Tracking climate impacts on the migratory monarch butterfly

ELISE F. ZIPKIN*†, LESLIE RIES†‡, RICK REEVES§, JAMES REGETZ§ and
KAREN S. OBERHAUSER¶

*USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708, USA, †Department of Biology,
University of Maryland, College Park, MD 20742, USA, ‡National Socio-environmental Synthesis Center, 1 Park Place, Suite
300, Annapolis, MD 24101, USA, §National Center for Ecological Analysis and Synthesis, University of California, Santa
Barbara, 735 State, Street, Santa Barbara, CA 92101, USA, ¶Department of Fisheries, Wildlife and Conservation Biology,
University of Minnesota, 1980 Folwell Ave., St. Paul, MN 55108, USA

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

Received 8 November 2011; revised version received 2 May 2012 and accepted 13 May 2012

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).

Present address: Rick Reeves, Foxgrove Solutions, 528 Foxen Drive, Santa Barbara, CA 93105, USA.

Correspondence: Elise F. Zipkin, tel. + 301 497 5810,
fax + 301 497 5545, email: ezipkin@usgs.gov

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
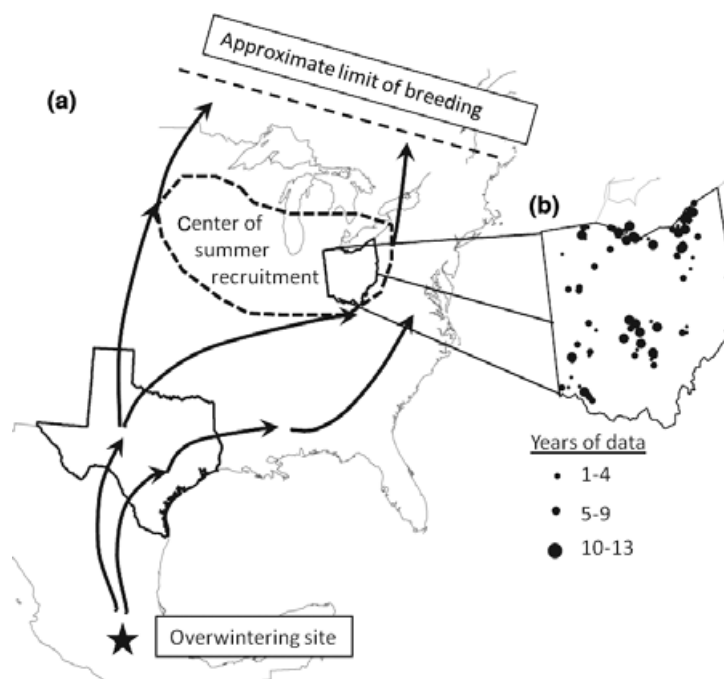
Fig. 1 Breeding dynamics of the eastern migratory monarch population (a) Adults overwinter in a small area in Mexico (star), then fly north in spring and lay eggs in the southern US with most known breeding in Texas. Adults emerge and fan out to occupy the rest of the breeding range over the summer. 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.

(Wassenaar & Hobson, 1998). 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 survey sites 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
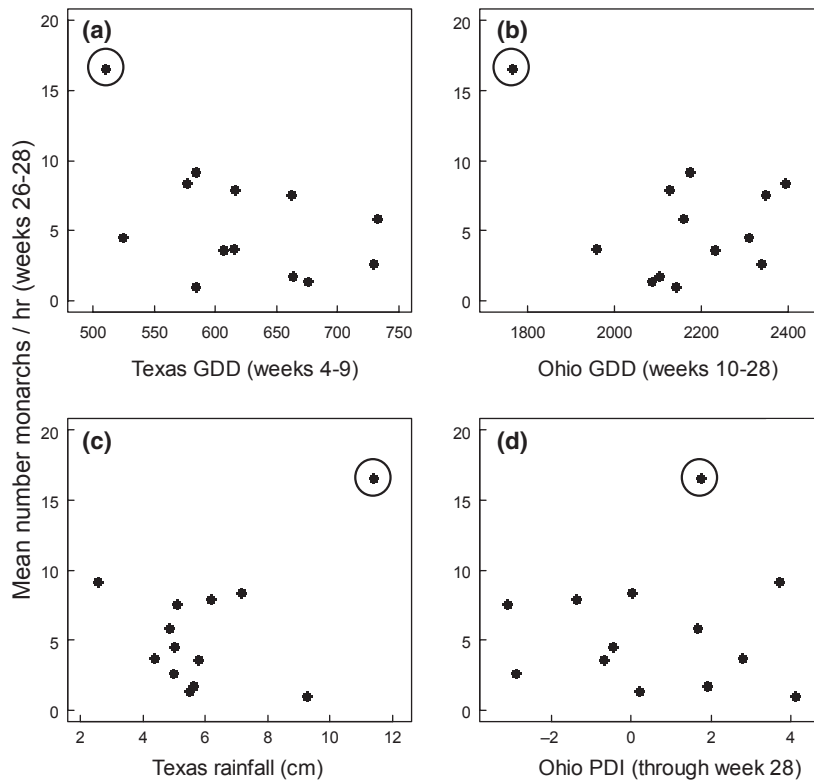
Fig. 2 The relationship between an index of monarch yearly abundance (averaged over all sites during weeks 26–28) and (a) spring growing degree days (GDD) in Texas (accumulated from weeks 4–9), (b) summer GDD in Ohio (accumulated from weeks 10–28), (c) February–April rainfall in Texas, and (d) mean Palmer Drought Index in Ohio. An outlier (1997) is circled in each panel. There is no statistically significant relationship between monarch abundance and any of the coarse-scale climate variables presented in panels a–d.

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).

This monitoring program was launched in 1995 by the Ohio Lepidopterist Society (www.ohiolepidopterists.org) and we include data from 1996 (the first year with multiple locations) through 2008 (the last year for which we have acquired and processed data). The annual number of survey locations increased from 13 in 1996 to 56 in 2008. These survey locations are spread throughout the state and, although several cluster around urban areas (Fig. 1b), none are closer than 1 km in distance and several kilometers usually separates the closest sites. Each location was surveyed by a volunteer who visited their assigned location approximately once weekly during the study period, although not all locations were visited every week or during every year. Survey protocols were based on those developed by Pollard (1977) and follow similar protocols to other butterfly monitoring programs in North America and Europe. At each survey point, the observer walked a fixed transect of variable length and recorded all butterflies seen within approximately 5 m. We note that these are general butterfly surveys and not focused on monarchs specifically. As such, no host plant data were collected during the surveys. However, all native milkweeds in the Midwest are perennial and their distribution is not likely to change markedly from year to year so we do not expect milkweed abundances to be a major factor driving annual differences in monarch distributions. Transect lengths vary between sites, but remained fixed at sites from year to year. To account for variable transect lengths and effort, observers recorded the time spent on each survey. A total of 9904 surveys were conducted at 94 unique locations in Ohio over the 13 years.

Climate data

To calculate GDD, we first acquired daily minimum and maximum temperatures throughout Texas (weeks 4–9) and Ohio (weeks 10–28) for 1996–2008 from NOAA's Global Summary of the Day network, a global network of weather stations that provides daily weather metrics (www.ncdc.noaa.gov/oa/gsod.html). For Texas, we used the daily minimum and maximum temperature values over the period of interest at each weather station in the state and averaged values across the entire state to arrive at a single GDD spring value for each year. In Ohio, we needed spatially specific temperature values at each butterfly survey location based on the network of weather stations. To obtain these data, we performed spatial interpolation in R (R Development Core Team, 2011) using an automatic kriging procedure implemented internally in the *automap* package (Hiemstra *et al.*, 2009) and carried out via the *intamap* package (Pebesma *et al.*, 2011). Using these time-series of interpolated minimum and maximum daily temperatures, we calculated GDD values for each survey location in Ohio on each day in each year, and accumulated them over phenologically relevant time periods as described below.

We obtained weekly PDI values from NOAA's Climate Data Center for each of the ten NOAA-defined climate divisions within Ohio (http://www.esrl.noaa.scr/psd/usclimate/map.html). In Texas, but not Ohio, there was a strong correlation between GDD and PDI, averaged across the state's ten climate divisions. We therefore used mean rainfall to account for yearly precipitation patterns, which were only weakly correlated with GDD values in Texas. We used totals from February, March, and April to align with the growing season of both milkweed and monarchs. We obtained state-wide summaries of monthly rainfall totals for the same period from NOAA's Climate at a Glance for each year (http://www.ncdc.noaa.gov/oa/climate/research/cag3/cag3.html).

Unlike the Texas data, which we used to capture large-scale conditions averaged across the state, the GDD data from Ohio were summarized at the temporal and spatial scale of the individual monarch surveys. Although monarchs are certainly able to move long distances, we assumed that once their migratory expansion was complete, populations remain fairly local and therefore respond to local climate conditions. Genetic analysis shows increased local population structure as the summer breeding season continues (Eanes & Koehn, 1978), suggesting that individual movement is more limited during the breeding season and supporting our assumption. For each survey location, we accumulated GDD from week 10 up to the week of each survey. To account for rainfall effects at survey locations in Ohio, we used the PDI calculated for week 28. Although it is possible that weekly changes in the drought index could affect monarch counts, PDI tended to be negatively correlated with week (i.e., the spring tends to be wetter than the summer in Ohio), an artifact that would bias our interpretation of the results. As such, we opted to characterize the annual precipitation conditions at sites for each year. We believe that this adequately captures the necessary variation in PDI because the index, which measures drought conditions and not simply precipitation, is designed to remain fairly stable over the season and does not experience high variation based on a weekly weather patterns (Heim, 2002).

Analysis

We modeled monarch abundance at each survey site within Ohio throughout the summer breeding season based on spring and summer climate metrics. We used Poisson regression to model expected counts $(\lambda j,t,k)$ at each location j that varied annually (by year t) and by week within season (denoted as k). The objective of our model is to characterize local monarch dynamics based on relevant climate variables during the spring and summer. We opted not to include spatial location (e.g., latitude and longitude) as a factor in the model but instead used a proxy for location in the form of mean GDD accumulated by the end of the season (averaged over the 13 year study period). This allowed us to capture the average overall condition of a site (i.e., whether it tended to be relatively warmer or cooler) while still allowing the model to remain general, increasing the potential to transfer it to other locations. (See Appendix S1 for more details on the ability of our model to capture spatial correlation in the monarch data without inclusion of specific spatial covariates.)

Although we incorporated variables from the spring, our model predicts expected counts during the summer breeding season (weeks 10–28). That week range roughly corresponds to the time period from just before the first arrival of most

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:

$$
\begin{aligned}
\log(\lambda_{j,t,k}) = {} & \alpha1 + \alpha2 \cdot week_k + \alpha3 \cdot spPREC_t + \alpha4 \cdot spPREC_t^2 \\
& + \alpha5 \cdot spGDD_t + \alpha6 \cdot spGDD_t^2 + \alpha7 \cdot spPREC_t \cdot week_k \\
& + \alpha8 \cdot spGDD_t \cdot week_k \\
& + \alpha9 \cdot GDDdiff_{j,t,k} \\
& + \alpha10 \cdot avgGDD_j + \alpha11 \cdot avgGDD_j^2 \\
& + \alpha12 \cdot GDDdiff_{j,t,k} \cdot week_k \\
& + \alpha13 \cdot GDDdiff_{j,t,k} \cdot avgGDD_j \cdot week_k \\
& + \alpha14 \cdot PDI_{j,t} \\
& + \alpha15 \cdot PDI_{j,t}^2 + \alpha16 \cdot PDI_{j,t} \cdot week_k + \alpha17 \cdot open_j \\
& + \log(effort_{j,t,k})
\end{aligned}
$$

with $\alpha1$ as the intercept term and $\alpha2$–$\alpha17$ 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 ($\alpha2$, linear term because monarch abundance in Ohio will generally be increasing during this time frame). The parameters $\alpha3$–$\alpha8$ deal with the effects of the spring conditions in Texas on monarch counts, where $\alpha3$ and $\alpha4$ are the linear and squared effects of cumulative precipitation in Texas, $spPREC_t$, and $\alpha5$ and $\alpha6$ are the linear and squared effects of GDD in Texas, $spGDD_t$. We also included parameters $\alpha7$ and $\alpha8$ 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 $\alpha9$–$\alpha13$ 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, $GDDdiff_{j,t,k}$, 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 ($\alpha9$) on $GDDdiff_{j,t,k}$ because a squared term did not come out as significant in earlier versions of the model. The average GDD, $avgGDD_j$, 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 ($\alpha10$) and squared ($\alpha11$) effects for $avgGDD_j$. We hypothesized that the importance of $GDDdiff_{j,t,k}$ 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 $avgGDD_j$ may be important in understanding how

variation in $GDDdiff_{j,t,k}$ 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 $\alpha12$ and $\alpha13$ account for these possible interactions. Parameters $\alpha14$–$\alpha16$ are effects related to site-specific PDI values. The covariate $PDI_{j,t}$ is the annual metric of the drought index at each survey location and we included linear ($\alpha14$) and squared ($\alpha15$) effects as well as an interaction with survey week ($\alpha16$).

We included two location-specific nuisance terms in our model: the covariate $open_j$ is the proportion of area along the jth transect that is unforested. Although we are not specifically interested in how differences in habitat affect monarch abundance, we included $\alpha17$ because milkweed tends to grow in open areas. Similarly, survey durations and transect lengths vary and we included an offset term, $\log(effort_{j,t,k})$, 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 one 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

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)

Parameter	Covariate	Description	Estimate	SD	95% PI
$\alpha 1$	NA	Intercept	-0.578	0.025	$(-0.63, -0.53)$
$\alpha 2$	$week_k$	Week in season	1.376	0.014	$(1.35, 1.40)$
$\alpha 3$	$spPREC_t$	Spring precipitation in Texas (linear)	-0.070	0.015	$(-0.10, -0.04)$
$\alpha 4$	$spPREC_t^2$	Spring precipitation in Texas (squared)	0.364	0.011	$(0.34, 0.39)$
$\alpha 5$	$spGDD_t$	Spring GDD in Texas (linear)	-0.198	0.022	$(-0.24, -0.15)$
$\alpha 6$	$spGDD_t^2$	Spring GDD in Texas (squared)	-0.229	0.014	$(-0.26, -0.20)$
$\alpha 7$	$spPREC_t\,week_k$	Spring precipitation and week interaction	0.100	0.017	$(0.07, 0.13)$
$\alpha 8$	$spGDD_t\,week_k$	Spring GDD and week interaction	0.109	0.013	$(0.08, 0.13)$
$\alpha 9$	$GDDdiff_{j,t,k}$	Weekly GDD differential at transects in Ohio	-0.049	0.020	$(-0.09, -0.01)$
$\alpha 10$	$avgGDD_j$	Average cumulative GDD at transects in Ohio (linear)	-0.091	0.011	$(-0.11, -0.07)$
$\alpha 11$	$avgGDD_j^2$	Average cumulative GDD at transects in Ohio (squared)	0.055	0.011	$(0.03, 0.08)$
$\alpha 12$	$GDDdiff_{j,t,k}\cdot week_k$	GDD differential and week interaction	0.080	0.015	$(0.05, 0.11)$
$\alpha 13$	$GDDdiff_{j,t,k}\cdot avgGDD_j\cdot week_k$	GDD differential, average GDD and week interaction	-0.031	0.006	$(-0.04, -0.02)$
$\alpha 14$	$PDI_{j,t}$	Annual PDI at transects in Ohio (linear)	-0.104	0.016	$(-0.14, -0.07)$
$\alpha 15$	$PDI_{j,t}^2$	Annual PDI at transects in Ohio (squared)	-0.059	0.009	$(-0.08, -0.04)$
$\alpha 16$	$PDI_{j,t}\cdot week_k$	Annual PDI and week interaction	-0.108	0.014	$(-0.14, -0.08)$
$\alpha 17$	$open_j$	Proportion of unforested habitat at transects in Ohio	0.303	0.010	$(0.28, 0.32)$

GDD, growing degree days; PDI, Palmer Drought Index; SD, standard deviation.

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 $avgGDD_j$ values) that had accumulated above average GDD ($GDDdiff_{j,t,k}$) 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,
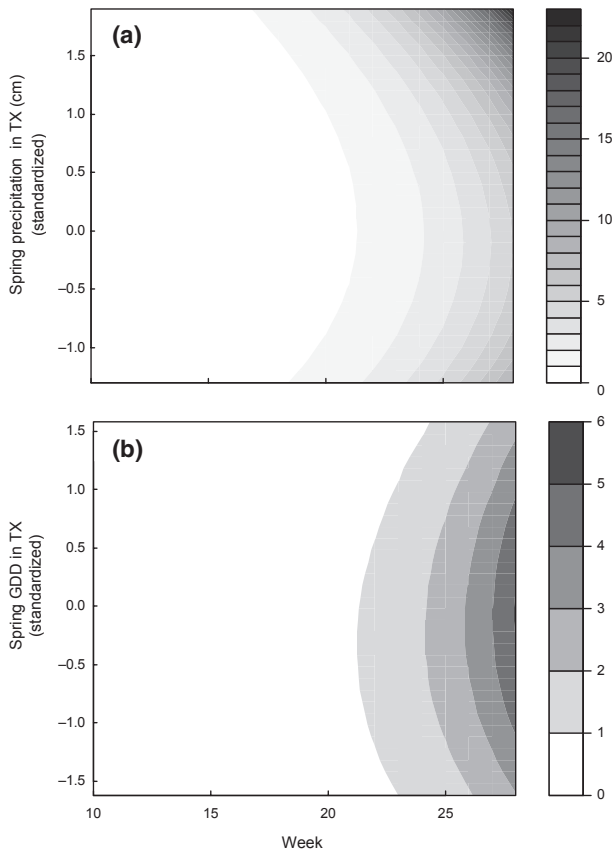
Fig. 3 Expected monarch count by week for the range of observed (a) spring precipitation in Texas and (b) spring growing degree days (GDD) in Texas where all other parameter values were held at their average values. The precipitation and GDD covariates are shown on a standardized scale such that the mean and standard deviation for each are 0 and 1, respectively.
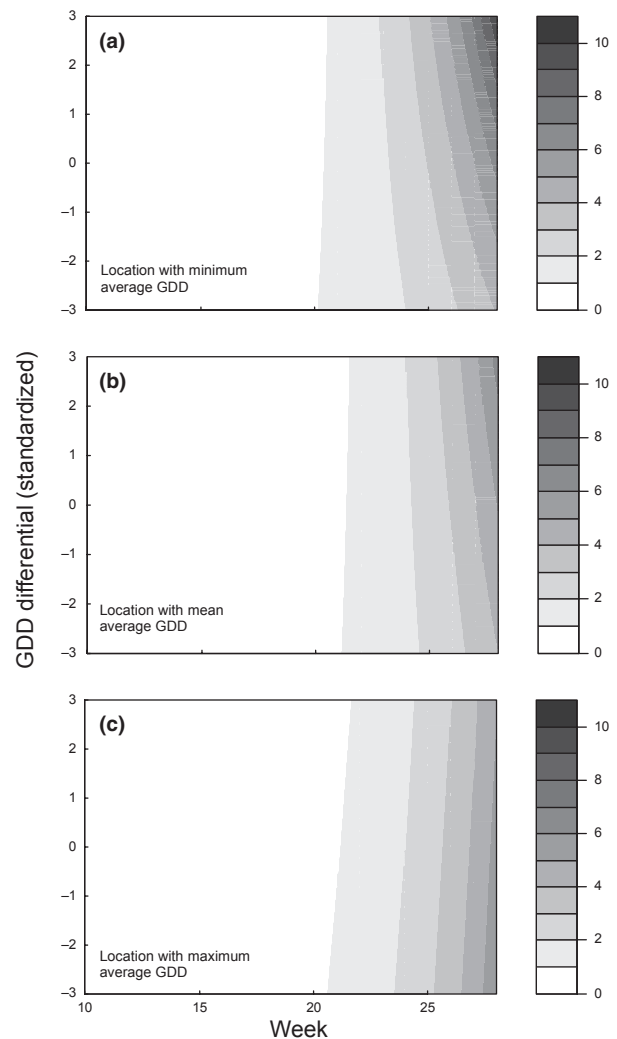

Fig. 4 Expected monarch count by week as plotted against the growing degree days (GDD) differential (standardized to have a mean of 0 and a standard deviation of 1) for (a) the coolest survey location in Ohio (minimum avgGDD); (b) a location with average temperatures (mean avgGDD); and (c) the warmest survey location (maximum avgGDD).

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 from1997. 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 (Prysby, 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.

Acknowledgements

References

Adamik P, Pietruszkova J (2008) Advances in spring but variable autumnal trends in timing of inland wader migration. *Acta Ornithologica*, **43**, 119–128.

Altizer SM, Oberhauser KS, Brower LP (2000) Associations between host migration and the prevalence of a protozoan parasite in natural populations of monarch butterflies. *Ecological Entomology*, **25**, 125–139.

Bartel R, Oberhauser K, DeRoode J, Altizer S (2011) Monarch migration and parasite transmission in eastern North America. *Ecology*, **92**, 342–351.

Batalden RV, Oberhauser K, Peterson AT (2007) Ecological niches in sequential generations of eastern North American monarch butterflies (Lepidoptera: Danaidae): the ecology of migration and likely climate change implications. *Population Ecology*, **36**, 1365–1373.

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.

Bowlin MS, Bisson IA, Shamoun-Baranes J et al. (2010) Grand challenges in migration biology. *Integrative and Comparative Biology*, **50**, 261–279.

Brattstrom O, Kjellen N, Alerstam T, Akesson S (2008) Effects of wind and weather on red admiral, *Vanessa atalanta*, migration at a coastal site in southern Sweden. *Animal Behaviour*, **76**, 335–344.

Brower LP (1986) New perspectives on the migration biology of the monarch butterfly, *Danaus plexippus* L. Migration: mechanisms and adaptive significance. In: *Migration: mechanisms and adaptive significance* (ed. Rankin MA), pp. 748–785. Marine Science Institute, The University of Texas at Austin, Port Aransas, TX.

Brower LP, Malcolm SB (1991) Animal migrations: endangered phenomena. *American Zoologist*, **31**, 265–276.

Brower LP, Kust DR, Rendon-Salinas E et al. (2004) Catastrophic winter storm mortality of monarch butterflies in Mexico during January 2002. In: *The Monarch Butterfly: Biology and Conservation* (eds. Oberhauser KS, Solensky MJ), pp. 151–166. Cornell University Press, Ithaca.

Brower LP, Taylor OR, Williams EH, Slayback DA, Zubieta RR, Ramirez MI (2012) Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity*, **5**, 95–100.

Chapman JW, Drake VA, Reynolds DR (2011) Recent insights from radar studies of insect flight. *Annual Review of Entomology*, **56**, 337–356.

Crozier L, Dwyer G (2006) Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *American Naturalist*, **167**, 853–866.

Dingle H (1996) *Migration: the biology of life on the move.* Oxford University Press, New York.

Dingle H, Rochester WA, Zalucki MP (2000) Relationships among climate, latitude and migration: Australian butterflies are not temperate-zone birds. *Oecologia*, **124**, 196–207.

Dingle H, Zalucki MP, Rochester WA, Armijo-Prewitt T (2005) Distribution of the monarch butterfly, *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae), in western North America. *Biological Journal of the Linnean Society*, **85**, 491–500.

Doi H, Gordo O, Katano I (2008) Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. *Climate Research*, **36**, 181–190.

Eanes WF, Koehn RK (1978) An analysis of genetic structure in the Monarch butterfly, *Danaus plexippus* L. *Evolution*, **32**, 784–797.

Forister ML, Shapiro AM (2003) Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology*, **9**, 1130–1135.

Forister ML, McCall AC, Sanders NJ et al. (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences*, **107**, 2088–2092.

Gelman A, Hill J (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York.

Girvetz EH, Zganjar C, Raber GT, Maurer EP, Kareiva P, Lawler JJ (2009) Applied Climate-Change Analysis: The Climate Wizard Tool. *PLoS One* **4**, e8320. doi: 10.1371/journal.pone.0008320.

Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, **35**, 37–58.

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, **80**, 4–18.

Heim RR Jr (2002) A review of twentieth-century drought indices used in the United States. *Bulletin of the American Meteorological Society*, **83**, 1149–1165.

Hiemstra PH, Pebesma EJ, Twenhofel CJW, Heuvelink GBM (2009) Real-time automatic interpolation of ambient gamma dose rates from the Dutch Radioactivity Monitoring Network. *Computers & Geosciences*, **35**, 1711–1721.

Hodgson JA, Thomas CD, Oliver TH, Anderson BJ, Brereton TM, Crone EE (2011) Predicting insect phenology across space and time. *Global Change Biology*, **17**, 1289–1300.

Howard E, Davis AK (2004) Documenting the spring movements of monarch butterflies with Journey North, a citizen science program. In: *The Monarch Butterfly: Biology and Conservation* (eds. Oberhauser KS, Solensky MJ), pp. 105–114. Cornell University Press, Ithaca.

Hu Q, Wilson GD (2000) Effects of temperature anomalies on the Palmer Drought Severity Index in the central United States. *International Journal of Climatology*, **20**, 1899–1911.

Kokko H (1999) Competition for early arrival in migratory birds. *Journal of Animal Ecology*, **68**, 940–950.

Konvicka M, Maradova M, Benes J, Fric Z, Kepka P (2003) Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecology and Biogeography*, **12**, 403–410.

Lindsay E, Mehta M, Dhulipala V, Oberhauser K, Altizer S (2009) Crowding and disease: effects of host density on response to infection in a butterfly-parasite interaction. *Ecological Entomology*, **34**, 551–561.

Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS–A Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325–337.

Maelzer DA, Zalucki MP (2000) Long range forecasts of the *Helicoverpa punctigera* and *H. armigera* (Noctuidae: Lepidoptera) in Australia using the SOI and the SST. *Bulletin of Entomological Research*, **90**, 133–146.

Malcolm SB, Cockrell BJ, Brower LP (1987) Monarch butterfly voltinism: effects of temperature constraints at different latitudes. *Oikos*, **49**, 77–82.

McMaster GS, Wilhelm WW (1997) Growing degree-days: one equation, two interpretations. *Agricultural and Forest Meteorology*, **87**, 291–300.

Mueller T, Fagan WF (2008) Search and navigation in dynamic environments–from individual behaviors to population distributions. *Oikos*, **117**, 654–664.

Norris DR, Marra PP (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor*, **109**, 535–547.

Oberhauser K, Peterson AT (2003) Modeling current and future potential wintering distributions of eastern North American monarch butterflies. *Proceedings of the National Academy of Sciences*, **100**, 14063–14068.

Palm V, Leito A, Truu J, Tomingas O (2009) The spring timing of arrival of migratory birds: dependence on climate variables and migration route. *Ornis Fennica*, **86**, 97–108.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*, **37**, 637–669.

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, **13**, 1860–1872.

Parmesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Pebesma E, Cornford D, Dubois G *et al.* (2011) INTAMAP: the design and implementation of an interoperable automated interpolation web service. *Computers and Geosciences*, **37**, 343–362.

Pleasants JM, Oberhauser KS (in press) Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. *Insect Conservation and Diversity*, doi: 10.1111/j.1752-4598.2012.00196.x.

Pollard E (1977) A method for assessing changes in the abundance of butterflies. *Biological Conservation*, **12**, 115–134.

Prysby MD (2004) Natural enemies and survival of monarch eggs and larvae. In: *The Monarch Butterfly: Biology and Conservation* (eds. Oberhauser KS, Solensky MJ), pp. 27–37. Cornell University Press, Ithaca.

Prysby M, Oberhauser KS (2004) Temporal and geographic variation in monarch densities: Citizen scientists document monarch population patterns. In: *The Monarch Butterfly: Biology and Conservation* (eds. Oberhauser KS, Solensky MJ), pp. 9–20. Cornell University Press, Ithaca.

R Development Core Team (2011) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at: http://www.R-project.org/ (accessed 15 September 2011).

Rendon-Salinas E, Valera-Bermejo CA, Cruz-Pina M, Martinez-Meza F (2011) *Monitoreo De Las Colonias De Hibernacion De Mariposa Monarca: Superficie Forestal De Ocupacion En Diciembre De 2010*. World Wildlife Fund, Mexico, Mexico City.

Rubolini D, Saino N, Moller AP (2010) Migratory behaviour constrains the phenological response of birds to climate change. *Climate Research*, **42**, 45–55.

Saino N, Ambrosini R, Rubolini D *et al.* (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 835–842.

Singer MC, Parmesan C (2010) Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**, 3161–3176.

Srygley RB, Dudley R, Oliveira EG, Aizprua R, Pelaez NZ, Riveros AJ (2010) El Nino and dry season rainfall influence hostplant phenology and an annual butterfly migration from Neotropical wet to dry forests. *Global Change Biology*, **16**, 936–945.

Stevens SR, Frey DF (2010) Host plant pattern and variation in climate predict the location of natal grounds for migratory monarch butterflies in western North America. *Journal of Insect Conservation*, **14**, 731–744.

Swengel AB (1995) Population fluctuations of the monarch (*Danaus plexippus*) in the 4th of July butterfly count 1977–1994. *American Midland Naturalist*, **134**, 205–214.

Vandenbosch R (2003) Fluctuations of *Vanessa cardui* butterfly abundance with El Nino and Pacific Decadal Oscillation climatic variables. *Global Change Biology*, **9**, 785–790.

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2561–2569.

Warren MS, Hill JK, Thomas JA *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Wassenaar LI, Hobson KA (1998) Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences*, **95**, 15436–15439.

Wilcove DS, Wikelski M (2008) Going, going, gone: is animal migration disappearing? *PLoS Biology*, **6**, 1361–1364.

York HA, Oberhauser KS (2002) Effects of duration and timing of heat stress on monarch butterfly (Danaus plexippus) (Lepidoptera: Nymphalidae) development. *Journal of the Kansas Entomological Society*, **75**, 290–298.

Zalucki MP (1982) Temperature and rate of development in *Danaus plexippus* L. and *D. chrysippus* L. *Autralian Entomological Society*, **21**, 241–246.

Zalucki MP, Clarke A (2004) Monarchs across the Pacific: the Columbus hypothesis revisited. *Biological Journal of the Linnean Society*, **82**, 111–121.

Zalucki MP, Rochester WA (2004) Spatial and temporal populations dynamics of monarchs down-under: lessons for North America. In: *The Monarch Butterfly: Biology and Conservation* (eds. Oberhauser KS, Solensky MJ), pp. 219–228. Cornell University Press, Ithaca, NY.

Zipkin EF, Gardner B, Gilbert AT, O'Connell A, Royle JA, Silverman ED (2010) Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics. *Oecologia*, **163**, 893–902.

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.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.