitoring network in Ohio, our results suggest that climate acts in conflicting ways during the spring and summer seasons. High spring precipitation in Texas is associated with the largest annual population growth in Ohio and the earliest arrival to the summer breeding ground, as are intermediate spring temperatures in Texas. On the other hand, the timing of monarch arrivals to the summer breeding grounds is not affected by climate conditions within Ohio. Once in Ohio for summer breeding, precipitation has minimal impacts on overall abundances, whereas warmer summer temperatures are generally associated with the highest expected abundances, yet this effect is mitigated by the average seasonal temperature of each location in that the warmest sites receive no benefit of above average summer temperatures. Our results highlight the complex relationship between climate and performance for a migrating species and suggest that attempts to understand how monarchs will be affected by future climate conditions will be challenging.

Keywords: breeding habitat, Danaus plexippus, growing degree day, palmer drought index, phenology, Poisson regression model, return migration

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Introduction

A primary goal of global climate change research is to understand the connections between climate and biological phenomena so that specific predictions can be made about how species will be affected by future climate regimes (Parmesan, 2006). While this is a difficult task for any organism, characterizing the responses of migratory species is particularly challenging. During the course of their life cycles, migratory species experience multiple climates that may be changing in different ways (Norris & Marra, 2007; Bowlin et al., 2010).

Perhaps not surprisingly, it has been suggested that climate change, along with other anthropogenic pressures, may be contributing to the overall decline of ‘flagship’ migrants (Brower & Malcolm, 1991; Wilcove & Wikelski, 2008). Here, we use the term migratory to refer to species that have a regular, long-distance pattern of return or ‘round-trip’ migration related to predictable, disjunct seasonal ranges and not species that track unpredictable resources over large areas (sensu Dingle, 1996; Mueller & Fagan, 2008).

Establishing cause and effect relationships between climate and migratory dynamics is complicated. In addition to direct impacts on physiology at each location along the migration cycle, which may be carried over into subsequent migratory phases (Harrison et al., 2011), climate can also have indirect effects on the abundance or timing of food resources (Zalucki & Rochester, 2004;...
Visser & Both, 2005; Srygley et al., 2010). Disentangling these multiple, interacting climate drivers is complex and studies are rarely designed to isolate causes to a particular migratory phase or effect (Gordo, 2007; Norris & Marra, 2007). Indeed, many studies have focused on large-scale climate dynamics like the North Atlantic Oscillations (NAO) in the northern hemisphere and the Southern Oscillation Index (SOI) in the southern hemisphere, which are often associated with broad-scale weather patterns and have thus been found to be good predictors of both phenology (e.g., Adamik & Pietruszkova, 2008; Palm et al., 2009; Srygley et al., 2010) and abundance (e.g., Maelzer & Zalucki, 2000; Vandenbosch et al., 2003; Zipkin et al., 2010). Yet the use of large-scale climate metrics, such as the Atlantic Oscillations, makes it difficult to isolate how specific climate factors may be impacting particular phases of migration or the performance of species (Gordo, 2007; Norris & Marra, 2007).

The vast majority of studies on the impacts of climate on terrestrial, migratory species have focused on bird phenology, with the bulk of that research studying spring arrival times at breeding grounds in North America and Europe (Gordo, 2007). In general, dates of spring arrival have been advancing for many species and those advancements are consistent with regional warming (Gordo, 2007). While there is a great deal of interspecific variability in this phenomenon, there is also general within-species consistency (Rubolini et al., 2010). Most studies have not specifically examined the climate conditions during the winter or migratory (stopover) phases, and instead have focused only on the environment at the point of arrival (Gordo, 2007), despite the fact that it is very unlikely that birds are able to assess conditions at summer breeding grounds prior to their arrival. While some climate variables may operate on a large enough scale so that metrics from the arrival point are correlated to stopover or wintering climates (e.g., the Atlantic Oscillations), this approach does not allow specific climate mechanisms to be identified (Norris & Marra, 2007).

Earlier arrivals to breeding locations can lead to either better access to resources (Kokko, 1999) or, conversely, a phenological mismatch where access to optimal resources is diminished, possibly leading to decreased fitness or even population declines (Both et al., 2006; Saino et al., 2011). Studies of how climate impacts population size have been less common and more inconsistent, possibly because breeding performance responds to more complex interactions of factors both on and off the breeding grounds (Norris & Marra, 2007).

Butterflies have received intensive focus on the climate impacts related to phenology (Parmesan, 2007), phenological mismatches (Doi et al., 2008; Singer & Parmesan, 2010), local abundances (Warren et al., 2001; Hodgson et al., 2011), and range and elevational dynamics (Parmesan et al., 1999; Konvicka et al., 2003; Crozier & Dwyer, 2006; Forister et al., 2010). Several butterfly species exhibit yearly migrations, some with exceptionally high “outbreak” years, and the timing and size of those events have been linked to large-scale oscillations like El Nino (Vadenbosch 2003, Srygley et al., 2010). While mounting evidence has shown that for some species, a portion of individuals do return to wintering ranges (Brattstrom et al., 2008, Chapman et al., 2011), the best known example of insect return migration is the monarch butterfly (Danaus plexippus) which completes a regular migratory circuit each year, but over multiple generations (Brower, 1986). Because of its spectacular migration, it has become a ‘flagship’ species for both migration and the conservation of migratory phenomenon (Brower & Malcolm, 1991; Wilcove & Wikelski, 2008). Understanding how climate impacts monarchs will be a key factor in its conservation (Oberhauser & Peterson, 2003; Batalden et al., 2007) and will expand our understanding of the impacts of climate on migratory species in general (Bowlin et al., 2010).

Study system

The monarch butterfly (Danaus plexippus) in North America has a regular seasonal migratory pattern that is completed over multiple generations rather than by single individuals (Brower, 1986). There are two distinct monarch populations in North America: the western migratory population, west of the Rocky Mountains that overwinters along the California coast (Dingle et al., 2005) and the eastern migratory population, east of the Rocky Mountains that overwinters in Mexico (Brower, 1986). There is also a small non-migratory population in southern Florida (Altizer et al., 2000). The eastern migratory population is the largest, and the focus of this study. Monarchs use host plants in the subfamily Asclepiadoideae (milkweeds), which are common throughout North America.

Individuals from the eastern population overwinter in a small forested area at the boundary of the Mexican states Michoacán and México (Brower, 1986; Fig. 1). During the winter, they remain clustered in dense colonies, which start breaking up in late February or early March as individuals begin moving northward. The spring migrants move into Texas and its surrounding areas (Fig. 1) by mid-March (Brower et al., 2004) and begin laying eggs in mid- to late-March. These eggs become the year’s first generation, which fans out over the rest of eastern North America (Fig. 1). Throughout the summer breeding season, the population grows as an additional 2–3 generations are produced, with the bulk of recruitment occurring in the Midwest.

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The size of the final generation, which migrates to Mexico, fluctuates substantially from year to year (Swengel, 1995; Prysby & Oberhauser, 2004; Pleasants & Oberhauser, in press). The causes of those fluctuations are currently unknown, although climate is assumed to be one contributing factor (Zalucki & Rochester, 2004). Around the first of September, most monarchs enter reproductive diapause, begin to move southward, and ultimately return to the Mexican overwintering sites (Brower, 1986).

Climate effects on monarchs can be direct, impacting adult activity and juvenile development, or indirect, by impacting growth and vitality of their host plants (Zalucki & Rochester, 2004). Niche models have suggested that monarchs during the breeding season have an optimal temperature and precipitation ‘envelope’ that tracks northward as the season progresses, starting in Texas during March and April. Although that climate envelope continually shifts position throughout the summer growing season, much of the optimal range persists in the Midwest (Batalden et al., 2007). These modeling results are largely consistent with laboratory studies that bracket the minimum and maximum temperatures that promote monarch juvenile development (Zalucki, 1982; York & Oberhauser, 2002) and suggest climate should underlie some of the year-to-year variability in population dynamics (Zalucki & Rochester, 2004). Studies in western populations suggest drought is a limiting factor (Stevens & Frey, 2010) and that higher winter temperatures and increases in the previous season’s rainfall can advance the onset of spring migration (Forister & Shapiro, 2003). Our goal is to examine how weather experienced during the spring and summer impacts phenology as well as inter-annual fluctuations in abundance of the monarch butterfly on its summer breeding grounds. We focus our analysis on patterns in Ohio because there is a well-established series of butterfly monitoring stations throughout the state (Fig. 1b) which falls within the major zone of monarch recruitment (Fig. 1a). We use climate variables from Texas as indicators of spring conditions because we know that the migratory population moves through Texas and lays at least a portion of their eggs there; the extent of spring breeding outside Texas is less known.

Materials and methods

Our analysis focuses on the impacts of climate experienced by the first generation in the southern US (developed from eggs laid by incoming spring migrants from Mexico) and during the main population growth phase in Ohio (from incoming first generation adults that emerged in Texas and the surrounding areas). We concentrated on temperature and precipitation, two main facets of weather known to affect

**Fig. 1** Breeding dynamics of the eastern migratory monarch population (a) Adults overwinter in a small area in Mexico (star), then fly north in spring and lay eggs in the southern US with most known breeding in Texas. Adults emerge and fan out to occupy the rest of the breeding range over the summer. Two or three more generations are produced during this time with most recruitment occurring in the Midwest, including (b) Ohio where there is a network of butterfly monitoring stations that was established in 1995. In September, most adults enter reproductive diapause and return to the overwintering sites in Mexico.
monarchs (Zalucki & Clarke, 2004; Batalden et al., 2007). Because initial explorations of the data suggested that coarse weather metrics could not explain inter-annual variations in abundance and phenology (Fig. 2), we developed a model that captured weekly dynamics at each Ohio survey site based on several climate metrics.

To account for timing in our model, we sequentially numbered each week in the season and we refer to those week designations throughout the rest of this article. The onset of migration from Mexico is approximately the beginning of March (week 1 always begins on March 1). Unfortunately, we had no data on the size of the population leaving Mexico each year, so it was not possible to include that factor in our model. Spring breeding in Texas occurs primarily between the last week in March through the end of April (weeks 4 – 9; Prysby & Oberhauser, 2004). The adults that emerge during spring breeding usually arrive in Ohio by the first week in May (week 10; Howard & Davis, 2004), but are relatively uncommon until mid-June to mid-July (weeks 15 – 20). Population growth continues through approximately the beginning of September (week 28; Brower, 1986).

Temperature impacts were captured by converting temperature into growing degree days (GDD). The GDD accumulate the number of degrees that can contribute to development, assuming a minimum temperature below which a species cannot develop and a maximum temperature beyond which growth is no longer benefited (McMaster & Wilhelm, 1997). The GDD calculations are based on physiological responses and temperature tolerances that are generally measured in a lab and are species-specific; the values we used were developed for the monarch by Zalucki (1982). The minimum temperature required for monarch growth is 11.5 °C while the maximum is 33 °C. GDD are accumulated over the season by summing the total GDD accumulated each day. Daily GDD are calculated using the mean of two daily values: the day’s high temperature (up to a maximum of 33 °C) and the day’s low temperature. Then, the minimum temperature required for growth (21.5 °C) is subtracted from that mean value to arrive at the daily GDD value. A total of 352 GDD are on average required for an egg to develop into an adult. Like temperature, the impacts of drought can accumulate over a season and the timing of rainfall is also critical. The Palmer Drought Index (PDI) integrates rainfall events, temperature, and other hydrological dynamics over the season to estimate water availability (Heim Jr, 2002). This metric can give more biologically relevant information than rainfall alone (Heim Jr, 2002), but PDI can be confounded with temperature (Hu & Wilson, 2000).

**Monarch data collection**

The Ohio data were collected at 90 locations that comprise a state-wide network of butterfly monitoring surveys (Fig. 1b).
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monarchs into Ohio (from Texas and the surrounding areas) to just prior to the southerly migration back to Mexico. We modeled expected monarch counts at each location \( j \) (1–90) in week \( k \) (10–28) within year \( t \) (1996–2008) on the log scale using the following model:

\[
\log(\hat{y}_{j,tk}) = \alpha + \beta_1 \cdot \text{week}_k + \beta_2 \cdot \text{spPREC}_t + \beta_3 \cdot \text{spPRED}_t^2 + \\
+ \beta_5 \cdot \text{spGDD}_t + \beta_6 \cdot \text{spGDD}_t^2 + \beta_7 \cdot \text{spPRED}_t \cdot \text{week}_k + \\
+ \beta_8 \cdot \text{spGDD}_t \cdot \text{week}_k + \\
+ \beta_9 \cdot \text{GDDdiff}_{j,t,k} + \\
+ \beta_{10} \cdot \text{avgGDD}_j + \beta_{11} \cdot \text{avgGDD}_t^2 + \\
+ \beta_{12} \cdot \text{GDDdiff}_{j,t,k} \cdot \text{week}_k + \\
+ \beta_{13} \cdot \text{GDDdiff}_{j,t,k} \cdot \text{avgGDD}_j \cdot \text{week}_k + \\
+ \beta_{14} \cdot \text{PDI}_{j,t} + \\
+ \beta_{15} \cdot \text{PDI}_{j,t}^2 + \beta_{16} \cdot \text{PDI}_{j,t} \cdot \text{week}_k + \beta_{17} \cdot \text{open}_{j,t} + \\
+ \log(\text{effort}_{j,tk})
\]

with \( \alpha \) as the intercept term and \( \beta_2 - \beta_{17} \) as parameters that affect the count annually, weekly, and by location. We standardized each covariate so that it had a mean of 0 and a standard deviation of 1. The annual migration northward retains a fairly consistent within-season temporal schedule. Because of this consistency and because we hypothesized that the effects of several of the weather covariates may vary over the course of the season, we included a covariate on week \( (\beta_2, \text{linear term because monarch abundance in Ohio will generally be increasing during this time frame}) \). The parameters \( \beta_3 - \beta_{12} \) deal with the effects of the spring conditions in Texas on monarch counts, where \( \beta_3 \) and \( \beta_4 \) are the linear and squared effects of cumulative precipitation in Texas, \( \text{spPREC}_t \), and \( \beta_5 \) and \( \beta_6 \) are the linear and squared effects of GDD in Texas, \( \text{spGDD}_t \). We also included parameters \( \beta_7 \) and \( \beta_8 \) as interaction terms with spring precipitation/GDD and week, respectively, because we hypothesized that spring conditions in Texas may affect monarch counts in Ohio differently over the course of the breeding season.

Parameters \( \beta_{9} - \beta_{13} \) are effects related to the accumulating GDD at the survey point \( j \). Because GDD increases throughout the spring and summer, we used the difference from the mean GDD, \( \text{GDDdiff}_{j,t,k} \), at a given point \( j \) across all 13 years of the survey (Hodgson et al., 2011). Thus, we were able to capture whether the GDD accumulated by the end of each week of the survey were above or below the average for that site at that time. We included only a linear effect (\( \beta_9 \)) on \( \text{GDDdiff}_{j,t,k} \) because a squared term did not come out as significant in earlier versions of the model. The average GDD, \( \text{avgGDD}_j \), accumulated at the end of the summer season (week 28 in our model) across all 13 years of sampling, accounted for location effects. This was confirmed by a lack of any structure in model residuals related to latitude or longitude (Appendix S1). We included linear (\( \beta_{10} \)) and squared (\( \beta_{11} \)) effects for \( \text{avgGDD}_j \). We hypothesized that the importance of \( \text{GDDdiff}_{j,t,k} \) might vary by week over the course of the sampling period and may have an increasing influence on monarch abundance as the season progresses (because abundance is always very low during the early part of the season). We similarly suspected that a site’s \( \text{avgGDD}_j \) may be important in understanding how variation in \( \text{GDDdiff}_{j,t,k} \) affects abundance over the spring and summer seasons (i.e., the effect of above average GDD may depend on whether or not that site is typically a warmer or cooler location). Covariates \( \beta_{12} \) and \( \beta_{13} \) account for these possible interactions. Parameters \( \beta_{14} - \beta_{16} \) are effects related to site-specific PDI values. The covariate \( \text{PDI}_{j,t} \) is the annual metric of the drought index at each survey location and we included linear (\( \beta_{14} \)) and squared (\( \beta_{15} \)) effects as well as an interaction with survey week (\( \beta_{16} \)).

We included two location-specific nuisance terms in our model: the covariate \( \text{open}_{j,t} \), is the proportion of area along the \( j \)th transect that is unforested. Although we are not specifically interested in how differences in habitat affect monarch abundance, we included \( \beta_{17} \) because milkweed tends to grow in open areas. Similarly, survey durations and transect lengths vary and we included an offset term, log(\( \text{effort}_{j,tk} \)), measured in survey minutes to account for variable effort.

Although our model is quite complicated, containing four main effects (spring precipitation, spring GDD, summer PDI, and summer GDD) as well as several interactions and square terms, this level of complexity was necessary to adequately describe the climate variables affecting the spatial and temporal changes in monarch abundances. During development, we built and analyzed a total of 12 versions of the model and performed a model selection procedure to determine which model to use in our analyses. Details on the candidate models and the selection process can be found in Appendix S1.

We analyzed our model using a Bayesian approach with the programs R and WinBUGS (Lunn et al., 2000). We ran three chains for 3000 iterations after a burn-in of 3000 iterations and thinned the chains by 3 assuming flat normal priors on each of the covariates. Model convergence was assessed using the R-hat statistic, which examines the variance ratio of the MCMC algorithm within and between chains across iterations for each parameter value (Gelman & Hill, 2007). R-hat values close to 1 indicate that the model has converged and values under 1.2 are considered acceptable (Gelman & Hill, 2007). The R-hat values for all parameters in our model were less than 1.03.

### Results

In contrast to coarse-scale comparisons which show no relationship between any single climate metric and yearly monarch abundance (Fig. 2), our model results suggest that climate in both Texas and Ohio does impact expected counts in Ohio. All parameters that were included in the model had significant effects, and standard deviations for each parameter were generally small (Table 1). The interactions between week and the spring climate variables (Texas GDD and precipitation) as well as the GDD differentials at locations in Ohio were all positive, suggesting that the importance of these climate variables increases over the course of the summer. This is an expected result because counts remain near zero for the first few weeks of the modeling period then increase rapidly through the remainder of the study period. This is shown in the results for both spring and summer climate impacts, which are
displayed in Figs 3 and 4; in all cases the displayed results assume that other covariates in the model are held at their mean values.

Spring weather conditions in Texas had significant effects on the magnitude of monarch counts later in the season in Ohio, with wetter springs and average spring temperatures leading to the highest predicted abundances at the end of the season (Fig. 3). Spring weather conditions in Texas also affected emergence phenology of monarchs in Ohio, with earlier observations and faster increases in expected abundance during the wettest and, to a lesser degree, driest springs (Fig. 3a), when other parameters are held constant. Our results further indicate that intermediate values of spring GDD were associated with earlier observations and greater increases of monarchs in Ohio (Fig. 3b), although the magnitude of the effect was not as great as that for spring precipitation (Fig. 3a).

Monarchs’ response to climate experienced on their summer breeding grounds in Ohio showed some key differences compared with spring effects. First, GDD was much more important than precipitation during summer (Table 1). The impacts of precipitation (as measured with annual PDI) were minor and did not have a consistent effect on timing or abundance (results not illustrated). Expected monarch abundance was greatest when GDD was above average for each site, but that effect was strongest for the coolest sites (Fig. 4a) and diminished as sites became warmer (Fig. 4b), with the pattern beginning to reverse at the warmest sites (Fig. 4c). The effect was increasingly pronounced as the season progressed. The highest observed counts were found late in the season in the coolest locations (min avgGDD values) that had accumulated above average GDD (GDDdiffi,t,k) values (Fig. 4a). Conditions in Ohio had no obvious impact on monarch arrival phenology (Fig. 4).

Discussion

Our results show that climate is a major driver of monarch population dynamics, but that the relationships are complex. We showed that no simple climate metric (seasonal summaries of temperature and precipitation) on either the spring or summer breeding grounds could explain annual abundances in Ohio (Fig. 2 and Appendix S1). Instead, a combination of interacting climate factors on both the spring and summer breeding grounds seems to set the stage for differences in migration phenology and annual population growth (Figs 3 and 4). These results emphasize the difficulties in trying to understand how climatic conditions impact migrating species and highlight the challenges associated with making predictions on the effects of changing climate regimes on monarchs and other migrating species. By not including specific spatial covariates, our model was designed to be general and to shed light on the climate factors affecting the eastern migratory population of monarchs. Results from our model can be used to make predictions about the relationships between monarchs and weather variables in other regions of eastern North America and can be validated using additional data from such locales. We further suggest the construction of similar models for the western migratory population.

Table 1  Parameter descriptions, point estimate (posterior mean), standard deviation, and 95% posterior interval. The subscripts represent transect location (j), survey year (t), and week within season (k).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Covariate</th>
<th>Description</th>
<th>Estimate</th>
<th>SD</th>
<th>95% PI</th>
</tr>
</thead>
<tbody>
<tr>
<td>a1</td>
<td>NA</td>
<td>Intercept</td>
<td>−0.578</td>
<td>0.025</td>
<td>(−0.63,−0.53)</td>
</tr>
<tr>
<td>a2</td>
<td>weekk</td>
<td>Week in season</td>
<td>1.376</td>
<td>0.014</td>
<td>(1.35,1.40)</td>
</tr>
<tr>
<td>a3</td>
<td>spPRECjt</td>
<td>Spring precipitation in Texas (linear)</td>
<td>−0.070</td>
<td>0.015</td>
<td>(−0.10,−0.04)</td>
</tr>
<tr>
<td>a4</td>
<td>spPREDjt²</td>
<td>Spring precipitation in Texas (squared)</td>
<td>0.364</td>
<td>0.011</td>
<td>(0.34,0.39)</td>
</tr>
<tr>
<td>a5</td>
<td>spGDDjt</td>
<td>Spring GDD in Texas (linear)</td>
<td>−0.198</td>
<td>0.022</td>
<td>(−0.24,−0.15)</td>
</tr>
<tr>
<td>a6</td>
<td>spGDDjt²</td>
<td>Spring GDD in Texas (squared)</td>
<td>−0.229</td>
<td>0.014</td>
<td>(−0.26,−0.20)</td>
</tr>
<tr>
<td>a7</td>
<td>spPRECjt weekk</td>
<td>Spring precipitation and week interaction</td>
<td>0.100</td>
<td>0.017</td>
<td>(0.07,0.13)</td>
</tr>
<tr>
<td>a8</td>
<td>spGDDjt weekk</td>
<td>Spring GDD and week interaction</td>
<td>0.109</td>
<td>0.013</td>
<td>(0.08,0.13)</td>
</tr>
<tr>
<td>a9</td>
<td>GDDdiffi,t,k</td>
<td>Weekly GDD differential at transects in Ohio</td>
<td>−0.049</td>
<td>0.020</td>
<td>(−0.09,−0.01)</td>
</tr>
<tr>
<td>a10</td>
<td>avgGDDjt</td>
<td>Average cumulative GDD at transects in Ohio (linear)</td>
<td>−0.091</td>
<td>0.011</td>
<td>(−0.11,−0.07)</td>
</tr>
<tr>
<td>a11</td>
<td>avgGDDjt²</td>
<td>Average cumulative GDD at transects in Ohio (squared)</td>
<td>0.055</td>
<td>0.011</td>
<td>(0.03,0.08)</td>
</tr>
<tr>
<td>a12</td>
<td>GDDdiffi,t,k weekk</td>
<td>GDD differential and week interaction</td>
<td>0.080</td>
<td>0.015</td>
<td>(0.05,0.11)</td>
</tr>
<tr>
<td>a13</td>
<td>GDDdiffi,t,k avgGDDjt weekk</td>
<td>GDD differential, average GDD and week interaction</td>
<td>−0.031</td>
<td>0.006</td>
<td>(−0.04,−0.02)</td>
</tr>
<tr>
<td>a14</td>
<td>PDIjt</td>
<td>Annual PDI at transects in Ohio (linear)</td>
<td>−0.104</td>
<td>0.016</td>
<td>(−0.14,−0.07)</td>
</tr>
<tr>
<td>a15</td>
<td>PDIjt²</td>
<td>Annual PDI at transects in Ohio (squared)</td>
<td>−0.059</td>
<td>0.009</td>
<td>(−0.08,−0.04)</td>
</tr>
<tr>
<td>a16</td>
<td>PDIjt weekk</td>
<td>Annual PDI and week interaction</td>
<td>−0.108</td>
<td>0.014</td>
<td>(−0.14,−0.08)</td>
</tr>
<tr>
<td>a17</td>
<td>openji</td>
<td>Proportion of unforested habitat at transects in Ohio</td>
<td>0.303</td>
<td>0.010</td>
<td>(0.28,0.32)</td>
</tr>
</tbody>
</table>

GDD, growing degree days; PDI, Palmer Drought Index; SD, standard deviation.
to determine the variability among monarchs in their responses to climate conditions.

According to our model, spring precipitation was the factor associated with the greatest potential for population growth, with the wettest springs leading to the highest population numbers (Fig. 3a). This relationship was curvilinear, with low precipitation also leading to slightly higher predicted values compared with average precipitation (Fig. 3a). Yet, this relationship is obviously complex. We first note that the year with the lowest population (2004) occurred during the second wettest spring (Fig. 2c). More in line with these results, the year with the highest population (1997) also occurred in the wettest spring (Fig. 2c), but monarchs this year were unusually abundant (highlighted as an outlier in all four panels of Fig. 2). This raises the question of whether the result could have been driven by that one potentially aberrant year. To explore this, we reran the model excluding the data from 1997. The results were strikingly similar to those illustrated in Figs 3 and 4 with two notable differences (Appendix S2). First, the strength of the effect for spring precipitation was weaker, with both wet and dry springs still leading to higher numbers, but in a weaker and more symmetrical fashion (Fig. S2a). Results were unchanged for spring GDD (Fig. S2b). Second, the strength of the effect of summer GDD was stronger (Fig. S2c–e), but the interaction effect with average site GDD, while still present, was weaker with no reversal of effect occurring at the warmest sites (compare Figs S2e and S4c).

Based on the results from the model runs with the full and reduced data sets, we conclude that the climate factors leading to optimal population growth include...
wetter or, to a lesser degree, drier springs, and intermediate temperature zones in Texas. In Texas, average temperatures are optimal (Fig. 3b) while in Ohio, warmer summers (within the range experienced during this 13 year study) generally lead to higher monarch numbers, except at the very warmest sites. Areas south of Ohio are too warm to support optimal growth during summer months (Malcolm et al., 1987; Batalden et al., 2007) and these results are in line with laboratory studies that highlight both lethal and sub-lethal effects of hot temperatures (York & Oberhauser, 2002). Our results suggest that future temperature regimes across monarchs’ growing range are likely to have divergent effects depending on latitude and also the time of the season. In both runs of the model, only spring climate metrics impacted the expected timing of arrival in a substantive way, with wetter or drier springs and average temperatures in Texas associated with earlier sightings in Ohio (Figs 3 and 4). This is consistent with our hypothesis that climate in Texas should have a bigger impact on arrival than conditions in Ohio.

Despite these general trends, these climate factors cannot in and of themselves explain all the observed year-to-year variability in monarch abundances. The purpose of our model was to determine how spring and summer climate conditions affect inter-annual monarch abundances and the phenology of arrival to breeding locations in Ohio. However, additional factors (all of which are likely climate-related) may also affect monarch population dynamics, including size of the wintering population and winter mortality, annual milkweed growth, and parasitism. If data become available for annual milkweed abundances, such information could potentially reduce the remaining variation in our model. Similarly, the area occupied by the wintering population is often used to indicate overall monarch population size (Brower et al., 2012; Pleasants & Oberhauser, in press), but the values available are measured near the start of the overwinter period and do not account for wintering mortality (Rendon-Salinas et al., 2011), which can be highly variable. Despite this, it is worth noting that 1997, which had an exceptionally cool spring and summer (factors associated with smaller population sizes) nevertheless produced an extremely large population (Fig. 2). This may or may not be related to the 1996–1997 overwinter colony sizes, which were the largest ever recorded (Rendon-Salinas et al., 2011). Similarly, overwinter mortality during 2003–2004 was high, possibly contributing to the small population size observed in 2004. Yearly milkweed growth is also likely to be an important factor in monarch population sizes, both in Texas and Ohio, and the timing of growth may be particularly important. Anecdotal evidence suggests that monarch arrivals sometimes occur when milkweed has barely emerged, leading to food depletion and crowding (K. Oberhauser, unpublished data), and potentially increased parasitism rates (Lindsay et al., 2009), which could have an effect on local population abundances. Parasitism and disease are other well studied and important factors in monarch biology (Prisby, 2004; Bartel et al., 2011) and it is currently unknown how they may interact with arrival phenology and climate.

Climate predictions across North America (Girvetz et al., 2009, implemented in www.climatewizard.org) suggest that springs in Texas may become hotter and drier while the summers throughout eastern North America may also be hotter and slightly wetter (based on a high emission, 50 year scenario). If spring precipitation in Texas remains within the range captured by our 1996–2008 study period, then our model results suggest that this could potentially have a slight benefit for monarchs as low precipitation is associated with earlier arrivals and more growth. However, we are cautious about this result and suggest further testing in other regions, especially as drought is associated with reduced population sizes in California (Stevens & Frey, 2010). Although our model indicates that drier spring conditions (as compared to average precipitation) are associated with elevated population sizes, if springs in Texas become too hot the result could be decreased abundances as the optimal spring temperature for monarchs is in the intermediate range of current conditions. The impacts of increased summer temperatures and precipitation are harder to gauge. Our model suggests that monarchs in Ohio are likely to experience increased growth with warmer summers, but at some point this relationship may slow or reverse (Fig. 4c). Recent studies have shown that warmer temperatures have been beneficial to many European butterflies, including migrants (Warren et al., 2001), but these regions do not experience the extreme heat waves that are sometimes observed in the southern and midwestern US. At a large scale, warming is expected to be more intense further north and west, which could be helpful to monarch growth, but again at some point, the heat may slow growth or even cause mortality.

These crude projections are in line with niche modeling that shows the optimal climate window tracking north based on a 50 year climate projection (Batalden et al., 2007). No modeling approach has yet captured the full complexity of how climate interacts with all the potential factors that influence monarch population growth, including the condition and number of incoming migrants from Mexico, milkweed growth and congruence with monarch arrivals, natural enemies, and appropriate climatic environments for activity and growth throughout each phase of their migratory cycle.
Further consideration of the effects of climate on monarchs will ultimately need to include changing climate during their overwinter and fall migration phases as well. Research has already shown that changes in climate in Mexico could have devastating consequences for this population (Oberhauser & Peterson, 2003). Piecing together the mechanisms that drive these dynamics will be crucial to understand monarch biology in general and how this unique species may respond to future climate scenarios.

Migrating species have an intricate and complicated relationship with climate variables that can vary geographically (Dingle et al., 2000) and cannot easily be described by simple weather variables. Our results elucidate how monarchs respond to both local and regional climate factors. They also demonstrate how optimal climate conditions can change for a species over the migration path and how phenology may be impacted more severely by climate conditions along the migratory route than at the destination, something that is rarely considered in studies of migratory species (Gordo, 2007). It would be easy to look at basic climate variables individually (e.g., Fig. 2) and conclude that climate plays no dominant role in observed patterns of monarch abundances. But here we show that monarch abundances are influenced by an interacting combination of spring and summer variables that impact populations differently across space. Therefore, it should not be surprising that relating a single annual summary index to major climate metrics does not reveal significant relationships. Instead, climate variables must be considered in conjunction with one another and also within the context of our best understanding of a species’ biology. Our findings highlight the importance of ongoing research into understanding the effects of climate on migrating species dynamics and particularly emphasize the need to determine which variables are most important along specific points of the migratory path.

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References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Model selection.

Appendix S2. Results from model run excluding data from the year 1997.

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