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

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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.

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25 **Running Header:** Lemoine et al: Warming effects on monarch development

26   **Abstract**

27   Climate warming will fundamentally alter the development of many ectothermic insects;

28   understanding how elevated temperatures affect insect development is becoming increasingly

29   important. Yet most studies examining the relationship between temperature and insect

30   development do so in highly controlled laboratory settings. While useful, laboratory studies

31   cannot incorporate natural variability in temperatures or behavioral thermoregulation by insects.

32   Using *in situ* field warming experiments, we assessed the impact of experimental warming on

33   development of monarch butterfly larvae (*Danaus plexippus*). Monarch larvae were reared on

34   butterfly weed (*Asclepias tuberosa*) grown under 'Ambient' and 'Warmed' conditions. We

35   quantified time to pupation, final pupal mass, and survivorship. Monarch larval development

36   proceeded more rapidly at higher temperatures, and this effect was even greater for monarch

37   larvae reared under 'Warmed' conditions. In contrast, survivorship and pupal mass were not

38   affected by warming. More rapid developmental rates of monarch larvae will alter their

39   ecological and evolutionary dynamics by potentially speeding up northward migrations and

40   increasing the number of generations during the summer breeding season. Our results contrast

41   those from laboratory experiments, wherein rising temperatures increase growth rates of

42   lepidopteran larvae, but also reduce final pupal mass and increase mortality. Therefore, more

43   studies assessing the impact of warming and climate change on monarch biology are needed.

Introduction

44

45   Modified temperature regimes caused by climate change will fundamentally alter insect

46 life cycles. As with other insects, lepidopteran larval development is temperature-dependent.

47 Warming increases growth rates and survivorship; however both growth and survival decline

48 rapidly once temperatures exceed an individual's thermal optimum (Kingsolver et al. 2006,

49 Kingsolver and Woods 1997). The effects of elevated temperatures on lepidopteran larval

50 development have, to date, been mostly examined in highly controlled lab settings. Such

51 laboratory experiments cannot incorporate natural temperature fluctuations that affect larval

52 development and survival (Zalucki 1982) or changes in insect behavior (*i.e.* behavioral

53 thermoregulation, predator avoidance). Furthermore, warming alters plant nutritional quality

54 (Veteli et al. 2002), and lab experiments often use artificial foods (Kingsolver et al. 2006, Lee

55 and Roh 2010) or leaf material that was not grown under elevated temperatures (Lemoine et al.

56 2014). Extrapolating results from laboratory experiments to natural settings is therefore

57 problematic. Field experiments are necessary to identify how elevated temperatures influence

58 insect development in a more natural, albeit, variable environment.

59   Monarch butterflies (*Danaus plexippus*) are a charismatic species found throughout North

60 America and are well known for their annual migrations between Mexico and northern United

61 States and southern Canada. Monarch migrations have been extensively studied, focusing on

62 factors that influence migration success and population size (Reppert et al. 2010, Flockhart et al.

63 2015), potential overwintering and migratory habitat loss (Oberhauser and Peterson 2003,

64 Pleasants and Oberhauser 2012, Sáenz-Romero et al. 2012), and overwintering behavior

65 (Masters et al. 1988). Reductions in overwintering and migratory habitat caused by changes in

66 climate and land-use have stimulated research on thermal constraints experienced by migratory

67   adults and larvae, the need for cool night time temperatures to induce reproductive diapause in

68   adult monarchs (Goehring and Oberhauser 2002, Guerra and Reppert 2013), and the threat posed

69   by spring droughts that reduce monarch population sizes in their summer breeding grounds

70   (Zipkin et al. 2012).

71   As with all insect species, monarch larval growth, consumption, and mortality rates

72   depend upon environmental temperatures (Zalucki 1982, Goehring and Oberhauser 2002, York

73   and Oberhauser 2002, Lemoine et al. 2014). Prolonged exposure to extreme heat reduces larval

74   growth and survival rates in laboratory experiments (Zalucki 1982, York and Oberhauser 2002).

75   Although warming alters the nutritional quality of monarchs' milkweed host plants (Couture et

76   al. 2015), few studies consider concurrent effects of warming on both monarch and milkweed

77   (*but see* Couture et al. 2015). Milkweed nitrogen, lignin, and fiber content increase under

78   elevated temperatures (Couture et al. 2015). Given that elevated temperatures affect both

79   monarchs and milkweeds simultaneously, the relationship between temperature and monarch

80   larval development and survival might be fundamentally different under climate warming. Field

81   experiments are necessary to explore how warming affects monarch larval development in a

82   scenario that incorporates natural temperature variability and changes in host plant quality.

83   Here, we report results from an *in situ* warming experiment designed to assess how

84   elevated temperatures influence growth, survival, and development of monarch larvae under

85   variable field conditions. We hypothesized that development time would decrease with rising

86   temperatures under ambient conditions, as has commonly been reported for monarch larvae

87   (Zalucki 1982). However, this relationship between development time and temperature would be

88   significantly stronger under warming since milkweed grown under elevated temperatures

89   contains significantly more nitrogen (Couture et al. 2015). We expected that pupal mass and

90 survival would decrease with rising temperatures (Zalucki 1982, York and Oberhauser 2002), but

91 that warming would weaken these effects due to the effects of elevated temperatures on

92 milkweed nutritional quality (Couture et al. 2015).

93

94 **Methods**

95   All experiments were conducted at the Smithsonian Environmental Research Center in

96 Edgewater, MD. The experiment consisted of 16 replicate 2 x 2 m garden beds. Garden beds

97 were assigned to temperature treatments in a completely randomized design. Warming

98 treatments were imposed using a single Kalglo MRM-1215 1500W (Kalglo Electronics

99 Company, Bethlehem, PA) heater installed 1.5 m from the ground over half of the garden beds.

100 An aluminum frame of the same shape and size as the heaters was hung over the remaining

101 garden beds to mimic any shading effects ($n = 8$ garden beds per temperature treatment). In each

102 garden bed, 1 m long, 20 cm high aluminum sheets were driven 10 cm into the soil to quarter the

103 2 x 2 m garden bed into four 1 x 1 m subplots. In the fall of 2013, butterfly weed *Asclepias*

104 *tuberosa* was sown into two of the subplots within each garden bed, resulting in a density of $\sim$ 4

105 plants per subplot (the remaining two subplots were used for other experiments). We chose *A.*

106 *tuberosa* over the *A. syriaca* because *A. syriaca* can grow to $>$ 2 m tall, surpassing the height of

107 our heaters. The experimental unit was therefore 32 1 x 1 m subplots ($n = 16$ per temperature)

108 within the sixteen garden beds.

109   We placed Onset HOBO temperature loggers in the center of each garden bed to record

110 air temperature in 10-minute intervals over the course of the experiment. In 'Ambient'

111 treatments, average daytime temperatures were $25.2 \pm 1.4°$ C and average nighttime temperatures

112 of $19.9 \pm 2.0°$ C. Maximum daytime temperatures at our study site were $30.7 \pm 2.5°$ C, while

113 minimum nighttime temperatures were $18.2 \pm 2.3°$ C. Since air temperature measurements may

114 not accurately reflect the heating achieved by infrared heaters (Kimball et al. 2008), we verified

115 heating treatments using a handheld IR thermometer to measure temperatures on a plastic sphere

116 mounted 0.5 m from the ground placed in the middle each experimental subplot at midnight.

117 Nighttime IR gun measurements verified that heaters raised surface temperatures by ~4° C on

118 average ($p < 0.001$), which is below severe projections of a 6° C increase in temperature but

119 above the more conservative estimate of a 2° C temperature increase by 2100 (IPCC 2007).

120   In August 2014, monarch eggs and larvae were gathered from *A. syriaca* within nearby

121 old-growth fields. Eggs and larvae were reared in mesh cages and fed fresh *A. syriaca* leaves

122 daily until they reached the third instar. Larval development was checked continuously

123 throughout the day. First or second instars escaped the mesh bags easily and thus were not used.

124 Immediately after molting to the third instar, larvae were randomly assigned to a temperature

125 treatment ('Ambient', 'Warmed') and a single larva was placed on a single *A. tuberosa* within a

126 randomly chosen plot ($n = 15$, $n = 18$ for 'Ambient' and 'Warmed' treatments, respectively). A

127 20 x 30.5 cm organza mesh bag was placed over the plant to retain the monarch. If the monarch

128 larva consumed the entire host plant, they were transferred to another plant within the same

129 subplot. Time to pupation was recorded as the number of hours between experiment initiation

130 and onset of chrysalis formation, and this number was converted to number of days

131 (development hour / 24). Dead individuals were recorded and removed from the host plant.

132 Chrysalids were transported to the lab and weighed to obtain final pupal mass.

133   We measured three plant traits (specific leaf area (SLA), water content, and latex

134 production) to determine whether warming effects on monarch development might be mediated

135 through warming effects on plant traits. At the end of the experiment, two newly expanded

136   leaves were collected from each plant. For one leaf, we measured leaf area, obtained a fresh wet

137   mass, and then dried the leaf to obtain a dry mass. We calculated specific leaf area (SLA) as area

138   / dry mass and percent water content as (1 – dry mass (g) / fresh mass (g))*100. Using the second

139   leaf, we determined latex production by cutting the tip of the leaf and blotting all latex onto a

140   dry, pre-weighed piece of filter paper (Agrawal 2005). The filter paper was dried again and latex

141   concentration calculated as the difference in post- and pre-latex filter weights divided by leaf

142   area (Agrawal 2005).

143   Although heaters raised temperatures of 'Warmed' plots by ~4˚ C on average, plots

144   varied considerably in temperature due to different light levels across the experimental garden

145   and varying plant biomass within each plot. We therefore measured temperature with a handheld

146   infrared thermometer in each subplot during the night at the end of the experiment. For

147   consistency, we recorded temperature of a white plastic sphere mounted 0.5 m from the ground

148   in the middle of each subplot. We then treated temperature as a quantitative rather than

149   categorical variable in all analyses. Note that these measures reflect relative differences in

150   temperature among plots that should be relatively constant over the experiment.

151   We used an ANCOVA design to regress days^{-1} until pupation and final pupal mass

152   against night-time temperatures as measured by the IR gun. We included temperature treatment

153   as a covariate, which allows for the possibility that slopes differ between temperature treatments.

154   Mortality was assessed using logistic regression that also included night-time temperature and its

155   interaction with temperature treatment, as in the ANCOVA. Although monarchs experience

156   mortality as pupae, brief exposure to prolonged temperatures did not alter pupal mortality rates

157   and third instars were the most sensitive to temperature increases (York and Oberhauser 2002).

158   Thus, our experiment likely captured most of the influence of temperature on larval survival.

159   Model assumptions were verified with residual plots where appropriate. All analyses

160   were conducted using Python v2.7 with the '*numpy*', '*pandas*', and '*statsmodels*' modules

161   (McKinney 2010, Seabold and Perktold 2010, Walt et al. 2011).

162

163   **Results**

164   Time to pupation decreased with increasing temperature, but did so differently under

165   'Ambient' and 'Warmed' conditions (interaction: $p < 0.041$) (Fig. 1). At the lowest temperature

166   in 'Ambient' treatments, 12.6° C, monarch larvae required 12.2 days to transition between third

167   instar and pupa. At the warmest temperature achieved in the 'Warmed' plots, monarch larvae

168   required only 10.0 days to pupate. Importantly, the relationship between temperature and time to

169   development varied among treatments (Fig. 1). When reared under 'Ambient' conditions, larval

170   development time decreased by ~ 0.4 days per 1° C increase in temperature. In 'Warmed' plots,

171   larval development time decreased by ~ 0.7 days per 1° C increase in temperature. Climate

172   change may therefore speed larval development by ~ 0.7 − 2.4 days, depending on the severity of

173   temperature increases.

174   Air temperature measurements do not accurately reflect the intensity of infrared heating

175   because infrared energy warms surfaces and not the air (Kimball et al. 2008), calculations of

176   degree-days may not accurately reflect the underlying temperature treatments. Still, we

177   calculated the number of degree days experienced by each individual for which there was

178   adequate temperature data following the simple averaging method, since temperatures remained

179   within the upper and lower thermal limits throughout the experiment (Allen 1976). Monarch

180   caterpillars experienced ~ 155 ± 17 degree days, and this did not differ between temperature

181   treatments ($p = 0.978$). Thus, monarch larvae accumulated their required number of degree days

182   faster in the warming treatment than in the ambient treatment.

183   Temperature had no effect on pupal mass ($p = 0.454$, $R^2 = 0.023$). Similarly, mortality

184   was low throughout the experiment (18%) and independent of temperature ($p = 0.610$, pseudo-R^2

185    $= 0.01$).

186   Warming had no effect on any measured plant trait. SLA ($p = 0.940$, $R^2 = 0$), percentage

187   water content ($p = 0.313$, $R^2 = 0.05$), and latex concentration ($p = 0.739$, $R^2 = 0.01$) all did not

188   vary with temperature. Thus, any effects of warming on monarch development time were direct

189   effects of temperature on monarch physiology rather than being mediated through the plant traits

190   we measured.

191

192   **Discussion**

193   Our study indicates that warming accelerates monarch larval development but has little

194   effect on larval mortality or pupal mass at our study site. This is consistent with numerous

195   studies showing positive correlations between larval development and temperature (Kingsolver

196   and Woods 1997, Bale et al. 2002). Since warming increases larval growth rates, lepidopteran

197   larvae reach critical mass needed for pupation earlier and proceed through larval stadia more

198   quickly. Monarch larvae developed more rapidly from the third instar but experienced roughly

199   the same number of degree days. Our results suggest that climate warming might facilitate

200   monarch larval development through later instars under moderate climate change scenarios at

201   sites with relatively cool temperatures, potentially increasing the number of generations in the

202   temperate summer breeding grounds of eastern migratory monarch populations.

203   Laboratory studies have consistently documented negative effects of extreme

204   temperatures on monarch caterpillar development and survival. Short-term, extreme heat stress

205   can have weak negative effects on pupal mass (York and Oberhauser 2002). Likewise, constant

206   temperatures above 28° C induced high mortality rates in monarch larvae (Zalucki 1982, York

207   and Oberhauser 2002). However, these studies used either pulses of extremely high temperatures

208   (*i.e.* 36° C) or held monarch larvae at a constant temperature (*i.e.* 28° C). Ambient, maximum

209   daytime temperatures averaged 30 °C during our experiment; warming increased this maximum

210   to 32-34° C. Although these temperatures are above the thermal optimum of monarch survival,

211   we found no effect of *in situ* warming on either pupal mass or survival of older monarch larvae.

212   Eggs and first instar larvae are resistant to high temperatures, with third instars, fourth instars,

213   and pupae being the most sensitive to extreme heat (Zalucki et al. 1982, York and Oberhauser

214   2002). As temperatures exceeded 28° C for less than 20% of the full 24 hour day, it is likely that

215   diel and daily temperature fluctuations mitigated the lethality of high temperatures.

216   Interestingly, our study site had warmer temperatures during our experiment than other

217   locations of the monarch breeding range. Monarchs typically experience cool temperatures

218   during their northward migration: maximum March temperatures in Texas average 23.5 ± 2.4° C,

219   maximum April temperatures in Iowa and the midwestern US average 20.7 ± 1.5° C, and

220   maximum May temperatures in the Great Lakes region average 18 ± 2.3° C (averages based on

221   50 year weather station data provided by WorldClim). Even maximum temperatures during the

222   summer breeding season in the Great Lakes region are typically lower than at our study site,

223   averaging 26.0 ± 2.3° C compared to 30.7 ± 2.5° C at during our experiment. We found no

224   influence of increased temperatures on larval monarch pupal mass and survival at our study site,

225   which had temperatures well above those in other important breeding ranges. Indeed,

226   temperatures in these ranges rarely exceed the thermal optimum of 28° C and do not exceed the

227   critical thermal maximum of 36° C (Zalucki 1982, York and Oberhauser 2002). Thus, climate

228   change is unlikely to raise temperatures to a range that is detrimental to monarch larval

229   performance.

230   Though monarch larval development proceeded more rapidly when exposed to high

231   temperatures, this effect was stronger on plants grown under warmed conditions. Increased

232   sensitivity to temperature in 'Warmed' plots likely stems from altered plant nutritional content.

233   Though we found no different in *A. tuberosa* leaf characteristics between 'Ambient' and

234   'Warmed' treatments, elevated temperatures alter foliar water content, nutritional content, and

235   secondary metabolite concentrations of numerous plant species (Zvereva and Kozlov 2006). In

236   particular, milkweed nitrogen content increases at elevated temperatures (Couture et al. 2015).

237   Insect development proceeds more rapidly at high temperatures on nitrogen-rich plants (Lemoine

238   et al. 2013, Lemoine et al. 2014). It is therefore likely that increased foliar nitrogen content of *A.*

239   *tuberosa* grown under elevated temperatures is responsible for the greater sensitivity of monarch

240   larvae to rising temperatures.

241   Our paper demonstrates that climate warming may minimally impact the development of

242   monarch larvae in temperate regions. Though numerous laboratory studies have reported

243   detrimental impacts of extreme temperatures on monarch larval development and survival

244   (Zalucki 1982, York and Oberhauser 2002), our field experiment demonstrated that *in situ*

245   warming had little influence on larval survival or pupal mass even in a site with extreme daytime

246   temperatures. Rising temperatures may, however, have other important effects on monarch

247   larvae. Monarch larvae may, for example, suffer higher parasitism rates at high temperatures as

248   occurs in other insect-parasitoid pairs (Bezemer et al. 1998). Predatory insects also increase their

249   attack and ingestion rates at high temperatures, suggesting that predation pressure on monarch

250   larvae may increase substantially under warming (Rall et al. 2010). Furthermore, landscape level

251   distributions of milkweed host plants may be substantially different at elevated temperatures.

252   Warming may reduce the availability of *Asclepias* host plants during the northward migration via

253   increased drought or drastically alter the geographic range of *Asclepias* host plants (Zipkin et al.

254   2012, Lemoine 2015). Thus, this research establishes an important baseline for future work

255   considering numerous other consequences of increased temperature on monarch larval

256   performance and survival.

257 **Acknowledgements**

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Figure 1(on next page)

Effects of temperate on monarch development time.

Monarch development time decreased as temperature increased in both Ambient (open circles) and Warmed (filled circles) plots. However, the effect of temperature on monarch larval development was stronger in Warmed plots.