Do growing degree days predict phenology across butterfly species?

HEATHER L. CAYTON,[1,6] NICK M. HADDAD,[1] KEVIN GROSS,[2] SARAH E. DIAMOND,[3] AND LESLIE RIES[4,5]

[1]*Department of Biological Sciences, North Carolina State University, Raleigh, North Carolina 27695 USA*
[2]*Biomathematics Program, North Carolina State University, Raleigh, North Carolina 27695 USA*
[3]*Department of Biology, Case Western Reserve University, Cleveland, Ohio 44106 USA*
[4]*National Socio-Environmental Synthesis Center, Annapolis, Maryland 21401 USA*
[5]*Biology Department, University of Maryland, College Park, Maryland 20742 USA*

Abstract. Global climate change is causing shifts in phenology across multiple species. We use a geographically and temporally extensive data set of butterfly abundance across the state of Ohio to ask whether phenological change can be predicted from climatological data. Our focus is on growing degree days (GDD), a commonly used measure of thermal accumulation, as the mechanistic link between climate change and species phenology. We used simple calculations of median absolute error associated with GDD and an alternative predictor of phenology, ordinal date, for both first emergence and peak abundance of 13 butterfly species. We show that GDD acts as a better predictor than date for first emergence in nearly all species, and for peak abundance in more than half of all species, especially univoltine species. Species with less ecological flexibility, in particular those with greater dietary specialization, had greater predictability with GDD. The new method we develop for predicting phenology using GDD offers a simple yet effective way to predict species' responses to climate change.

Key words: climate change; first emergence; growing degree days; Lepidoptera; Ohio, USA; ordinal date; peak abundance; phenology; temperature.

INTRODUCTION

Global climate change is causing shifts in phenology, or the timing of life cycle events, across plants and animals (Root et al. 2003, Parmesan 2006). There are many examples of advanced timing, such as egg-laying in birds (Møller et al. 2010) and emergence in butterflies (Forister and Shapiro 2003). Given that these phenological shifts are occurring, an important step is to determine how predictable these shifts are. As yet, there is no simple and reliable approach to predict phenological shifts across multiple species (Visser and Both 2005) and biogeographic regions. In this paper, we use a long-term, geographically extensive data set of butterfly abundance across the U.S. state of Ohio to ask whether phenological change can be predicted across species using models of thermal accumulation.

One of the many species' traits (Altermatt 2010, Diamond et al. 2011) and climate variables (Laws and Belovsky 2010) that have been used to link climate change to phenological shifts is thermal tolerance for development, which can be measured with growing degree days (GDD). GDD is a time-based integral of heat accumulation, measured annually by accumulating the daily total of degrees (°C) that occur between minimum and maximum temperature thresholds (D_{min} and D_{max}). GDD has a long history of use in predicting plant and insect phenology in agriculture (Parry and

Carter 1985, Bonhomme 2000), and temperature has been shown to be a major driver of phenology (Miller-Rushing et al. 2010, Diamond et al. 2014). Only more recently have ecologists adopted GDD as a link between changes in climate and phenology (Nufio et al. 2010, Hodgson et al. 2011).

GDD should be a strong, integrative measure of climate change because it can account for both spatial and temporal variation in temperature, and it explicitly constrains the thermal limits within which growth is possible. Models that forecast the impacts of future climate change can incorporate GDD as a localized, specific variable directly related to organismal development. As global temperatures rise, GDD will accumulate faster and with more interannual variation than ordinal date. However, these two measurements will always remain correlated to some extent, and other abiotic factors that may influence phenology, such as precipitation, might be better predicted by date than by GDD. Therefore, a test is needed to determine when and for which species GDD can more accurately predict species' responses in place of date, or whether date alone can act as a good predictor of phenology.

In this study, we are able to distinguish the abilities of GDD and date to predict phenology in an unusually large data set on butterfly species abundance across 120 sites in Ohio for 17 years, where we observe high levels of both interannual and latitudinal variation in GDD (Fig. 1). This analysis joins a growing body of work using butterfly monitoring programs that uniquely benefits from having a long time series of data (Roy
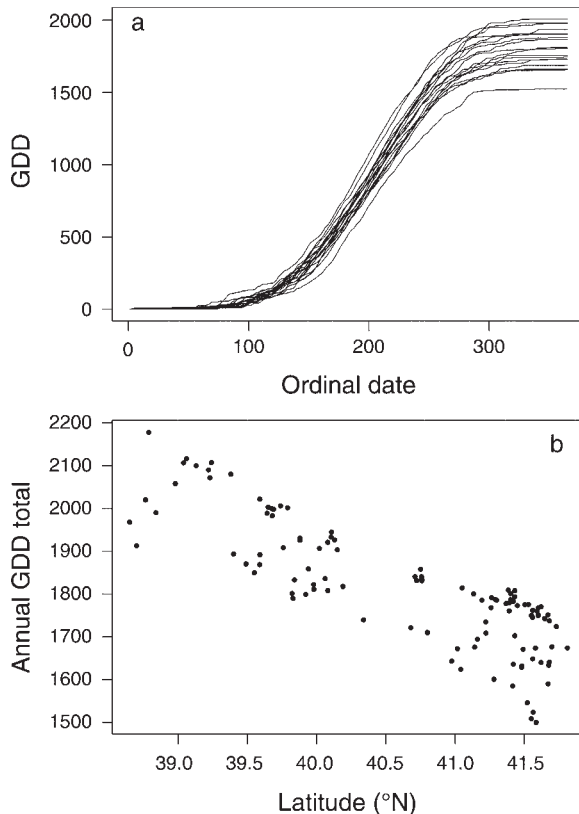
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FIG. 1. Total accumulated growing degree days (GDD) for (a) each of 17 years averaged across all sites and (b) each of 120 sites averaged across all years, ordered by latitude from south to north.

and Sparks 2000, Forister and Shapiro 2003, Stefanescu et al. 2003). With these data, we asked whether GDD or date better predicted phenology in terms of first emergence and peak abundance for 13 common butterfly species across the state. We define predictability as the ability to predict date of emergence or date of peak abundance with the least amount of error from year to year as measured in days. We then quantitatively measure the forecasting accuracy of GDD compared to date. With this method, we have highlighted a simple yet powerful approach that can be used to predict how species may respond to future climate change.

METHODS

Butterfly data collection

We obtained survey data on butterfly abundances across the state of Ohio that were collected between 1996 and 2012 by the Ohio Lepidopterists. Surveys typically run from early April until late October and are conducted by volunteers at approximately one-week intervals. Survey protocols are based on those developed by Pollard (Pollard 1977) and are similar to other butterfly monitoring programs in North America and Europe. At each survey point, one observer walks a fixed transect and records all butterfly species seen and their abundances within approximately 5 m of the transect. Survey lengths vary between sites, although they are always consistent within a site each year.

To conduct our analysis, we chose 13 species that were among the most common resident species within Ohio, and whose emergence occurred late enough to be captured within the time frame of most surveys: pearl crescent (*Phyciodes tharos*), great spangled fritillary (*Speyeria cybele*), silver-spotted skipper (*Epargyreus clarus*), little wood satyr (*Megisto cymela*), common wood nymph (*Cercyonis pegala*), orange sulphur (*Colias eurytheme*), eastern-tailed blue (*Cupido comyntas*), least skipper (*Ancyloxypha numitor*), European skipper (*Thymelicus lineola*), spicebush swallowtail (*Papilio troilus*), Peck's skipper (*Polites peckius*), viceroy (*Limenitis archippus*), and hackberry emperor (*Asterocampa celtis*). We classified these species according to four species traits: larval host-plant category (legume, grass, forb, or woody), larval host-plant diversity (the number of different plant species used), over-wintering stage (egg, larvae, or pupae) and voltinism (univoltine, bivoltine, or multivoltine) (Scott 1986, Daniels 2004). We focus on these four traits in particular, as they have been suggested as central traits that may influence the ability of butterflies to respond to climate change (Dennis 1993, Diamond et al. 2011, 2014).

We used the portion of the data set that met the following criteria, and for which we had sufficient repeated observations to estimate emergence and peak abundance. For each combination of site, species, and year, we used emergence data in the analysis if (1) at least five individuals were seen at the site; (2) there was at least one survey record of absence before the emergence date; (3) the species was seen on more than one survey date; and (4) there was at least one survey date within 14 days prior to the emergence date. We used date of first observation as a proxy for emergence date. Because there were so few occurrences prior to 1 April, we did not use emergence dates that occurred before then. For multivoltine species, we analyzed emergence date of the first flight period only. With an average interval of 8 days between surveys, we did not expect to detect exact emergence date, but rather obtain a reasonable estimate of emergence given the challenges of collecting large-scale data with volunteers.

We also analyzed date of peak abundance as a complement to emergence date. Peak abundance is generally less sensitive to variation in sampling size and imperfect detectability (Moussus et al. 2010). To calculate peak abundance, we fit curves of butterfly abundance over time using nonlinear least squares (based on a standard three-parameter Gaussian function, $y = a \times \exp(-1/2 \times ((x - b)/c)^2)$ for each species at each site within each year. Ordinal dates of peak abundance were estimated as the dates of the maximal abundance values from the nonlinear regression models (parameter b above [a represents the amplitude of the

curve, and c represents the width of the curve]). For multivoltine species, we estimated peak abundance of the first flight period only. There were not enough data for *L. archippus* to calculate peak abundance of the first flight period, so we used peak abundance of the second flight period. Descriptive statistics of butterfly phenology (peak abundance estimated as the mean and median ordinal date, both unweighted and weighted by abundance, not presented) yielded qualitatively similar results as estimates of phenology from the nonlinear regression models. Here, we focus on the nonlinear regression estimates to limit potential sensitivity to extreme values.

There has been some criticism of focusing on emergence timing as opposed to date of peak abundance in that it can generate bias relating to changes in sampling effort or population abundance over time (Von Strien et al. 2008, Ellwood et al. 2012). We have minimized potential bias in missing early emergence dates or emergence in small populations by eliminating the earliest emerging species, and by creating a threshold of species appearance at each site below which we avoid using data. In addition, our focus is on the relative predictive ability of GDD vs. date rather than estimating their individual effects. Because both GDD and date are derived from the same data set, these indices will be subject to the same estimation biases, such that assessment of their relative predictive ability will not be influenced.

Climate data

To calculate GDD, we used the Daymet daily surface weather and climatological summaries produced by Oak Ridge National Laboratory (data *available online*).[7] We extracted the temperature values from the Daymet grid pixel measuring 1×1 km that contained each of the site points, for each day and year of the study duration. These temperatures were used to perform the daily GDD time series calculation, which used the single-sine growing degree day method with a fixed spacing of 12 hours between daily minimum and maximum temperatures (Baskerville and Emin 1969, Roltsch et al. 1999). We started accumulating GDD on 1 January each year, so that each emergence date and peak date was associated with a site- and year-specific GDD value.

We used a minimum threshold of 10°C and a maximum of 30°C to calculate GDD. These thresholds were first developed in agriculture and correspond to generally accepted thermal thresholds for several economically important crops (Dethier and Vittum 1967) and other insects (Nufio et al. 2010). To our knowledge, there are only two butterfly species in North America for which thermal tolerance limits for development have been specifically calculated. Monarchs (*Danaus plexippus*) are known to have a minimum threshold (D_{min}) of 11.5°C and a maximum threshold (D_{max}) of 33°C

(Zalucki 1982), although, as a migrant species of tropical origin, this is likely a warmer range than might be seen for resident species in temperate Ohio, especially for the lower thermal limit (Sunday et al. 2011). A warm-adapted species, the sachem skipper (*Atalopedes campestris*), is known to have a D_{min} of 15.5°C but no measured D_{max}, and is an uncommon stray to Ohio (Crozier and Dwyer 2006). In the absence of known species-specific thresholds, and given that butterfly development is generally tied to seasonal variation in host-plant growth, we feel it is reasonable to use general agricultural thresholds, especially given that these roughly correspond to the only other known thresholds.

Analysis

We identified the date of emergence and peak abundance for all species at each site-year combination and calculated the GDD for these dates. For each species, at each site with at least three years of observed values, we excluded each year in turn and calculated the median date and median GDD of emergence and peak abundance from the remaining values. As a result, each observed value had a unique median value associated with it. We then recorded the absolute difference between each observed value and median value, which we considered to be the amount of error associated with that variable. Median values for GDD were converted back to a date specific to each site and year, so that we were able to calculate the difference between median value and observed value of GDD on the same scale as ordinal date. Finally, for each site–year combination, we tallied whether date or GDD did better (i.e., had less error). To determine whether the number of site-year combinations with less error associated with GDD compared to date was significantly different for each species, we performed a chi-squared test (df = 1).

We also conducted a time series analysis to determine the forecasting ability of GDD and ordinal date on emergence and peak abundance. We excluded the final year of observation from each site for each species and used an autoregressive integrated moving average (ARIMA) model to predict the GDD or date of emergence and peak abundance. By generating a prediction of emergence and peak abundance for the last year for which we have data and comparing the amount of error associated with it for both GDD and date, we specifically address the temporal variation in the data and outline a practical method for predicting phenology (see Appendix A for details).

We also performed model selection analysis to examine the influence of butterfly species' traits (larval host-plant class, larval host-plant diversity, overwintering stage, and voltinism) on the predictability of emergence and peak abundance based on GDD. Higher values of predictability indicate GDD was a better predictor of emergence or peak abundance compared with ordinal date. We used AIC_c (AIC corrected for small sample size) to identify a subset of best-fitting

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TABLE 1. Number of site-year observations for 13 butterfly species for which growing degree days (GDD) or date had less error, or for which they were equal, when compared to a median value based on all other years at the site.

	First emergence				Peak abundance			
	No. sites with less error		No. sites with equal error	P	No. sites with less error		No. sites with equal error	P
Species	Date	GDD			Date	GDD		
Megisto cymela	148	256	21	**<0.001**	114	144	14	0.062
Colias eurytheme	189	245	16	**0.007**	161	122	7	**0.02**
Epargyreus clarus	197	230	19	0.11	181	161	6	0.279
Phycoides tharos	154	212	24	**0.002**	101	77	16	0.072
Speyeria cybele	148	205	19	**0.002**	111	145	10	**0.034**
Cupido comyntas	184	203	18	0.334	208	95	14	**<0.001**
Cercyonis pegala	134	168	13	**0.05**	98	113	10	0.302
Ancyloxpha numitor	114	142	16	0.08	39	37	5	0.818
Polites peckius	107	120	18	0.388	29	35	2	0.453
Papilio troilus	72	108	11	**0.007**	34	54	2	**0.033**
Thymelicus lineola	73	102	14	**0.028**	26	58	8	**<0.001**
Asterocampa celtis	52	69	7	0.122	14	26	4	0.058
Limenitis archippus	57	57	2	1	23	7	2	**0.003**

Note: The total number of site-year observations is not equal for emergence and peak abundance within a species because it was not always possible at every site in every year to calculate both emergence and peak.

models for each of the two responses (see Appendix B for details).

All analyses were performed using program R (R Development Core Team 2015).

RESULTS

The data set included 16 444 surveys conducted over 17 years among 120 sites. From this data set, we included 3918 dates of first emergence, with an average of 301 dates used per species (average 18 per year per species). We included 2319 peak abundance dates, with an average of 178 dates used per species (average 10 per year per species).

Total accumulated annual GDD averaged among all sites ranged from 1271 (SD = 127) to 1729 (SD = 150; Fig. 1a). Total accumulated GDD averaged among all years at each site ranged from 1247 (SD = 120) to 1899 (SD = 147; Fig. 1b).

GDD outperformed date and more accurately predicted emergence in 13 of 14 species (Table 1, Fig. 2a). The difference between the numbers of site-year observations where GDD performed better compared to date was significant for *M. cymela*, *C. eurytheme*, *P. tharos*, *S. cybele*, *C. pegala*, *P. troilus*, and *T. lineola* ($P \leq 0.05$) and marginally significant for *A. numitor* ($0.05 < P \leq 0.10$). GDD performed equally well as date for the one species, *L. archippus*.

GDD outperformed date in predicting peak abundance in 7 of 13 species (Table 1, Fig. 2b). GDD was significantly better than date for *S. cybele*, *T. lineola*, and *P. troilus*, while date was significantly better than GDD for *L. archippus*, *C. eurytheme*, and *C. comyntas*. In addition, GDD was marginally significantly better for *M. cymela* and *A. celtis*, while date was marginally significantly better for *P. tharos*.

Site-year combinations where GDD and date had equal error were present for almost all species, but

constituted a small proportion of all site–year combinations tested (Table 1). The highest rate of combinations where GDD and date had equal amount of error was seen with *T. lineola* for emergence (14 out of 189, 7%) and with *A. celtis* for peak abundance (4 out of 44, 9%).

In the time series analysis, we used 3405 emergence dates to predict future emergence across 81 sites, and we used 1941 peak dates to predict future peak abundance across 76 sites. GDD did better than date at predicting emergence for all but three species, and GDD did better than date at predicting peak abundance for six species. Predictability of peak abundance varied with voltinism (see Appendix A for details).

We found larval host-plant diversity to be the strongest predictor for predictability of emergence and peak abundance from GDD. Voltinism was the next strongest factor for predictability of emergence, and overwintering stage was the next strongest factor for predictability of peak abundance (see Appendix B for details).

DISCUSSION

We show that growing degree days (GDD), a variable that provides a mechanistic link between thermal accumulation and organismal performance, improved predictions of phenological responses to interannual variation in temperature for several species. For common butterfly species found across the state of Ohio, GDD was as good as or better a predictor of first emergence than date for all species, and also a better predictor of peak abundance for over half of the species we examined. Specifically, we found that GDD exhibits lower error based on predicted values compared with ordinal date, which lacks an explicit mechanistic basis. In our development of a new approach to test GDD against other reasonable predictors, we provide results that support the use of GDD in predicting ecological
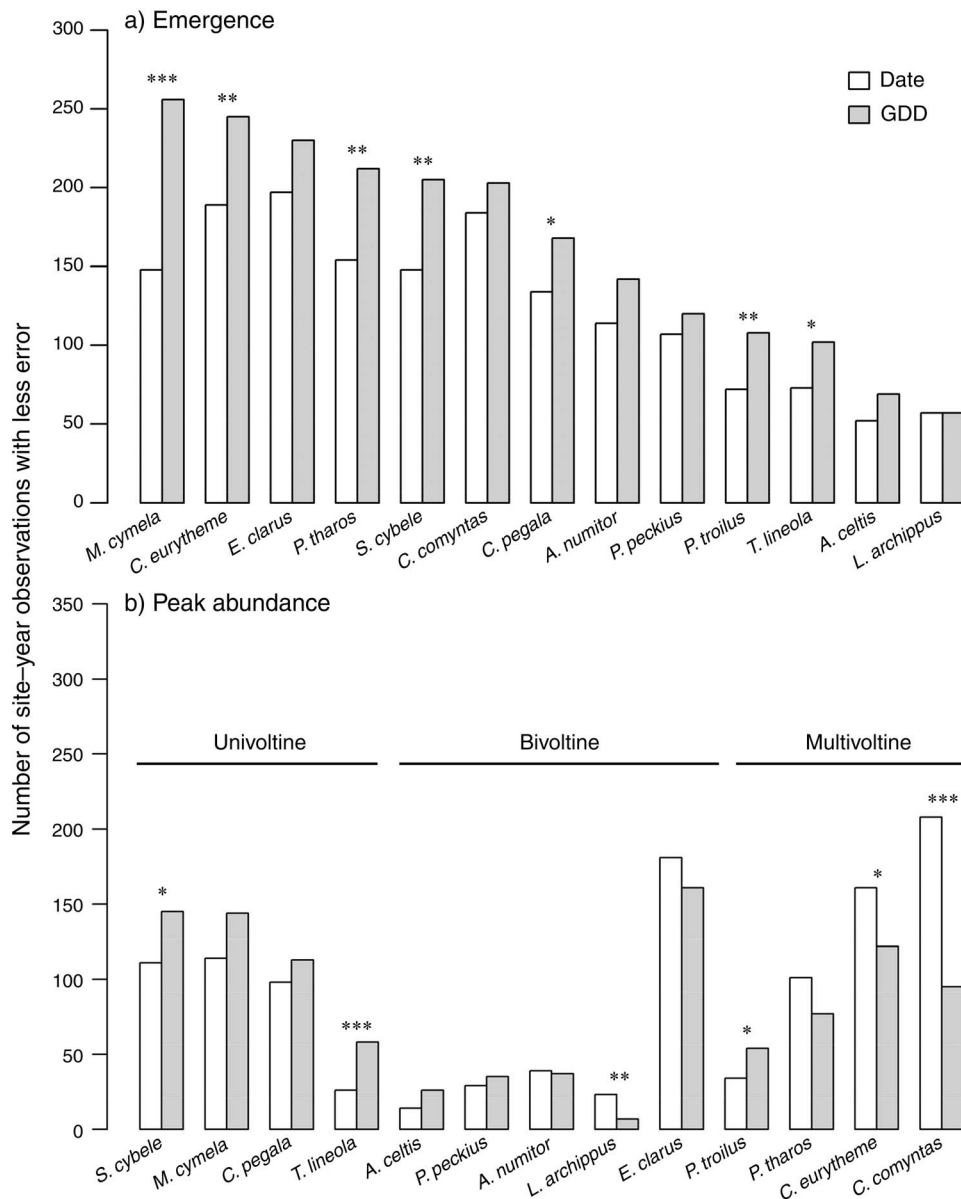
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Fig. 2. Number of site-year observations with less error associated with either GDD or date for (a) emergence and (b) peak abundance. Error was calculated based on the median of the difference between the observed value in a year and the median value for all other years at a site. Species are *Megisto cymela*, *Colias eurytheme*, *Epargyreus clarus*, *Phycoides tharos*, *Speyeria cybele*, *Cupido comyntas*, *Cercyonis pegala*, *Ancyloxpha numitor*, *Polites peckius*, *Papilio troilus*, *Thymelicus lineola*, *Asterocampa celtis*, and *Limenitis archippus*.
    * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

responses to climate change of butterflies, and perhaps additional ectothermic taxa.

In predicting first emergence, GDD showed less or equal error at more sites than date for all 13 species. This strong trend was mirrored in our time series analysis, with emergence better predicted using GDD compared to date for 10 species. That this pattern of GDD outperforming date held across such a varied group of species indicates its great potential to be applicable to many species outside the scope of this analysis.

Our results for predictions of peak abundance were more mixed, but with GDD still outperforming date for at least half of all species in both analyses. We detected a clear trend of GDD outperforming date for univoltine species, while date outperformed GDD for multivoltine species. However, the fact that several species with significant differences favored date, and that two species (*C. eurytheme* and *C. comyntas*) showed inconsistent patterns of predictability between emergence date and peak abundance, underlies the complexity of using

GDD to predict multiple phenological stages. It is possible that peak abundance is more difficult to predict because it is influenced by additional ecological factors such as predation or disease incidence that can vary from year to year, in ways that first emergence does not. As such, GDD remains a promising predictor for peak abundance for some species, especially univoltine species where date of peak abundance is likely easier to isolate.

We found larval host-plant diversity to be a strong predictor of the predictability of both emergence and peak abundance based on GDD, such that species with greater dietary specialization had greater predictability with GDD. Butterfly species with more restricted diets are more closely tied to their host plants, and therefore it may be unsurprising that dietary specialists are more sensitive to the impacts of temperature on this trophic interaction compared with butterfly species with more flexible diets. Further, we found that species with fewer annual generations had greater emergence predictability with GDD, and species with less mobile overwintering stages (egg and pupa vs. larva) had greater emergence peak abundance predictability with GDD. Again, a general pattern emerged such that species with less ecological flexibility exhibited greater predictability with GDD.

One inherent source of variation in the data set is that surveys were not conducted on a daily basis, so that we could not determine the exact emergence date. Daily surveys allow for more precise determination of phenology, and can lead to a tighter relationship between GDD and emergence (Kuefler et al. 2008). In addition, with a data set compiled by so many different observers, there are likely differences in detection among observers (MacKenzie et al. 2002). However, any systematic errors in detection, such as late detection of first emergence due to insufficiently frequent surveying, would be similar for both date and GDD. Despite the observer and survey error inherent in our large and citizen-run data set, we still detected a signal showing that GDD predicts phenological change in response to temperature variation in a number of species, and would anticipate an even higher signal with more precise measures of phenology.

Spatial variation in emergence dates within species implies that there is no value of GDD or date intrinsic to a species, indicating that other abiotic and biotic factors (e.g., microclimate, individual physiology) do play a role in species phenology. This variation can have several different outcomes in terms of species' responses to climate change. For example, more thermally sensitive species are more likely to exhibit phenological shifts under changing climates (Edwards and Richardson 2004). This could potentially be beneficial if a shift toward earlier emergence leads to more generations per year or priority of access to limited resources, but alternatively could be disastrous if that shift causes a mismatch with their host plant's phenology. Our results indicate that future climate change and associated increases in the rate of thermal accumulation are likely to advance emergence dates, potentially most dramati-

cally in dietary specialist species, and could alter flight period lengths if environmental temperatures exceed species tolerance limits for development. The incorporation of abiotic weather variables in future analyses may further explain the observed variation and highlight more fine-scale trends in the data.

More work is needed on the link between phenological changes in butterflies and their host plants to understand whether phenological changes occur concurrently, or whether a mismatch arises between the emergence of butterflies and the productivity of their hosts (Miller-Rushing et al. 2010, Singer and Parmesan 2010). As such data continue to accumulate, through continued efforts in Ohio as well as other programs that exist in other states, synthesis across studies will be able to pinpoint how GDD can be used to predict emergence and peak abundance, and also the consistency of predictability among sites and years. In addition, there is considerable interspecific variation in upper, and particularly lower, lethal and critical thermal limits (Sunday et al. 2011). In knowing that two butterfly species (D. plexippus and A. campestris) have disparate lower thermal limits and (in the case of A. campestris) unknown upper thermal limits, it is likely that interspecific variation in butterfly thermal limits is the norm. Given this variability, model predictions of phenology based on GDD will be even further improved when incorporating species-specific thermal limits, potentially across multiple life stages (Briscoe et al. 2012) or with additional measures of thermal accumulation (ex. heating degree days). In accumulating larger data sets and combining these with species-specific thermal limits, we would be able to tailor GDD models to specific species, or suites of species with common traits.

In sum, we show that GDD is a good predictor of butterfly phenology, in particular emergence, supporting its use in ecological studies. Further, we present a novel method for predicting butterfly phenology that can be applied across multiple species, providing a framework for future, community-wide investigations using GDD to predict responses to climate change. The benefits of being able to anticipate phenological shifts are great, as the consequences of such shifts can potentially include temporal and/or spatial mismatches between dependent species (Hegland et al. 2009). The commonplace nature of the temperature data used to develop GDD models of phenology makes it a promising tool for future use. For those species that do respond to GDD, we can now predict, rather than simply describe, ecological responses as global temperatures rise.

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Supplemental Material

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/15-0131.1.sm