**Effects of *in situ* climate warming on monarch caterpillar (*Danaus plexippus*) development**

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**Abstract**

Climate warming will fundamentally alter basic life history strategies of many ectothermic insects. In the lab, rising temperatures increase growth rates of lepidopteran larvae, but also reduce final pupal mass and increase mortality. Using *in situ* field warming experiments on their natural host plants, we assessed the impact of climate warming on development of monarch (*Danaus plexippus*) larvae. Monarchs were reared on *Asclepias tuberosa* grown under 'Ambient' and 'Warmed' conditions. We quantified time to pupation, final pupal mass, and survivorship. Warming significantly decreased time to pupation, such that an increase of 1˚ C corresponded to a 0.5 day decrease in pupation time. In contrast, survivorship and pupal mass were not affected by warming. Our results indicate that climate warming will speed the developmental rate of monarchs, influencing their ecological and evolutionary dynamics. However, the effects of climate warming on larval development in other monarch populations and at different times of year should be investigated.

**Keywords:** temperature, pupal mass, survivorship, climate change, growth

## Introduction

Modified temperature regimes caused by climate change may fundamentally alter insect life cycles. Indeed, many aspects of lepidopteran larval development exhibit considerably temperature-dependence. For many species, warming increases growth rates and survivorship; however both growth and survival decline rapidly once temperatures exceed an individual's thermal optimum (Kingsolver et al. 2006, Kingsolver and Woods 1997). To date, most temperature manipulation experiments have been conducted in highly controlled lab settings. Such laboratory experiments overlook natural temperature fluctuations that affect larval development and survival (Zalucki 1982) and which may not accurately reflect real climate warming patterns. Furthermore, lab experiments often use artificial foods (Kingsolver et al. 2006, Lee and Roh 2010) or leaf material that was not grown under elevated temperatures (Lemoine et al. 2014). Given that plant nutritional quality also changes under warming (Veteli et al. 2002), extrapolating results from laboratory experiments is potentially misleading. Few studies address how realistic climate warming influences lepidopteran development using *in situ* field warming experiments that simultaneously warm both insects and their host plants while realistically mimicking climate warming.

Monarchs (*Danaus plexippus*) are a charismatic species found throughout North America and are well-known for their annual migrations between Mexico and the Great Lakes region. To date, monarch migrations have been extensively studied, focusing on factors that influence migration success and population size (Reppert et al. 2010, Flockhart et al. 2015), potential overwintering and migratory habitat loss (Oberhauser and Peterson 2003, Pleasants and Oberhauser 2012, Sáenz-Romero et al. 2012), and overwintering behavior (Masters et al. 1988). Climate change has shifted research focus towards thermal constraints on monarch migration and

**Comment [LH1]:** True for all species of insects

**Comment [LH2]:** An individual insect experiences weather, not climate. Climate is long term, weather is short term. I think you need to be more precise in your use of terms here and elsewhere.

**Comment [LH3]:** I do not find your arguments here convincing. Diet definitely influences development rate, but the argument that temperature is a huge determinant in food quality is demonstrably untrue. I do not deny that in some circumstances temperature may influence food quality, but the highlighted statement is not, generally, true. Rather than malign laboratory studies (or exaggerate potential issues), I think you study can be justified on other, more relevant grounds. For instance, in a field setting, insects have greater ability to thermoregulate because of the heterogenicity of the environment. Moreover, the influence of temperature on the totality of insect behavior (feeding, predator and parasite avoidance, thermoregulation, etc.) is better accommodated in a natural setting.

development; cool night time temperatures induce reproductive diapause in adult monarchs (Goehring and Oberhauser 2002, Guerra and Reppert 2013) and spring droughts reduce monarch population sizes in their summer breeding grounds (Zipkin et al. 2012). Thus, climate change may have considerable negative effects on monarch populations by reducing available overwintering and migratory habitat.

In addition to indirect effects on monarchs via habitat loss, climate change might directly alter monarch physiology. Monarch larval growth, consumption, and mortality rates all depend upon environmental temperatures (Zalucki 1982, Goehring and Oberhauser 2002, York and Oberhauser 2002, Lemoine et al. 2014). For example, prolonged exposure to extreme heat in reduces larval survival rates in laboratory experiments (Zalucki 1982, York and Oberhauser 2002). However, laboratory experiments often use extreme temperature regimes that monarchs may not encounter during their lifetime and lie outside the normal temperature range experienced by monarchs. Furthermore, warming can alter the nutritional quality of monarchs' milkweed host plants (Couture et al. 2015), yet few studies consider concurrent effects of warming on both monarch and milkweed (*but see* Couture et al. 2015). Indeed, studies that expose both monarchs and milkweed to realistic climate change scenarios that include diel ~~and daily~~ temperature fluctuations remain rare.

Here, we report results from an *in situ* warming experiment designed to assess how climate warming influences growth, survival, and development of monarch larvae. We hypothesized that warming would reduce larval development time, as has commonly been reported for monarch larvae (Zalucki 1982), but would also decrease pupal mass and survivorship (Zalucki 1982, York and Oberhauser 2002).

**Comment [LH4]:** Again, these points are essentially true of all insect species. I think you need to avoid the inference that monarchs are somehow unique in these attributes.

**Comment [LH5]:** Again, I don't see how this is an issue, or particularly relevant. Experiments to test physiological limits, by definition, explore temperatures or other conditions a species would rarely experience. I find statements like these offputting.

**Comment [LH6]:** "diel and daily" is redundant

**Comment [LH7]:** You have written yourself into a corner with this approach to your introduction. You argue that development must be studied in the context of diel temperature patterns, altered host quality associated with temperature, and survivorship issues associated with temperature, but to sort out such an array of complex issues would require multiple experiments, with multiple forms of controls, to allow for any potential assigning of cause and effect. In that this is not what you did, it leaves the reader (me) thinking your study is inadequate before I read anything about the actual study.

The more appropriate approach, in my view is to recognize that there are, and will always be, questions that cannot be addressed in a laboratory setting; specifically, because laboratory experimentation is designed to reduce complexity so cause and effect can be determined. Without trying to do a massive series of observational studies or field experiment necessary to directly address the interaction of multiple factors, it is very useful to examine phenomena, like development, in field experiments to identify key variables that interact with simple processes, like the temperature-development relationship.

**Methods**

All experiments were conducted at the Smithsonian Environmental Research Center in Edgewater, MD. Over the summer of 2013, sixteen 2 x 2 m garden beds were installed in an open field. In each plot, 1 m long aluminum sheets were driven into the soil to quarter the plot into four 1 x 1 m subplots. Two subplots were used for other experiments. The two remaining subplots were seeded with *Asclepias tuberosa* in the fall of 2013. Warming treatments were imposed by installing a single Kalglo MRM-1215 1500W (Kalglo Electronics Company, Bethlehem, PA) heater over half of the plots. An aluminum frame of the same shape and size as the heaters was hung over each control plot to mimic any shading effects ($n$ = 8 per temperature treatment). Heaters were suspended ~1.5 m from the soil surface. In October 2013, after the end of the growing season, heaters were turned off and *A. tuberosa* overwintered under natural conditions. At the beginning of the 2014 growing season, heaters were turned on and remained on throughout the experiment. *Asclepias tuberosa* was therefore germinated and grown under warming treatments for two growing seasons.

Temperature data loggers (Onset HOBO loggers) in each plot recorded average daytime temperatures of 25.2 ± 1.4˚ C and average nighttime temperatures of 19.9 ± 2.0˚ C in ambient conditions. Maximum daytime temperatures averaged 30.7 ± 2.5˚ C, while minimum nighttime temperatures averaged 18.2 ± 2.3˚ C. Since infrared heaters do not warm the air but instead warm surfaces, we verified heating treatments using a handheld IR thermometer (Kimball et al. 2008). Nighttime IR gun measurements verified that heaters raised surface temperatures by ~4˚ C on average ($p$ < 0.001), which is below severe projections of a 6˚ C increase in temperature but above the more conservative estimate of a 2˚ C temperature increase by 2100 (IPCC 2007).

**Comment [LH8]:** I don't understand why researchers don't adopt a standard policy in reporting experimental design. Please take my advice, and always have at least two sentences that state: (1) "The experimental unit was ____", and "The treatments were _____, and all treatments were replicated ____." You also need to describe the experimental arrangement. Is this randomized complete block, randomized complete block with split plots, etc?

As described, I literally cannot determine the experimental design – and you don't want editors, reviewers, or readers to have to guess about this stuff! My guess (and my rewrite of part of this paragraph is:

The experiment used a randomized complete block (16 replications) treatment arrangement with two treatments: warmed and ambient (=control). The experimental unit was a 1 x 1 plot with a heater (warm treatment) or frame 1.5 meter above the soil surface. Treatments within a replication were randomly assigned to two of four adjacent locations in a 2 x 2 m square with individual plots separated by aluminum sheets (you didn't specify how high). (The two plots not used in this experiment were employed in other experiments reported elsewhere.)

Note that my version of the experimental description gives the reader a picture of the treatment arrangement, it leads the reader to an expectation of the analysis (which must conform to the design), and it remains succinct. If I was incorrect in my interpretation, please make appropriate modifications.

In August 2014, monarch eggs and larvae were gathered from *A. syriaca* within nearby old-growth fields. Eggs and larvae were reared in mesh cages and fed fresh *A. syriaca* leaves daily until they reached the third instar. Larval development was checked continuously throughout the day. Immediately after molting to the third instar, larvae were randomly assigned to a temperature treatment ('Ambient', 'Warmed') and placed on a single *A. tuberosa* within a randomly chosen plot ($n$ = 15, $n$ = 18 for 'Ambient' and 'Warmed' treatments, respectively). A mesh bag was placed over the plant to retain the monarch. First or second instar larvae escaped the mesh bags easily and thus were not used. If the monarch consumed the entire host plant, they were transferred to another plant within the same subplot. Time to pupation was recorded as the number of hours between experiment initiation and onset of chrysalis formation, and this number was converted to number of days (development hour / 24). Dead individuals were recorded and removed from the host plant. Chrysalids were carefully transported back to the lab and weighed to obtain final pupal mass.

We measured three plant traits (specific leaf area (SLA), water content, and latex production) to determine whether warming effects on monarch development might be mediated through warming effects on plant traits. At the end of the experiment, two newly expanded leaves were collected from each plant. For one leaf, we measured leaf area, obtained a fresh wet mass, and then dried the leaf to obtain a dry mass. We calculated specific leaf area (SLA) as area / dry mass and percent water content as (1 – dry mass (g) / fresh mass (g))*100. Using the second leaf, we determined latex production by cutting the tip of the leaf and blotting all latex onto a dry, pre-weighed piece of filter paper. The filter paper was dried again and latex concentration calculated as the difference in post- and pre-latex filter weights divided by leaf area (Agrawal 2005).

Although heaters raised temperatures of 'Warmed' plots by ~4˚ C on average, plots varied considerably in temperature due to different light levels across the experimental garden and varying plant biomass within each plot. We therefore measured temperature with a handheld infrared thermometer in each subplot during the night at the end of the experiment. For consistency, we recorded temperature of a white plastic sphere mounted 0.5 m from the ground in the middle of each subplot. We then treated temperature as a quantitative, rather than categorical, variable in all analyses. Note that these measures reflect relative differences in temperature among plots that should be relatively constant over the experiment.

We regressed all response variables against night-time temperatures as measured by the IR gun using OLS regressions. We regressed mortality against temperature using logistic regression, where the response variable was dichotomous with survival = 0 and dead = 1. Although monarchs experience mortality as pupae, brief exposure to prolonged temperatures did not alter pupal mortality rates and third instar individuals were the most sensitive to temperature increases (York and Oberhauser 2002). Thus, our experiment likely captured most of the influence of temperature on larval survival.

Model assumptions were verified with residual plots where appropriate. All analyses were conducted using Python v2.7 with the '*numpy*', '*pandas*', and '*statsmodels*' modules (McKinney 2010, Seabold and Perktold 2010, Walt et al. 2011).

**Results**

Time to pupation declined rapidly with increasing temperature ($p < 0.001$, $R^2 = 0.57$) (Fig. 1). At the lowest temperature, 12.6˚ C, monarchs required 12.5 ± 0.24 days to transition between third instar and pupa. At the warmest temperature, 17.3˚ C, third instar monarchs

**Comment [LH9]:** Let me warn you, I haven't looked at your analysis yet, but I am immediately skeptical of your approach based on this description. You have two treatments, this says to me that you have only two points if you are using regression. Thus, a regression that includes the warm and ambient data in a single model faces the problem that with essentially two "levels" (here, of temperature) so you will necessarily get a good fitting line (because you only have two points. I understand that you won't be fitting just two points (you have the replications, you have the range of temperatures within each treatment), but that doesn't change the fundamental "only two point issue"

I have seen this error many, many times in my career (as reviewer and reader), and I think I have become hypersensitive to it. The solution in your case is to regress the temperature by treatment, and then compare the resulting regression models by treatment to identify differences. Of particular value here would be a comparison of slopes, as it would indicate a change in the fundamental relationship between temperature and development. Why might such a thing occur? For some of the reasons you previously mentioned: altered food quality, increased or decreased time feeding (perhaps to thermoregulate or because of some interaction between natural enemies and temperature).

The reason I am going on at length here, rather than after looking at your analysis, is that I want to emphasize the point that you could have made the closing paragraph of the intro much more specific (by speculating on possible outcomes as I did in the end of the previous paragraph). For instance, if the warmed treatment has a lower slope in the development curve than that of the ambient curve, this is cle ...

**Comment [LH10]:** Caught you! Not only is combining the treatment data in a single regression inappropriate, but in looking at your data points, I'm relatively certain you are missing key information from your experiment. I say this because it seems to me that separate regressions would show that the warmed treatments are taking longer than expected. Also, the convention in the insect development literature is to analyze 1/development time versus temperature (so that a greater slope corresponds to faster development), and I think your data presentation would greatly benefit from that conversion.

154 required only 10.3 ± 0.2 days to reach pupation. The slope was -0.46 ± 0.08, suggesting that 1˚ C
155 of warming reduces time to pupation by roughly half a day. Thus, in future climates, time to
156 pupation may be reduced by 1 – 3 days, depending on location and severity of warming. Air
157 temperature measurements do not accurately reflect the intensity of infrared heating because
158 infrared energy warms surfaces and not the air (Kimball et al. 2008), calculations of degree-days
159 may not accurately reflect the underlying temperature treatments. Still, we calculated the number
160 of degree days experienced by each individual for which there was adequate temperature data
161 following the simple averaging method, since temperatures remained within the upper and lower
162 thermal limits throughout the experiment (Allen 1976). Monarch caterpillars experienced ~ 155
163 ± 17 degree days, and this did not differ between temperature treatments ($p = 0.978$). Thus,
164 monarchs accumulated their required number of degree days faster in the warming treatment
165 than in the ambient treatment.
166 Temperature had no effect on pupal mass ($p = 0.454$, $R^2 = 0.023$, Fig. 2). Similarly,
167 mortality was low throughout the experiment (18%) and independent of temperature ($p = 0.610$,
168 pseudo-$R^2 = 0.01$, Fig. 3).
169 Warming had no effect on any measured plant trait. SLA ($p = 0.940$, $R^2 = 0$), percent
170 water content ($p = 0.313$, $R^2 = 0.05$), and latex concentration ($p = 0.739$, $R^2 = 0.01$) all did not
171 vary with temperature. Thus, any effects of warming on monarch development time were direct
172 effects of temperature on monarch physiology rather than being mediated through the plant traits
173 we measured.
174
175 **Discussion**

Our study indicates that climate warming will accelerate monarch larval development but likely have little effect on larval mortality or pupal mass at our study site. This is consistent with numerous studies showing positive correlations between larval development and temperature (Kingsolver and Woods 1997). Since warming increases larval growth rates, lepidopteran larvae reach critical mass needed for pupation earlier and proceed through larval stadia more quickly. This is demonstrated by the fact that monarch larvae developed more rapidly but experienced roughly the same number of degree days. Our results suggest that climate warming might actually facilitate monarch development under moderate climate change scenarios at sites with relatively cool temperatures, potentially increasing the number of generations in the temperate summer breeding grounds of eastern migratory monarch populations.

Laboratory studies have consistently documented negative effects of extreme temperatures on monarch caterpillar development and survival. Short-term, extreme heat stress can have weak negative effects on pupal mass (York and Oberhauser 2002). Likewise, constant temperatures above 28˚ C induced high mortality rates in monarch larvae (Zalucki 1982, York and Oberhauser 2002). However, these studies used either pulses of extremely high temperatures (*i.e.* 36˚ C) or held monarchs at a constant temperature (*i.e.* 28˚ C). Ambient, maximum daytime temperatures averaged 30 ˚C during our experiment; warming increased this maximum to 32-34˚ C. Although these temperatures are above the thermal optimum of monarch survival, we found no effect of *in situ* warming on either pupal mass or survival. As temperatures exceeded 28˚ C for less than 20% of the full 24 hour day, it is likely that diel and daily temperature fluctuations mitigated the lethality of high temperatures.

Interestingly, our study site had warmer temperatures during our experiment than other locations of the monarch breeding range. Monarchs typically experience cool temperatures

during their northward migration: maximum March temperatures in Texas average 23.5 ± 2.4˚ C, maximum April temperatures in Iowa and the midwestern US average 20.7 ± 1.5˚ C, and maximum May temperatures in the Great Lakes region average 18 ± 2.3˚ C (averages based on 50 year weather station data provided by WorldClim). Even maximum temperatures during the summer breeding season in the Great Lakes region are typically lower than at our study site, averaging 26.0 ± 2.3˚ C compared to 30.7 ± 2.5˚ C at during our experiment. Thus, our study site represents the upper thermal limits monarchs experience during their migrations and breeding season.

Climate change can also alter foliar water content, nutritional quality, and secondary metabolite concentrations (Zvereva and Kozlov 2006, Couture et al. 2015). However, we found little effect of temperature on *A. tuberosa* traits. Indeed, temperature often has negligible effects on secondary metabolites and nutritional content (Aerts et al. 2009, Veteli et al. 2002, Williams et al. 2000). Thus, effects of climate change on monarch development time appear related to direct effects of temperature on monarch physiology, rather than any change in host plant quality.

Although our results suggest that warming may minimally impact monarch larvae older than the third instar in temperate regions, climate change still poses a considerable threat to monarch populations. For example, increased incidence of drought may reduce the availability of *Asclepias* host plants during the northward migration, decreasing the population size of eastern migratory monarchs (Zipkin et al. 2012). Climate warming may also delay initiation of reproductive diapause in the fall, advance the cessation of reproductive diapause in the spring, and potentially cause monarchs to migrate further south than ordinary, missing their overwintering habitat or migrating north later in the year (Goehring and Oberhauser 2002,

222 Guerra and Reppert 2013). Climate warming will also increase the incidence of freezing rains
223 during the overwintering period, leading to increased adult mortality in overwintering
224 populations (Oberhauser and Peterson 2003). Furthermore, warming may have strong effects on
225 monarch larvae in more tropical environments or earlier in the season. Thus, researchers and
226 conservationists must understand how climate change will affect all parts of the monarch life
227 cycle in order to protect this important species.

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