



Warming experiments test the temperature sensitivity of an endangered butterfly across life history stages

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Abstract

The Karner blue butterfly (*Lycaeides melissa samuelis*) (hereafter Karner blue) is a federally listed endangered species occurring in disjunct locations within the Midwest and Eastern United States. As a hostplant specialist and an ectotherm, the Karner blue is likely to be susceptible to effects of climate change. We undertook warming experiments to explore the temperature sensitivity of various Karner blue life history stages and traits. Over a two-year period, we exposed all Karner blue life stages to temperature increases of +2, +4, and +6 °C above 1952–1999 mean temperatures. We analyzed the effect of these treatments on life history parameters likely related to fitness and population size, including development time, voltinism, degree-day accumulation, body weight, and morphology. Warming treatments resulted in earlier emergence and accelerated development, leading to additional generations. Warming also increased the number of degree-days accumulated during pre-adult development (i.e., egg hatch to eclosion). Results suggest that Karner blues developed in fewer days, in part, by putting on less mass as temperatures increased. As treatment temperature increased, adult body mass, length, and area decreased and voltinism increased. Females with lower adult mass and smaller body size produced fewer eggs. These results suggest a trade-off between accelerated development and decreased body size with decrease in adult mass and abdominal area being associated with reduced fecundity.

Implications for insect conservation Changes in development timing and in voltinism can negatively affect phenological matching between the Karner blue and its obligate host plant, Wild lupine (*Lupinus perennis*), resulting in population decrease. Poorer phenological matching between insect and hostplant can occur across multiple generations, for example, negatively affecting overwintering population size. With increasing temperatures, smaller females will produce fewer eggs, which can also lead to poorer population outcomes across generations.

Keywords Climate change · Development time · Endangered species · Karner blue butterfly · Phenology · Voltinism

Introduction

Multi-decadal declines of insect populations have been documented globally, showing significant reductions in abundance and distribution among multiple insect orders

(Gardiner and Didham 2020; Hallmann et al. 2020; Montgomery et al. 2020; Powney et al. 2019; Roth et al. 2020; Sánchez-Bayo and Wyckhuys 2019; Stepanian et al. 2020; Theng et al. 2020; van Klink et al. 2020; Wagner 2020). Despite those trends, population change is not uniform

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among species, in part, because of the variety of threats associated with declines (Crossley et al. 2020; Didham et al. 2020). To understand and predict population change, we document how physiological and demographic processes respond to changing conditions to improve our mechanistic understanding of factors leading to decline. To this end, we conducted a series of temperature manipulation experiments on the Karner blue butterfly (*Lycadeides melissa samuelis*) to improve our ability to understand documented declines of this species (Patterson et al. 2020) as part of the effort to conserve and recovery this endangered species.

The Karner blue is a monophagous, wild lupine (*Lupinus perennis*) (hereafter “lupine”) feeding specialist butterfly, listed as a federally endangered species in the United States and extirpated in Canada (Clough 1992). The Karner blue butterfly requires landscapes with heterogeneous canopy cover that enhance microclimatic diversity, and lupine population viability benefits from heterogeneous microscale temperature, moisture, shade, and soil conditions (Pavlovic and Grundel 2009; Grundel et al. 1998b). These traits suggest several climate-sensitive mechanisms that might affect species viability. The Karner blue’s life history stages have been examined via population modeling approaches (Fuller 2008; Thurman et al. 2020a, b; Li 2020) but possible climate sensitivity of the Karner blue butterfly (hereafter Karner blue) is not well understood mechanistically. As a specialist species with isolated populations and limited dispersal ability (Hess and Hess 2015; Knutson et al. 1999), the Karner blue butterfly is unlikely to disperse to distant alternative habitats in response to changing climate conditions. In situ responses to changing conditions are therefore pertinent for creating conservation plans for this species.

We performed experimental tests of warming on different life history stages of the Karner blue, focusing on life history parameters affecting fitness and population size. This experimental testing can help us understand mechanisms by which climate change might affect Karner blue populations (García-Barros 2000; Nylin and Gotthard 1998). Different temperature treatments were used to test five predictions, based on published observations of how temperature has affected other butterflies.

Prediction 1: *Exposure to higher temperatures accelerates development* (Sibly and Atkinson 1994). Specifically, warming will decrease developmental time during the larval and pupal stages. At warmer temperatures, butterflies spend less time developing when diapause is facultatively affected by temperature rather than being solely dependent on light and dark cycles (McWatters and Saunders 1998). Additionally, higher temperatures increase growth rates and shorten developmental time before eclosion (Atkinson 1994; Davies 2019; Kingsolver 1989; Van der Have and De Jong 1996).

Prediction 2: *Warming will cause earlier egg hatching, possibly cued by a more rapid accumulation of*

degree-days. Developmental changes lead to changes in insect phenology (Cayton et al. 2015), and growing degree-days (GDD) provide a metric linking climatic conditions and insect phenology (Nufio et al. 2010). Changes in diurnal temperature ranges can substantially change degree-day accumulation and alter insect life history (Chen et al. 2015; Patterson et al. 2020). If individuals are exposed to warmer temperatures, accumulation of a specified level of GDD will occur in fewer days (Tobin et al. 2008) and this could trigger earlier initiation of transitions, such as egg hatching, that are often associated with accumulation of a minimum number of GDD. Therefore, more rapid accumulation of GDD could shorten diapause duration (Hahn and Denlinger 2007; Kerr et al. 2020; Leather et al. 1995).

Prediction 3: *Warming temperature will delay the onset of diapause, which, in this species, could result in additional generations* (Davies 2019; Schiesari and O’Connor 2013). Typically, Karner blue eggs laid in mid-summer (e.g., July) by second- or summer-generation females enter diapause that is broken the following spring. However, field observations suggest extra Karner blue generations occur occasionally when second-generation eggs develop into adults in the summer they are produced rather than enter diapause which isn’t broken until the following spring (USFWS 2012). We ask whether three, or more, generations of adults across the spring and summer, might be related to development timing of prior generations and to increased temperatures.

Prediction 4: *Warmer temperatures will produce smaller Karner blue adults*. Body size is a product of development time and mass accumulation (Davidowitz et al. 2004). However, accelerated development rate can decrease metabolic rate and enzyme kinetics (Atkinson 1994; Gotthard 2001) and therefore reduce adult size (Van der Have and De Jong 1996). Body size influences many aspects of an organism’s physiology (Kingsolver and Huey 2008) and can influence overall fecundity (Peters and Peters 1986). Larger body size may also lead to stronger propensity for dispersal, which has been confirmed for butterflies and many other insects (e.g. odonates) (Stevens et al. 2012; Reim et al. 2018).

Prediction 5: *Warming and accelerated development result in reduced egg production or fecundity*. The complex relationship between temperature and development creates a size-dependent allocation tradeoff in ectotherms (Berger et al. 2008; Gotthard 2001). Previous insect studies have found that larger females often exhibit higher fecundity (Clifford and Boerger 1974; Hough and Pimentel 1978; Tyndale-Biscoe and Hughes 1969), and some have linked this to the mother’s extended development (Kamm 1972; Masaki 1972). If adult females become smaller with exposure to higher temperatures, their fecundity could decrease in response (Berger et al. 2008; Kozłowski 1992).

Methods

Karner blue life history and distribution

Historically, the Karner blue occurred between approximately 41°–46° N latitude and 93–71° W longitude, extending from Minnesota to Maine in the United States and Southern Ontario, Canada (Bried et al. 2014). The Karner blue is typically bivoltine across its range, overwintering as eggs that hatch in early spring, often in April, and producing a first generation of adults in May and June. These first-generation adults breed and produce a second generation of adults from about June–August. Females from that second generation lay eggs that overwinter, restarting the cycle. At the time of this study, the Karner blue was present in disjunct populations in the Midwest and Northeast U.S. states of Wisconsin, Michigan, Indiana, New Hampshire, and New York, with New York, Wisconsin and Michigan supporting the largest populations (Bried et al. 2014; Hess & Hess 2015; USFWS 2012;). The Indiana laboratory populations used in the present study were derived, in 2010, from an Indiana population that was reported as extinct in the wild by 2014 (Patterson et al. 2020).

Study system

Between 1992 and 2014, the Karner blue was monitored and studied at the Indiana Dunes National Park (hereafter, Indiana Dunes) in northwest Indiana, USA. During this period, Karner blue populations declined steadily, even with extensive habitat management by the National Park Service (NPS). Habitat monitoring within species recovery units included sampling units for habitat requirements, and synthesizing rating categories for habitat potential (Bried et al. 2014). Recovery criteria were used to estimate habitat potential and implement restoration activities towards recovering this endangered species. Despite these efforts, the species went regionally extinct at the Indiana Dunes by 2014 (Patterson 2020).

During the final phase of Karner blue population decline (2012–2014), the relationship between spring and summer temperatures and rapid decline was documented (Patterson et al. 2020). Historically high spring temperatures were associated with phenological mismatching between larvae and the larval hostplant (lupine, *Lupinus perennis*). High summer temperatures were associated with early senescence of lupine, decreasing lupine availability for developing summer larvae. The result of these two climate related effects was a final decline of the Karner blue. Intensive landscape management by the NPS during

the final two decades (1992–2012) of the Indiana Dunes population also provided increased habitat and resources for the Karner blue, suggesting that habitat availability was not the prime cause of decline. To understand warming effects further, we undertook a series of laboratory studies to examine how changes in mean temperatures might have affected Karner blue populations leading up to its end-stage precipitous decline (Erenler et al. 2020).

Temperature treatments

We performed warming experiments in the laboratory throughout the life cycle of the Karner blue. An experimental colony was started from 75 s-generation pupae from an Indiana Dunes captive-rearing program and 30 wild-caught second-generation females from two Indiana Dunes locations (Inland Marsh (since renamed to Tolleston Dunes by NPS), and Miller Woods). The laboratory colony was started in 2010. Treatments were maintained for generations from the fall of 2010 to summer of 2011 (Year 1) and again from fall of 2011 to summer of 2012 (Year 2). Year 2 individuals were direct descendants of Year 1 individuals such that diapaused offspring from final generations of Year 1 were first-generation individuals in Year 2.

Karner blue individuals were reared in two types of experimental growth chambers, depending on the temperature required. During the growing season and until late fall (October), they were reared in environmental chambers (Conviron® MTR30) that have a thermal operating envelope between 10 and 45 °C. When the experimental temperature treatment fell below the lower operating temperature of the environmental treatment (10 °C), we transferred the eggs to custom-constructed, remotely-monitored “cold simulation chambers” constructed from consumer-grade chest freezers. The cold simulation chambers were capable of a colder thermal profile (– 32 to 10 °C).

Temperatures were controlled by a script (MATLAB 2012) running on a continuous loop. When temperature deviated from set conditions, the freezer’s compressor was turned on or off to regulate towards the desired temperature. All chambers were held within + 0.4 and – 0.4 °C of set point. In both chamber types, we simulated daylight patterns or photoperiod using full-spectrum, cold cathode, 60-W light bulbs.

Climate projections for the greater Chicago region available at the time of this study (Hayhoe et al. 2010) suggested that regional temperatures would show steep increases starting around 2010 with mean 30-year interval increases projected at 1.4 °C from 2010 to 2040, 2–3 °C from 2040 to 2070, and 3–5 °C from 2070 to 2100, depending on emission scenarios. To approximate those 30-year interval projections, we selected baseline comparison temperatures as mean daily temperatures from 1952–1999, a period prior to

the steep increases projected starting around 2010 and for which a complete record of Indiana Dunes temperatures was available. Hereafter, we term those historic mean temperatures as “+0 °C”. We tested the effects of +2 °C, +4 °C, and +6 °C above the +0 °C baseline on Karner blue development. Those temperature increments were 1 °C higher than highest projected mean annual temperature increases from start to end of the 30-year intervals from 2010 to 2100, allowing us to examine possible effects on Karner blue development of extremes of temperature increases projected for the twenty-first century, while still capturing temperature increases that are very likely to occur.

Historic (+0 °C) temperatures were set from daily mean minimum and maximum temperatures using data from a weather station within the current boundary of Indiana Dunes at Ogden Dunes, Indiana from 1952 to 1989 and at the Indiana Dunes NPS headquarters in Porter, Indiana from 1989 to 1999. We set the minimum temperature based on the mean minimum 1952–1999 temperature near sunrise, and we set the maximum, based on the mean maximum 1952–1999 temperature in the late-afternoon. We increased the temperature hourly from the minimum and decreased temperatures from the maximum according to average hourly rates of temperature change observed during the day from the 1952–1999 data. We maintained a given daily mean temperature pattern for a ten-day interval and then reset the pattern to reflect temperatures observed within the next ten-day interval.

Colony maintenance and data collection

Each year of experimentation began with overwintering (“first-generation”) eggs that were laid in mid to late summer of a year, would subsequently overwinter, and hatch in spring of the next calendar year. Eggs were held in small plastic containers and monitored daily in the spring for hatching. Larvae that emerged from hatched eggs were removed and placed in individual small transparent plastic cups and supplied with lupine leaves.

We harvested large, green lupine leaves that were not yet withering, from wild lupines at Indiana Dunes and lupine grown in a greenhouse. All treatments were fed from the same batch of collected or grown leaves on a given day. Since lupine senescens as the summer progresses, lupine quality may have declined for larvae later in the experiment, but equally among treatments. Based on previous Karner blue rearing protocol, we fed adults sex-specific nectar solutions that contained specific concentrations of honey, water, and other nutrients.

Upon pupation, we weighed and placed individuals into containers with an appropriate substrate to aid in proper eclosion positioning. Individuals were monitored daily for signs of pupation marked by the darkening of the pupal

case. Specific success rates, such as hatching, pupation, and eclosion were recorded throughout each generation among treatments. This demographic information is not included within this study, as we focused on development time, egg hatching, degree-day accumulation, body size and mass, and egg output.

Once adults emerged, we recorded eclosion date, adult mass, and sex. Individuals were marked on their wings with identifying information. We took high-resolution photos of left, right and ventral perspectives of each adult. We used an image processing program (ImageJ; Schneider et al. 2012) to measure total wing area, snout-ventral length, thorax-ventral length, and abdominal area in the photographs (length in cm or area in cm²).

We mated adults, avoiding near relatives, to the extent possible, within each temperature treatment group. To enhance likelihood of mating, we temporarily removed adults from environmental chambers and exposed them to natural light and humidity. Mating cages, with males and females, were placed in a greenhouse or outdoor setting with both natural and artificial nectar resources. The mating period was monitored for a fixed period of four hours and each mating pair was recorded within that period. The result eggs would have a unique identification (ID) that included genealogy and experimental treatment information from both parents. To collect eggs, mated females were placed in oviposition cages. We recorded the number of eggs laid by each female. Egg containers were placed in the same temperature treatment as their mother.

We analyzed development and life stage timing from the two years of our experiments. With both years conducted back-to-back, overwintering individuals from Year 1 were kept and bred within their respective treatments. This allowed for complete exposure to one experimental treatment from egg to mating adulthood. Therefore, the two generations are interdependent within treatments in continuation of the experiment from Year 1 to Year 2. We analyzed development and life stage timing using similar methodology from the two years of our experiments. Not every individual in the experiment was tracked to death because excess individuals were returned to the field.

Data analysis

We used growing degree-days (GDD) as a metric to evaluate effects of temperature on development differences among treatments. GDD describe the number of thermal units an organism accumulates between a minimum or maximum temperature, measuring total accumulated degrees (°C) (Damos and Savopoulou-Soultani 2011; Hodgson et al. 2011; Nufio et al. 2010). Accumulation was based on hourly temperatures. We evaluated the temperature and degree-day accumulation at egg hatch and calculated an overall mean for

each of the four treatments (Year 1, first generation only). We calculated the total accumulated degree-days above 12 °C at egg hatching and at eclosion for Year 1 individuals. In Patterson et al. (2020), eggs maintained at a constant 10 °C did not hatch while eggs maintained at 12.2 °C did hatch suggesting that the minimum threshold temperature for accumulating GDD was between those temperatures. Therefore, in this study we used 12 °C as the threshold temperature for calculating GDD.

We examined how emergence and life stage timing differed among temperature treatments and generations using analysis of variance (ANOVA) (R Core Team 2014). These data were used to compare likely timing of Karner blue generations in relation to lupine emergence, flowering, and senescence records derived from a year-long lupine phenology field study completed by Dirig (1994). Linear regressions and analysis of variance (One-Way ANOVA) were calculated with statistical software (Systat 13 (Software, San Jose, CA) and R (R Core Team 2014)). We grouped all generations and treatment data within a year and then performed regression and ANOVA. We performed post hoc pairwise comparisons following one-way ANOVA using Tukey's Honestly Significant Difference (HSD) multiple comparisons' test to evaluate significant differences (F-ratios, p-values < 0.05) among groups.

We examined development rates, degree-day accumulation, body mass, and morphological attributes for male–female differences within each temperature treatment and found none (ANOVA p-value > 0.05) (Bristow 2017). Therefore, we combined male and female data together when examining effects of temperature on these variables. We examined how emergence and life stage timing differed among temperature treatments and generations by plotting the average dates for each life stage by treatment. For predicting adult mass and egg production response variables, we used generalized linear models, including three categorical explanatory variables (temperature, four levels;

generation, three levels; sex, two levels) and two continuous variables (development duration, adult mass). Confidence and prediction interval outputs were used to plot lower and upper 95% confidence levels (LCL and UCL, respectively).

Results

Development time (prediction 1)

Warming treatments accelerated development in both years. Development time (total number of days from egg hatch to eclosion) decreased significantly as treatment temperature increased (Year 1, Fig. 1a; Year 2: Fig. 1b). Individuals in the second generation within each year experienced shorter mean development times compared to those in the first generation (Appendix S1).

Egg hatching and degree-day accumulation (prediction 2)

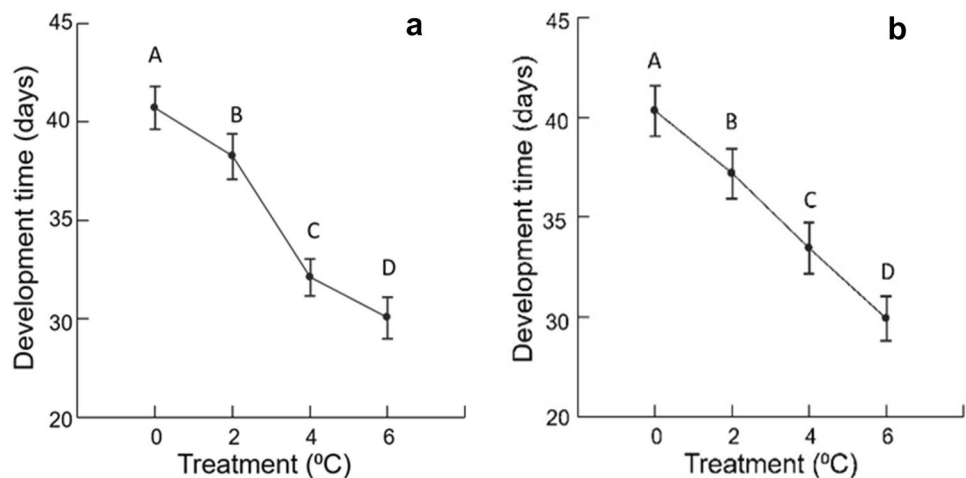
In both years, warmer treatments produced significantly earlier average first generation (spring) egg hatch dates than the +0 °C historic control (Table 1). Mean hatching dates were between 9 and 21 days earlier for +6 °C eggs than for +0 °C eggs in the two years. In Year 1, individuals in the

Table 1 Average spring hatch date by the Karner blue butterfly (*Lycadeides melissa samuelis*) date by year and treatment

Year	Treatment			
	+0	+2	+4	+6
1	April 20 ^A	April 19 ^B	April 9 ^C	March 28 ^D
2	April 24 ^A	April 19 ^B	April 19 ^B	April 15 ^C

Letters indicate treatments that are statistically different (ANOVA p < 0.05) from treatments within that year

Fig. 1 Average development time (days as larvae and pupae) for the Karner blue butterfly (*Lycadeides melissa samuelis*) by treatment and each year (Year 1: **a** Analysis of variance (ANOVA) p < 0.0001, F = 84.7, R² = 0.17, df = 3, n = 1311; Year 2: **b** ANOVA p < 0.0001, F = 54.3, R² = 0.20, df = 3, n = 704). Error bars represent standard deviation. Treatments labeled with different upper-case letters are significantly different from each other based on Tukey's Honest Significant Difference (HSD) multiple comparisons' test (p < 0.05)



warming treatments accumulated significantly more growing degree-days (GDD) above the thermal developmental minimum temperature of 12 °C at egg hatch than did the control (Fig. 2a). Mean temperatures at hatch are within 1–3 °C among treatments (Fig. 2b), but significantly different among most treatments. Accumulated degree-days at eclosion were significantly lower for +0 °C and +2 °C than for the other treatments (Appendix S2). This occurred across generations in both years of study. First-generation individuals accumulated significantly fewer GDD above 12 °C at eclosion than in second and third generations (Appendix S2).

Phenology (prediction 3)

Earlier hatching led to additional generations beyond the typical bivoltine (two generation) life history. All warming treatments (+2 °C, +4 °C, +6 °C) produced a third generation in both years. A partial fourth generation occurred in Year 1 in the +6 °C treatment as larvae, although no larvae

($n_{\text{larvae}} = 5$) pupated in that treatment. In Year 2, there was a fourth generation for the +6 °C treatment only ($n = 41$ fourth generation individuals) that successfully pupated and resulting adult females mated and laid eggs.

Within the historic temperature scenario (+0 °C, Fig. 3a), lupine phenology and availability of lupine host leaves (Dirig 1994) aligns with larval emergence, even in the second generation. Earlier hatch dates and extra generations in the warming treatments (Table 1) extended the total Karner blue generation season (i.e., time from first generation egg hatch to last generation adult emergence). For both Year 1 and Year 2, the +2, +4, and +6 °C treatment larvae individuals experienced an extended summer period, likely beyond the typical lupine growth season (Fig. 3b, c).

Body mass and morphology (prediction 4)

Pupal mass differed significantly among temperature treatments (one-way ANOVA, $F = 4.4$, $R^2 = 0.01$, $df = 3$, $n_{\text{pupae}} = 1157$). Pupal mass differed among generations

Fig. 2 Average degree-day accumulation at hatch for the Karner blue butterfly (*Lycaides melissa samuelis*) by treatment **a** Analysis of variance (ANOVA $p < 0.0001$, $F = 18.7$, $R^2 = 0.11$, $df = 3$, $n = 480$) and average temperature at hatch by treatment **b** ANOVA ($p < 0.0001$, $F = 95.9$, $R^2 = 0.40$, $df = 3$, $n = 479$) for Year 1 individuals. Error bars and uppercase letters follow Fig. 1

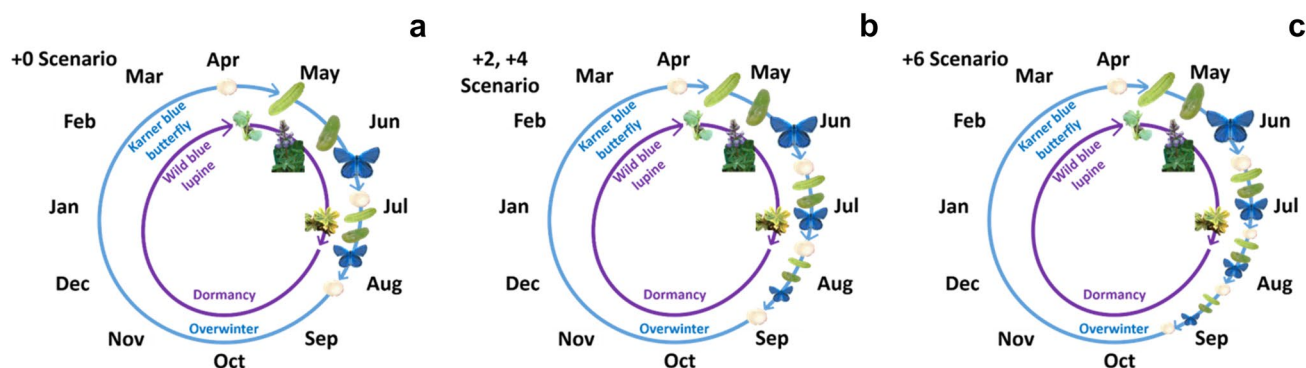
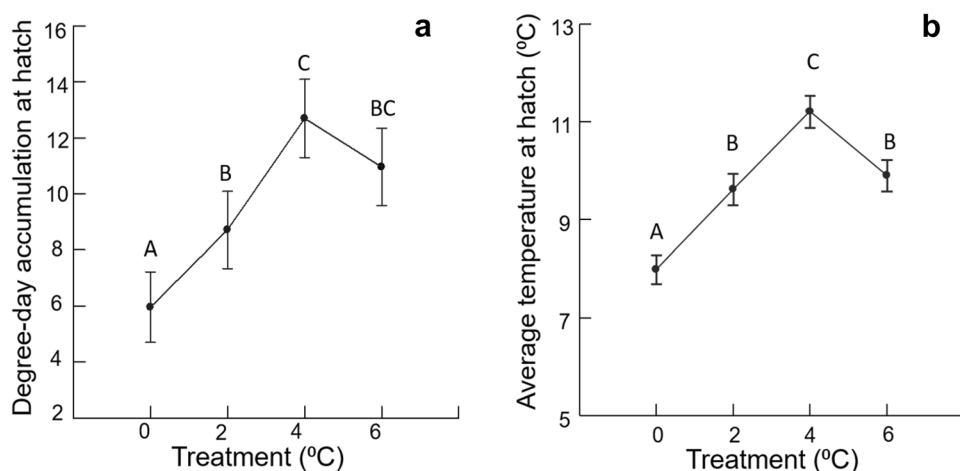


Fig. 3 Timing of each Karner blue butterfly generation in the +0, +2 and +4, and +6 climate change scenarios **a–c** using Year 2 Karner blue butterfly data, in relation to lupine phenology records from Dirig (1994). Each Karner blue butterfly symbol represents the average

date for start of that life stage (egg, larva, pupa, adult; respectively) among treatments. The three symbols for wild lupine (*Lupinus perennis*) correspond to: emergence, flowering, senescence (symbols shown respectively)

Fig. 4 Adult mass (mg) for the Karner blue butterfly (*Lycadeides melissa samuelis*) by treatment in Year 1 (**a** Analysis of variance (ANOVA) $p < 0.0001$, $F = 24.4$, $R^2 = 0.05$, $df = 3$, $n = 1307$), and Adult mass (mg) in Year 2 (**b** ANOVA $p < 0.0001$, $F = 10.1$, $R^2 = 0.04$, $df = 3$, $n = 768$). Error bars and uppercase letters follow Fig. 1

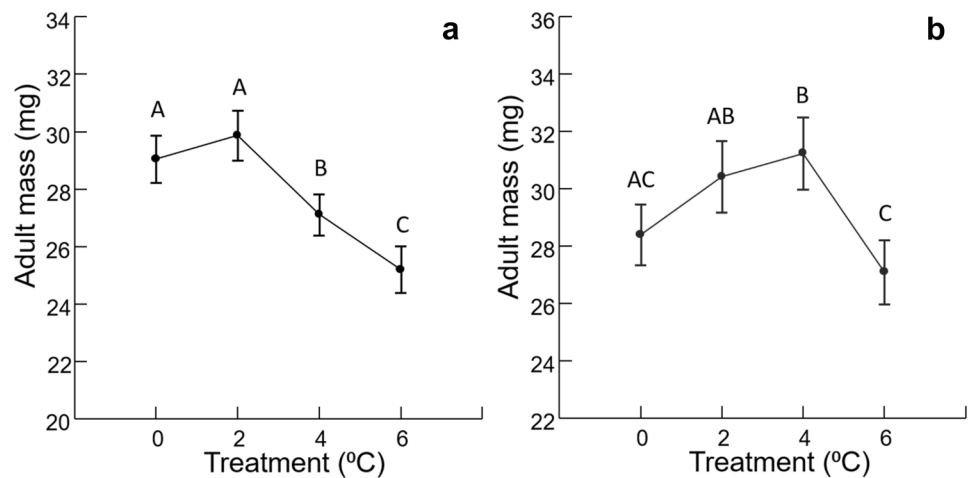
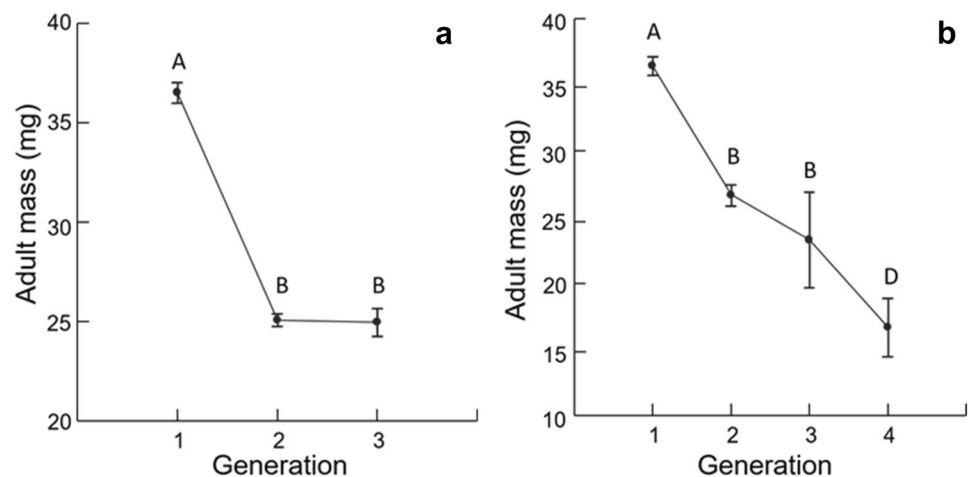


Fig. 5 Adult mass (mg) for the Karner blue butterfly (*Lycadeides melissa samuelis*) by generation for Year 1 (**a** Analysis of variance (ANOVA) $p < 0.0001$, $F = 703.9$, $R^2 = 0.52$, $df = 2$, $n = 1307$), Adult mass (mg) by generation for Year 2 (**b** ANOVA $p < 0.0001$, $F = 10.1$, $R^2 = 0.41$, $df = 3$, $n = 768$). Error bars and uppercase letters follow Fig. 1



($p < 0.0001$, $F = 436.9$, $R^2 = 0.43$, $df = 2$, $n_{\text{pupae}} = 1157$) (Appendix S3). Pupal mass was lower in the warmer treatments and later generations.

In Year 1, adult mass was significantly lower for the +4 °C and +6 °C treatments compared to the control (Fig. 4a). In Year 2, adult mass was significantly lower for the +6 °C treatment compared to the +2 °C and +4 °C treatments (Fig. 4b). In both years, mean adult mass was lowest in the highest temperature treatment, +6 °C. When compared to the first generation, adult mass decreased in the later (and additional) generations in both Year 1 and Year 2 (Fig. 5). Combining all treatments and generations in Year 1, we found that individuals with higher degree-day accumulation from egg hatch to eclosion had lower adult mass (Fig. 6).

As with adult mass, a maximum was reached in adult body size measurements at intermediate treatment temperatures. There were slight increases, not always significant, in mean snout-ventral length, thorax-ventral length, abdominal area, and wing area in the +2 °C and +4 °C treatments compared to +0 °C (Fig. 7a–d). The +6 °C treatment showed

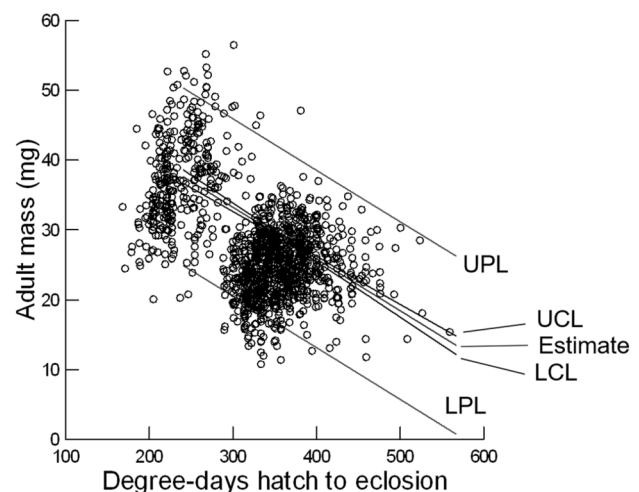


Fig. 6 Adult mass for the Karner blue butterfly (*Lycadeides melissa samuelis*) by degree-day accumulation at eclosion for Year 1 individuals (Linear Regression, $\text{Adult mass} = 48.015 - 0.062 \text{ Degree-Days}$, $F = 471.9$, $p < 0.0001$, $R^2 = 0.27$, $n = 1294$). Lower and upper 95% confidence levels (LCL and UCL, respectively), and lower and upper 95% prediction levels (LPL and UPL respectively)

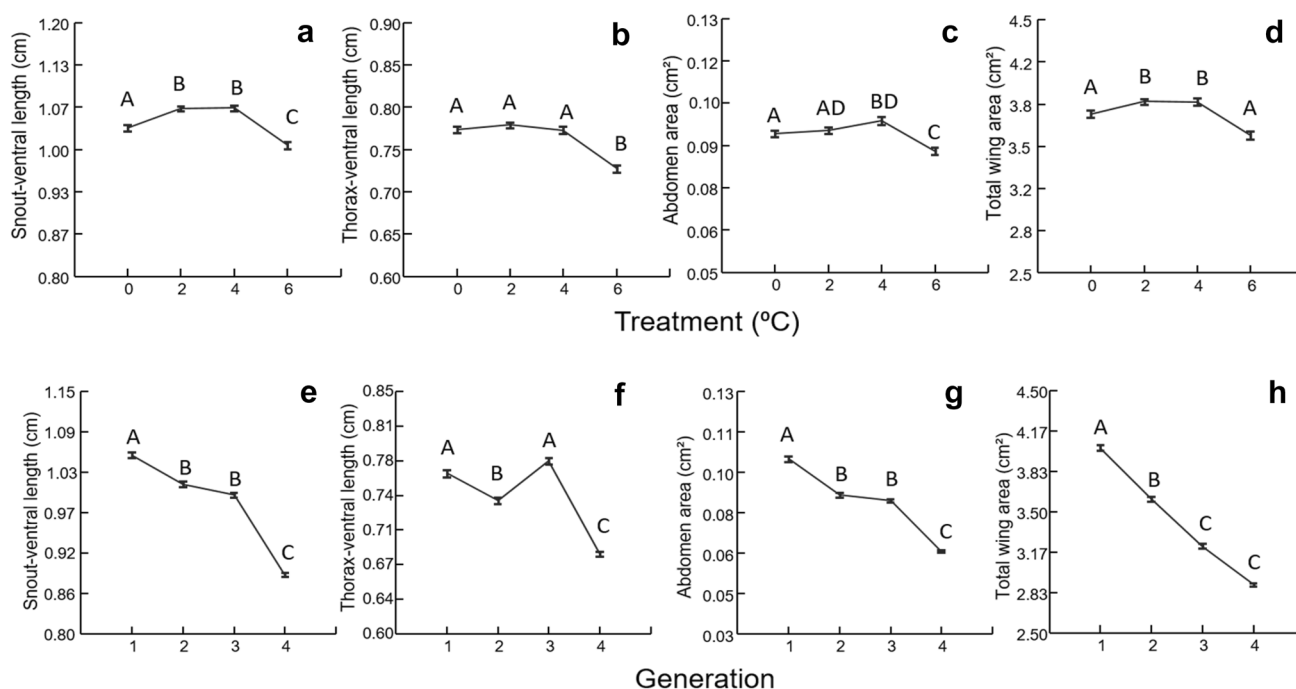


Fig. 7 Body size measurements for the Karner blue butterfly (*Lycaideides melissa samuelis*) by temperature treatment (**a** snout-ventral length, Analysis of variance (ANOVA $p < 0.0001$, $F = 23.10$, $R^2 = 0.09$, $df = 3$; **b** thorax-ventral length, ANOVA $p < 0.0001$, $F = 30.8$, $R^2 = 0.11$, $df = 3$; **c** abdominal area, ANOVA $p < 0.0001$, $F = 11.49$, $R^2 = 0.05$, $df = 3$; **d** total wing area, ANOVA $p < 0.0001$, $F = 11.52$, $R^2 = 0.09$, $df = 3$, $n = 694$), and generation **e** snout-ventral

length, ANOVA $p < 0.0001$, $F = 101.79$, $R^2 = 0.30$, $df = 3$; **f** thorax-ventral length, ANOVA $p < 0.0001$, $F = 60.27$, $R^2 = 0.20$, $df = 3$; **g** abdominal area, ANOVA $p < 0.0001$, $F = 113.92$, $R^2 = 0.32$, $df = 3$; **h** total wing area, ANOVA $p < 0.0001$, $F = 448.10$, $R^2 = 0.63$, $df = 1$, $n = 694$) for Year 2 individuals. Error bars and uppercase letters follow Fig. 1

a significant decrease in body size when compared to the control, except for wing area. There was a statistically significant decline in body size measurements from the first to subsequent generations. Body size measurements for generation four were lower than those of generation two, and generation two was lower than generation one. (Fig. 7 e–h).

Reproduction (prediction 5)

Analysis of covariance of year (2011/2012), temperature treatment (+0 °C, +2 °C, +4 °C, +6 °C), flight (1/2), log(Female Mass) on log(Egg Production Per Female) with all interactions indicated that temperature treatment ($F_{3,257} = 2.93$, $p = 0.034$) and log(Female Mass) ($F_{1,257} = 4.87$, $p = 0.028$) were significant factors and covariates respectively, while other terms and interactions were not significant ($P > 0.05$, $R^2 = 0.09$) (Appendix S4 top). Tukey's post hoc test on temperature treatment indicated that +0 °C had significantly greater egg output (1.86 eggs per female) than +2 °C ($t = 2.74$, $p = 0.034$) (Appendix S4 middle). Appendix S4 (bottom) shows mean ($\pm$ standard deviation) number of eggs per female as a function of temperature treatment and year and flight. Although only +0 °C and +2 °C counts (log transformed) were significantly different overall,

in both flights in Year 2 and in the first flight females in Year 1, mean egg count values generally declined with increased temperature.

When combining females from all treatments and generations within the year, we observed that as female mass increased, the number of eggs produced per female increased (Fig. 8a; Fig. 8b). Adult mass correlation with egg count was statistically significant (Bonferroni-adjusted $p < 0.05$). Additionally, females with larger abdominal area produced more eggs (Fig. 8c).

Discussion

This study investigated effects of temperatures on the life history stages of the Karner blue and how those effects might affect butterfly synchrony with its host plant. Five predictions were tested, and all were supported to some degree across treatments. Results showed that warmer temperatures led to faster development, earlier egg hatching, and smaller adult body mass. However, warming tended to increase the number of degree-days accumulated during development, indicating that Karner blues developed in fewer days by putting on less mass as temperatures increased. High

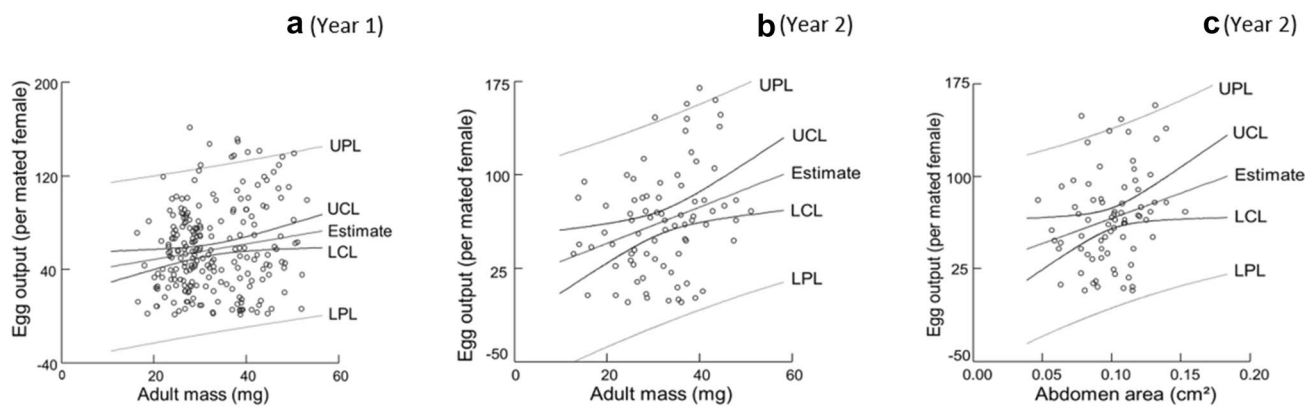


Fig. 8 Egg output per mated Karner blue butterfly (*Lycadeides melissa samuelis*) female plotted against their corresponding adult mass for Year 1 (**a** Linear Regression $p=0.02$, $F=5.05$, $r=0.15$, $R^2=0.02$, $df=1$, $n=225$) and Year 2 (**b** Linear Regression $p=0.0078$, $F=7.45$, $r=0.31$, $R^2=0.08$, $df=1$, $n=79$). Number of

eggs laid plotted with female abdominal area for Year 2 individuals only (**c** Analysis of variance (ANOVA) $p=0.03$, $F=4.424$, $df=1$, $r=0.26$, $R^2=0.06$, $n=74$). Lower and upper 95% confidence levels (LCL and UCL, respectively), and lower and upper 95% prediction levels (LPL and UPL respectively)

temperatures had negative impacts on larval development, leading to a shorter development period and decreased body mass accumulation in the Karner blue. Additionally, the adverse effects of high temperatures resulted in lighter females that produced a reduced number of eggs. Further, increased temperatures led to more generations, and additional generations led to smaller Karner blues. If the Karner blue has an upper thermal threshold for growth, high temperatures may impede optimal development and adult body mass. Smaller females produced significantly fewer eggs, as has been observed in other Lepidoptera (Buckley 2022; Diamond and Martin 2020; Clifford and Boerger 1974; Hough and Pimentel 1978; Tyndale-Biscoe and Hughes 1969; Kerr et al. 2020; Van Dyck et al. 2015; Yang et al. 2021).

Extra generations arising from the warming treatments, beyond the two nominal generations per year, may produce larvae after the host plant senesces or dies for the year, increasing larval mortality. With high mortality in the final generation, the number of offspring that hatch the following season would subsequently decrease (Cayton et al. 2015). These trends have been documented in other Lepidoptera (Huey and Kingsolver 1993; Kingsolver and Huey 2008; Diamond et al. 2014; Miller-Rushing et al. 2010). If this phenomenon continued over several years, reduced per capita fecundity could decrease population size. On the other hand, additional generations could allow for increased reproductive output, and population sizes might grow larger than a two-generation situation (Abrams et al. 1996). However, lupine survival late into the summer when those additional generations would occur is limited. Regardless of how the risks or benefits from extra voltinism counteract each other, having fewer individuals in additional generations may decrease genetic diversity and thus overall population fitness (Van Asch et al. 2007).

Many of the observed trends in response to increasing temperatures can have demographic consequences that are maladaptive. For example, earlier egg hatching can result in phenological mismatches with larval host plants, potentially leading to reduced fitness (Patterson et al. 2020). Additionally, if extra generations occur beyond the nominal two per year, larvae may be present after most host plants have senesced, further reducing the fitness of the population. Furthermore, females experiencing higher temperatures exhibited decreased body mass, which is positively correlated with egg production, suggesting lowered fecundity (Patterson et al. 2020). The perennial host plant of the Karner blue typically emerges in early spring, likely before eggs hatch, ensuring food availability for subsequent larvae. However, if the rate of advancement in the timing of spring egg hatching with rising temperatures is faster than for lupine emergence, the response to increased temperatures in the first generation may be maladaptive or overly sensitive to changes in temperature. Advanced spring egg hatching was observed in the final stages of Karner blue extinction at Indiana Dunes (Patterson et al. 2020; Ault et al. 2013).

Assumptions and future research

This study examined responses to warming in the Karner blue. Additional study on larval host plants is justified because warming could affect temporal variations in lupine quality or quantity and thereby affect larval survival. In contrast, any nectar-mediated impact of climate change on adults is likely to occur across the entire flower community or several dominant nectar species and thus may have more distributed or moderated effects. Whether the Karner blue and its hostplant have the adaptive capacity to resynchronize under such temperature related changes

in developmental timing of each species is not clear but worthy of study (Thurman et al. 2020a, b). Determining whether selective pressures on developmental timing created by climate change might eventually result in evolutionary rescue, or butterfly-hostplant synchronization over a wider range of climatic conditions could help guide conservation efforts (Carlson et al. 2014). Lastly, Fuller (2008) conducted a comprehensive analysis of the Karner blue life history tables, concluding that egg survivorship plays a predominant role in Karner blue demography. Further research could better predict the direction and magnitude of population change related to extra broods resulting from increased temperatures.

Management implications for the Karner blue butterfly

This study comprises a series of laboratory experiments that are linked across various life stages and our results offer insights into how individual-level responses may scale up to the population level. Specifically, land managers could develop strategies to decrease exposure and sensitivity to climate change while enhancing adaptive capacity; several techniques for this are suggested by our studies. New management strategies could address these challenges (Schuurman et al. 2022). Creating a more diverse genetic and abundance base from which evolutionary rescue might operate during selection during extreme weather years might be one such novel approach.

Some processes suggested in laboratory experiments may be playing out in Karner blue populations already. Specifically, microclimatic variation has previously been identified as critical for enabling suitable timing of insect and host plant development for the Karner blue (Grundel and Pavlovic 2007; Grundel et al. 1998a, b; Lane 1999; Maxwell 1998), and the experiments in this study suggest that warming may generate additional generations that will need suitable host plants. Yet, phenological matching has been underappreciated in many herbaceous insects due to our limited understanding of the factors that aligning these critical interactions (Kharouba et al. 2018; Lindén 2018). Even in the Karner blue, past management actions to create a range of microclimates by manipulating canopy cover may not have been sufficiently aggressive to address mismatches that appear to occur between the emergence of host plants and early egg hatching in warm spring conditions or hot, dry summer conditions (Patterson et al. 2020). New management approaches to creating microclimatic diversity based on how existing microclimatic variation at Indiana Dunes failed to provide refugia for lupine during especially dry, hot years may provide insight (Woods et al. 2015).

Generalizing to other species

This study examines multiple life history processes that might combine to determine the Karner blue response to climate change at different spatial scales. Process-based modeling is one approach for understanding responses to climate change and is contrasted to niche-based approaches that are frequently used to understand broadly, but less mechanistically, a species' response to climate change (Morin and Thuiller 2009). These approaches can be complementary, so it is generally useful to undertake both types of studies to describe response to climate change, regardless of species. Our evolving understanding of the extinction risk the Karner blue faces benefits from undertaking both more statistical, less mechanistic, evaluations of climate threats (e.g., Li 2020) and more mechanistic studies that examine constraints on multiple life stages (e.g., Fuller 2008).

Numerous studies have shown that endemic or specialized insect species are particularly vulnerable to population declines associated with climate change and habitat loss (Cornelissen 2011; Nooten et al. 2014; Villalpando et al. 2009). The Karner blue exhibits traits, such as limited diet breadth and dispersal ability, that it shares with many other members of the butterfly family *Lycenidae* (Thurman et al. 2022) and that contributes to frequent endangerment. These traits can contribute to limited climatic niche breadth across this family (Thurman et al. 2020a, b). Therefore, we might expect some of the same life history stage responses to climate change in other members of this butterfly family that we documented here for the Karner blue. Implementing adaptive conservation strategies can enhance population resilience and resistance to environmental change across such similar species (Poiani et al. 2001; McNeely et al. 2005; Lindenmayer et al. 2007).

To ensure effective conservation, it is essential to evaluate vulnerabilities, devise strategies to mitigate them, and allocate conservation efforts accordingly (Foden et al. 2013; Fischlin et al. 2007; Harris et al. 2006; Liebesman and Peterson 2009; Parmesan and Yohe 2003). The dynamic nature of ecological communities under global change necessitates a comprehensive assessment of vulnerabilities and the implementation of management strategies to ensure the persistence of species within the landscape (Sgrò et al. 2011). Additionally, considering the urgency of the situation, it may be necessary to prioritize conservation efforts for species impacted by climate change, even if they are not currently in immediate danger of extinction (Parmesan and Yohe 2003; Kareiva and Marvier 2011; Sax 2013).

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Data availability The datasets generated during and/or analyzed during the current study are available in the U.S. Geological Survey repository, <https://doi.org/10.5066/P967LATZ>.

Declarations

Competing interests The authors have no competing interests, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

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