

Warming affects hatching time and early season survival of eastern tent caterpillars

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Received: 4 December 2014 / Accepted: 3 June 2015 / Published online: 21 June 2015
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Abstract Climate change is disrupting species interactions by altering the timing of phenological events such as budburst for plants and hatching for insects. We combined field observations with laboratory manipulations to investigate the consequences of climate warming on the phenology and performance of the eastern tent caterpillar (*Malacosoma americanum*). We evaluated the effects of warmer winter and spring regimes on caterpillar hatching patterns and starvation endurance, traits likely to be under selection in populations experiencing phenological asynchrony, using individuals from two different populations (Washington, DC, and Roswell, GA). We also quantified the proximate and extended fitness effects of early food deprivation and recorded spring phenology of local caterpillars and their host plants. In addition, we conducted laboratory assays to determine if caterpillars are using plant chemical cues to fine-tune their hatching times. Warmer winter temperatures induced earlier hatching and caterpillars from GA survived starvation for periods that were 30 % longer than caterpillars from DC. Warmer spring regimes reduced the starvation endurance of caterpillars overwintering in the wild but not in the laboratory. Early starvation dramatically reduced hatchling survival; however, surviving caterpillars did not show detrimental effects on pupal mass or development time. In the field, hatching preceded budburst in both 2013 and 2014 and the period of optimal foliage quality was 2 weeks shorter in 2013. Hatching time was unaffected

by exposure to plant volatiles. Overall, we found that warmer temperatures can trigger late-season asynchrony by accelerating plant phenology and caterpillars from different populations exhibit differential abilities to cope with environmental unreliability.

Keywords Starvation endurance · Synchrony · Phenology · *Prunus serotina* · *Malacosoma americanum*

Introduction

Spring in temperate ecosystems is the time for numerous species to resume development and begin a new season of resource acquisition. The transition between winter and spring is often characterized by irregular periods with warm episodes followed by late storms and cold snaps. Therefore, spring biota is often faced with a developmental tradeoff in which species can delay development and avoid frost risk or advance it and maximize resource exploitation (Leinonen and Hänninen 2002). Consumers face a further challenge since they need not only to synchronize their life cycle with favorable weather conditions but also with the availability of food resources such as pollen, foliage or prey/hosts (Stenseth and Mysterud 2002; Yang and Rudolf 2010). Consistent with these predictions, temperate spring herbivores have been shown to exhibit higher temporal variation in population densities than species feeding later in the season (Forkner et al. 2008).

Spring weather is being significantly altered by recent climate change (Schwartz et al. 2013), resulting in phenological changes that are particularly pronounced in temperate ecosystems (Miller-Rushing and Primack 2008; Primack et al. 2009). For example, Ellwood et al. (2013) documented record early flowering times for 27 plant

Communicated by Julia Koricheva.

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species in 2010 and 2012 in North America. One species, the highbush blueberry, *Vaccinium corymbosum*, flowered 6 weeks earlier than in the mid-1800s. These phenological alterations in response to warmer temperature regimes are occurring across diverse taxa, including vertebrates, invertebrates, woody plants and herbs (Walther et al. 2002; Parmesan and Yohe 2003; Gordo and Sanz 2006; Laube et al. 2014). Because the magnitude of phenological responses to warmer temperatures varies among regions and taxonomic groups (Parmesan 2007), these phenological changes are affecting communities (Forrest et al. 2010) and disrupting multispecies interactions (Visser and Both 2005). Environmental factors such as temperature may act as physiological restrictions, directly controlling the timing of phenological events, and/or as cues that set the organisms' biological clock (Gwinner 1996; Ausin et al. 2005). Most insect species time their life cycle events using a combination of temperature and photoperiod (Tauber et al. 1986); however, the relative importance of different environmental factors and the specific physiological processes regulating phenology remain unexplored for most taxa (Forrest and Miller-Rushing 2010).

Temperature sensitivity often differs among trophic levels (Voigt et al. 2003; Berggren et al. 2009) and insects usually exhibit stronger responses than plants to climate change (Gordo and Sanz 2005; Parmesan 2007), most likely because their metabolism is more sensitive to increases in temperature (Bale et al. 2002; Berggren et al. 2009). Rising winter temperatures have been shown to increase herbivore overwintering survival in non-diapausing herbivores (Bale et al. 2002; Battisti et al. 2005). However, augmented metabolic activity induced by warmer winter temperatures can lead to the depletion of energy reserves in diapausing organisms, resulting in lower fecundity and higher overwintering mortality (Irwin et al. 2003), as has been shown for monarch butterflies (Brower et al. 2009), goldenrod gall flies (Irwin et al. 2003), and woodland ringlet butterflies (Brower et al. 2009; Stuhldreher et al. 2014). This energy depletion during the winter may affect the ability of herbivores to tolerate phenological mismatches once they reach the energetically demanding feeding stage.

Phenological mismatches, such as larvae hatching before the budburst of their host plants, are expected to have the most severe detrimental effects on specialists that exploit ephemeral resources because when mismatches occur, these consumers lack other feeding options (Bale et al. 2002). Similarly, species that experience phenological constraints both early and late in development are likely to be particularly vulnerable, because either an advance or a delay relative to their associated host plant(s) can adversely affect fitness (Singer and Parmesan 2010). For example, larvae of the winter moth (*Operophtera brumata*) successfully feed only on newly expanding foliage of oaks,

performing poorly on both unopened hard buds and on mature leaves, so their fitness decreases dramatically when they miss the optimal period of leaf expansion (Feeny 1970). In this species, asynchrony occurred stochastically under pre-warming conditions, but warmer springs are increasing the frequency of caterpillar mortality because climate change is further disrupting the synchrony of winter moths and their host plants (Visser and Holleman 2001). In the face of these temporal constraints, many spring herbivores have evolved a measure of tolerance to starvation enabling them to survive even when hatching occurs well in advance of foliage availability. This is the case with the oak processionary caterpillar, *Thaumetopoea processionea*. Larvae of this species feed on the buds of *Quercus robur* and can endure starvation for up to 3 weeks while searching for edible buds (Wagenhoff et al. 2013). Similarly, a recent study found that colonies of the western tent caterpillar (*Malacosoma californicum pluviale*) hatching in advance of their host plant budburst tolerated starvation for about 3 weeks without showing negative effects on final colony size (Kharouba et al. 2015).

Spring temperature, through its effects on herbivore survival and plant–herbivore synchrony, is an important factor influencing the temporal course of defoliator outbreaks in temperate ecosystems (Fitzgerald 1995; Weed et al. 2013). While an increased temporal variability in local spring weather (e.g., late winter storms, cold snaps, and wide temperature fluctuations) is generally predicted to increase under many climate change scenarios (IPCC 2014), it is difficult to predict how these changes will influence forest herbivores (and amounts of herbivory) more generally (Schwartzberg et al. 2014; Jamieson et al. 2014; Dukes et al. 2009; Rodenhouse et al. 2009). Forest defoliation during insect outbreak periods has severe effects on tree growth and mortality, affecting habitat heterogeneity, nutrient cycling and ultimately ecosystem function (Yang 2012). Climate change has been documented to exacerbate the onset of pine beetle outbreaks through enhanced winter survival and development rates (reviewed in Weed et al. 2013); however, for many forest species, there is still uncertainty whether climate change will reduce or increase the incidence of outbreaks (Klapwijk et al. 2012). Some of this uncertainty stems from the observation that geographically widespread populations vary markedly in the magnitude of annual variation in 'spring' conditions they experience and to which they are therefore locally adapted; investigations that explore among-population variation in responses to climate change are clearly necessary to advance, model and predict its effects on species interactions.

Here, we integrated phenology observations in the field with warming manipulations in the laboratory to evaluate the effects of warmer temperature regimes on the performance of a widespread forest herbivore, the eastern tent

caterpillar (*Malacosoma americanum*). In addition, we assessed their tolerance to phenological mismatches with their main food plant, black cherry (*Prunus serotina*). The distribution of *M. americanum* extends from northern Florida to southern Canada (Fitzgerald 1995), so widespread populations experience very different environmental conditions. As a species, *M. americanum* tolerates a variety of winter and spring temperature regimes; however, specific populations are unlikely to express the full range of climatic tolerance. To test if distant populations differ in their seasonality-related responses, we collected *M. americanum* egg masses from two distinct localities in the USA—Washington, DC, and Roswell, GA (ca. 870 km apart)—and compared their responses under altered winter and spring temperature regimes. We expected warmer conditions to increase hatchling survival (particularly for the southern population) and to accelerate caterpillar metabolism, resulting in advanced hatching time and a reduction of larval starvation endurance due to faster depletion of energy reserves.

Using growth chambers, we manipulated late winter and spring temperature conditions to evaluate the effects of warming on winter survival, hatching phenology and starvation endurance of caterpillars from both DC and GA. In addition, we evaluated the long-term effects of hatchling starvation on two fitness correlates: insect development time and pupal mass. Finally, we followed early season phenology of *P. serotina* and *M. americanum* under ambient conditions in Washington, DC to document the current relative timing of caterpillar hatching and foliage development. Given the high levels of synchrony between *M. americanum* hatching and *P. serotina* budburst that have been recorded in the past, it has been suggested that caterpillars inside their eggs could be utilizing plant volatile cues to fine-tune hatching when foliage is available (Fitzgerald 1995); here, we experimentally tested that hypothesis.

Materials and methods

Study system

Eastern tent caterpillars are a common and widespread forest herbivore that inhabits much of the central and eastern USA. Their populations fluctuate widely among years, alternating between outbreak and low density years (Fitzgerald 1995). Eggs of *M. americanum* hatch early in the spring, around the time of budburst of their most common host, black cherry (*Prunus serotina*). Larvae feed gregariously on the expanding foliage; they are central place foragers, and colonies build and inhabit silken tents, which provide shelter from some predators and a site for thermoregulation (Fitzgerald 1995). Last instar larvae leave the

tents to disperse and pupate. Adults emerge and mate at the beginning of the summer. Females deposit all of their eggs in a single egg mass shortly after mating and embryonic development proceeds rapidly. In mid-summer, pharate larvae (fully developed caterpillars that remain inside the egg) enter summer diapause and remain dormant inside their eggs until the following spring. A protective coating about 0.5 mm thick of a substance called spumaline covers the egg masses and allows them to regulate moisture levels. A period of exposure to cold temperatures is required for diapause termination and pharate larvae that fail to experience this period do not hatch (Fitzgerald 1995). Heat accumulation is the main predictor of *M. americanum* hatching time (Neal et al. 1997), and caterpillars typically hatch a few days before or after budburst of the particular tree they were laid on (Neal et al. 1997; Fitzgerald 1995). There is a strong selective pressure to synchronize hatching time with host plant budburst because caterpillars hatching too early are likely to face harsh spring conditions and the risk of starvation, while caterpillars hatching too late cannot complete development due to declining leaf quality (fully hardened leaves are poor quality; Fitzgerald 1995). Synchrony between caterpillar hatching and host plant budburst could be a major factor affecting *M. americanum* populations, which are predicted to grow when in synchrony and collapse under asynchrony (Fitzgerald 1995); however, other factors such as direct effects of weather and diseases also contribute to population fluctuations (Fitzgerald 1995).

Effects of source population and temperatures on caterpillar performance

To assess the effects of winter and spring temperature regimes on caterpillar survival, hatching phenology and starvation endurance, we subjected egg masses from Roswell, Georgia (34.0339°N, 84.3442°W, $n = 15$; GA, hereafter) and from Washington, DC (38.9047°N, 77.0164°W, $n = 17$; DC, hereafter) to controlled winter and spring temperature conditions using growth chambers (Model I36VLC8; Percival, IA, USA). Both populations occur in the central region of *M. americanum*'s range and experience similar photoperiods, but winter and spring temperatures are slightly lower in DC than GA (Table 1). We collected GA egg masses in late November 2013 and transported them back to DC on November 25th.

All egg masses included in this experiment overwintered for 12 weeks at 3 °C to meet diapause termination requirements. Following incubation, each egg mass was split longitudinally and assigned to each of two winter treatments: cold winter (3 °C day/3 °C night) or warm winter (6 °C day/6 °C night) for a period of 4 weeks. After that, we exposed all egg masses to a common spring regime (17 °C day/10 °C night) to stimulate caterpillar hatching.

Table 1 Normal winter and spring temperatures (minimum, average and maximum) and amount of light (in days) that each locality accumulates over the season

Locality	Winter (°C) (min, ave, max)	Spring (°C) (min, ave, max)	Seasonal light sum (days) (spring, summer, fall, winter)
Roswell, GA	−0.8, 4.94, 10.67	7.88, 14.39, 20.89	52.6, 52.4, 40.3, 40.4
Washington, DC	−1.94, 3.17, 8.22	7.5, 13.44, 19.3	53.7, 53.5, 39.3, 39.4

Data are taken from NOAA weather stations located at Alpharetta 4 SSW, GA, and the U.S. National Arboretum, DC. To calculate seasonal light availability, we summed the hours of light experienced in each locality during each season (spring: March 21–June 21; summer: June 22–September 22; fall: September 23–December 21; winter: December 22–March 20) using data from 2012

Table 2 Temperature regimes experienced by eastern tent caterpillar (*Malacosoma americanum*) colonies under controlled winter and spring conditions

Treatment	Diapause (12 weeks)	Latency (4 weeks)	Hatch (~1 w)	Starvation
Cold cold	3 °C/3 °C day/night	3 °C/3 °C day/night	17 °C/10 °C day/night	17 °C/10 °C
Cold warm				21 °C/10 °C
Warm cold		6 °C/6 °C day/night		17 °C/10 °C
Warm warm				21 °C/10 °C

We performed egg mass inspections daily and collected all hatchlings, assigning half of them to each of two treatments: cold spring (17 °C day/10 °C night) or warm spring (21 °C day/10 °C night). This fully crossed design allowed us to control for genotype in all four treatments and to distinguish between the effects of winter vs. spring temperature conditions (Table 2). We adjusted the chamber's photoperiod systematically to simulate the ambient light increments for DC. These were the same for all treatments and ranged from 10:40 h/day of light during the winter to 12:50 h/day of light in April, at the end of the experiment. Georgia photoperiod was not simulated separately because it is very similar to DC for this time period (DC = 1767.283 h of light, GA = 1797.3 h, a difference of only 1.67 %). We expected caterpillars in the warm winter, warm spring combination to exhibit the lowest levels of starvation endurance due to early depletion of metabolic energy reserves.

We recorded the number of caterpillars hatching daily and transferred all hatchlings to Petri dishes (one dish per egg mass per treatment, $n_{GA} = 60$, $n_{DC} = 80$) with moist filter paper to evaluate their starvation endurance (days to die of starvation without water deprivation). A caterpillar was considered dead when it did not move after being gently prodded with a paintbrush. All Petri dishes were surveyed daily and we calculated the date to median hatch (when 50 % of the caterpillars hatched), the date to median death (when 50 % of the caterpillars had died) and the median life interval (days between median hatch and median death) for each Petri dish. Eastern tent caterpillars form colonies and hatchlings kept in isolation die prematurely and do not feed. Because we could not distinguish among individual caterpillars kept together, and siblings hatch over a number of days, we measured starvation endurance at the colony level, instead of calculating the mean of individual life spans.

We compared winter survival (total caterpillars hatching/egg mass) among populations and treatments using a fixed effects ANOVA, with population and winter regime (cold vs. warm) as predictor variables. To compare cumulative degree-days (base 6 °C) required to reach median hatch between treatments and populations we used a Kruskal–Wallis test followed by pairwise comparisons (Wilcoxon rank sum test) with Bonferroni-adjusted P values. To investigate the effect of source population, winter (pre-hatching) and spring (post-hatching) temperatures on the ability of caterpillars to endure starvation, we compared the median life interval among treatments and populations using fixed effects ANOVA.

Because egg mass size is an important maternal effect that could influence larval energy reserves and therefore affect caterpillar starvation endurance, we measured the length of all egg masses before splitting them and without removing the spumaline. After caterpillars finished hatching, we took pictures of the egg masses using a stereoscopic microscope (Nikon SMZ18; software: NIS-Elements 4.3, 2014) to count all the hatched and unhatched eggs. We compared egg mass length, total eggs and the proportion of hatched eggs between populations using Wilcoxon rank-sum tests, because data did not meet assumptions of parametric tests. To explore the relationships between egg mass length and total eggs, as well as egg mass length and the proportion of hatched eggs we used linear regressions.

Effect of post-hatching temperature regime on caterpillar performance

Egg masses overwintering in the field experience different temperature and humidity conditions than those kept in growth chambers in the laboratory. Therefore, to gain

insight into the hatching success and starvation endurance of naturally occurring egg masses, we exposed 11 DC egg masses to ambient temperatures on black cherry trees in a common garden at The George Washington University. When caterpillars started hatching, we transferred the egg mass to a growth chamber (17 °C day/10 °C night) and then we transferred hatchlings to Petri dishes as described above, assigning half of the caterpillars to the warm spring regime (21 °C day/10 °C night) and the other half to the cold spring regime (17 °C day/10 °C night). We monitored all caterpillars daily and calculated the median life interval as described above. We used a Wilcoxon rank sum test to compare median life interval between spring temperature treatments.

Long-term effects of early starvation

To investigate if hatchlings surviving starvation exhibit long-lasting detrimental effects, we starved caterpillars for periods of 2–10 days, in 1-day increments. We assigned groups of 10 caterpillars taken from three different egg masses to each treatment (3 replicates \times 10 caterpillars \times 9 treatments) for a total of 270 caterpillars. All individuals included in this assay overwintered at 3 °C for 14 weeks. Caterpillars hatched under a 17 °C day/10 °C night regime (cool spring temperatures) and were kept at room temperature (\sim 23 °C) during the starvation and rearing period. Surviving caterpillars were placed directly on top of expanding foliage of black cherry trees at the end of their assigned starvation period and regularly fed until pupation. We recorded caterpillar survival to second instar, fifth instar, and emergence, as well as pupal mass using an analytical balance (Mettler Toledo, Switzerland). We recorded feeding development time (days from first feeding to adult moth emergence) and used linear regression to analyze the effects of starvation period length on survival and pupal mass. Males and females are highly dimorphic, so we separated sexes for pupal mass analyses. All statistical analyses were performed using R (R Core Team 2013).

Relative timing of caterpillar and foliage spring development

To examine natural variation in *M. americanum* and *P. serotina* spring phenology, we monitored pairs of egg masses and trees in Rock Creek Park, Washington, DC (38.9575°N, 77.0450°W) during the springs of 2013 and 2014. Most egg masses (12 out of 15 in 2013 and 7 out of 16 in 2014) were initially laid on the same large tree. Since colonies inhabiting the same tree are likely to merge after hatching, we relocated surplus egg masses to neighboring trees (less than a mile away) on March 2, 2013 and on March 10, 2014 (prior to hatching). Having only one

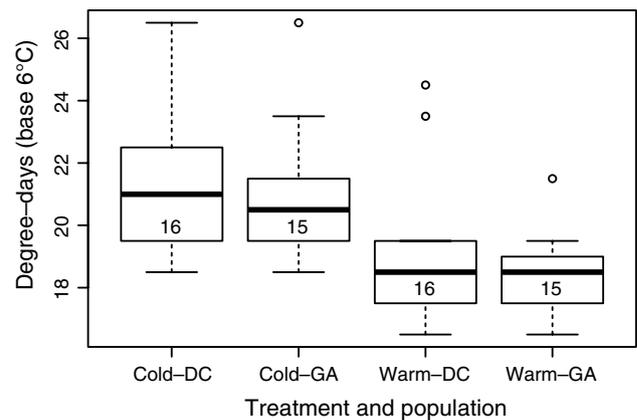


Fig. 1 Degree-days (base 6 °C) accumulated to the time of median hatch of eastern tent caterpillar (*Malacosoma americanum*) egg mass halves from DC and GA under cold and warm overwintering conditions ($n_{DC} = 16$, $n_{GA} = 15$ halves per treatment). Numbers in boxes indicate sample size

egg mass per tree allowed us to monitor each colony individually. We visited all trees biweekly during the onset of spring (throughout March) and weekly afterwards (April–May). For black cherry trees, we recognized the following phenological stages: closed buds (not edible for caterpillars), elongating buds (edible); expanding foliage (including open buds and new leaves), maturing foliage (when at least one leaf of the tree was hardened) and mature foliage (when at least 90 % of the leaves of a tree were hardened). For *M. americanum*, we recorded the presence of: hatchlings, a tent, feeding stage caterpillars (instars 1–5) and wandering individuals (5th instar caterpillars that stop feeding and disperse to pupate). Caterpillar development rates vary within colonies and some individuals linger after most of the colony wanders off to pupate; because these individuals are often parasitized or fail to pupate, we considered a colony to have completed the feeding stage when the majority of its caterpillars had reached the wandering stage.

We used data available through NOAA from a nearby weather station (Washington National Airport; 38.848°N, 77.034°W) to calculate mean spring temperatures using the daily minimum and maximum records corresponding to January 1 to March 21 for both 2013 and 2014. We also computed degree-day accumulation for both years using two different developmental thresholds (4 and 9 °C) starting on January 1, using BizEE (degree days.net) and climate data from weather station KADW, Andrews Airforce Base, MD. Neal et al. (1997) reported 9.1 °C as the developmental threshold temperature for eastern tent caterpillars; however, our data suggest that caterpillar development can proceed at lower temperatures (Fig. 1), so we included both thresholds (4 and 9 °C) to provide a visualization of spring temperatures likely to be relevant for this species.

Table 3 ANOVA table showing the effects of population, winter and spring temperature regimes on starvation endurance (median life interval duration)

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i> value	<i>P</i>
Spring temperature	1	0.99	0.99	0.1107	0.7401
Winter temperature	1	16.81	16.81	1.8834	0.1730
Population	1	339.59	339.59	38.0465	<0.0001*
Residuals	100	892.57	8.93		

* $P < 0.0001$

We calculated asynchrony indexes for each tree-caterpillar pair following the methods of Van Asch and Visser (2007), measuring the degree to which hatching occurred in synchrony with bud swelling. We calculated this index according to bud elongation and not budburst because caterpillars can feed on green swollen buds: $Q_n = H_n - B_n$, where H_n = hatching time of the n th egg mass and B_n = bud swelling time of the n th tree (at least one swollen bud per tree). We also calculated Q_i which indicates the synchrony levels that would have occurred if the egg masses had remained on their original tree (without being relocated); to calculate this index, we used the bud swelling dates of the trees on which each egg mass was originally laid. Q values correspond to the number of days between events, so positive numbers indicate that hatching occurred when foliage was available. We used Wilcoxon Mann–Whitney rank sum tests (R Package coin; Hothorn et al. 2006) to compare Q versus Q_i , for each year and Q between years.

The role of foliage cues for caterpillar hatching

To test Fitzgerald's hypothesis (1995) that caterpillars may be using foliage cues to fine-tune hatching time, we compared the hatching patterns of eggs exposed versus not exposed to black cherry expanding foliage. To control for genetic differences in hatching patterns, we split egg masses longitudinally and assigned one half to each treatment. To control for the possibility that black cherry branches might also emit signaling chemicals, we used two controls: no stimulus and a bare twig. Therefore, we performed two paired assays, one for each control type. Other studies have successfully used severed twigs to evaluate insect responses to plant volatiles (Witzgall et al. 2005), and it has been shown that severing branches stimulates their emission of organic volatile compounds (Vuorinen et al. 2005). For this experiment, we used laboratory-reared egg masses from the DC area that overwintered at standard temperatures (14 weeks at 3 °C). After overwintering, the surfaces of all egg masses were sterilized to prevent infection by dipping them in a 5 % hypochlorite solution and rinsing them thoroughly with tap water (as recommended

in Fitzgerald 1995). Following sterilization, we split the egg masses longitudinally and assigned them to their respective treatments (control vs. +volatile cues). We placed all halves in Petri dishes with moist filter paper in a growth chamber set to 17 °C day/10 °C night temperature regime. Each Petri dish was placed inside a sealed transparent storage bag to prevent airflow among treatments. In the first assay, control dishes included just the egg mass and a piece of filter paper (control 1) while in the second assay they included filter paper plus a dead twig of black cherry (control 2). In both assays, the experimental treatment (+volatiles) included a freshly excised twig bearing an expanding bud. To ensure foliage freshness, we wrapped the cut end of each fresh twig with a moist cotton ball and replaced them with freshly cut twigs every few days. The initial sample size was 22 and 21 pairs, respectively, but we excluded from the analyses those egg masses with less than ten caterpillars hatching per treatment, and those that were split unevenly. For each Petri dish (egg mass half), we compared time to median hatch (days from the onset of spring conditions to the day when 50 % of the caterpillars hatched) and the hatching period length (number of days between first and last hatch). Median hatch data from the first assay (+volatiles vs. control 1, $n = 12$ pairs) met normality assumptions and were analyzed using a paired t test. Median hatch data from the second assay (+volatiles vs. control 2, $n = 12$ pairs) did not meet normality assumptions, so treatments were compared using an exact Wilcoxon Mann–Whitney rank sum test (Hothorn et al. 2006). We used paired t tests to compare hatching period lengths between treatments for both assays.

Results

Effect of source population and temperatures on caterpillar performance

The total number of caterpillars hatching per egg mass did not vary among temperature regimes or source populations (overall model $F_{3,56} = 0.4338$ $P = 0.73$); the mean number of caterpillars hatching per egg mass was 157 ± 21 (mean \pm SE) for DC and 177 ± 25 for GA. However, overwintering temperature regime significantly influenced the timing of egg hatch. Colonies exposed to warmer temperatures (6 °C) hatched after accumulating 18 degree-days, 2 natural days earlier than caterpillars overwintering at 4 °C ($\chi^2 = 23.6617$, $df = 3$, $P < 0.0001$; Fig. 1). Both populations exhibited this same pattern (GA: $Z = 3.77$, $P = 0.01146$, $n = 15$; DC: $Z = 3.41$, $P = 0.00193$, $n = 16$), with caterpillars overwintering at lower temperatures requiring the accumulation of 10 % more degree-days to hatch (Fig. 1).

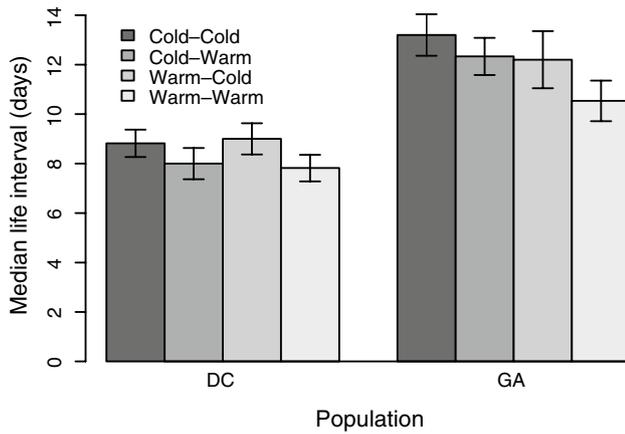


Fig. 2 Median life intervals of DC and GA caterpillar colonies under four different temperature regimes. Life intervals correspond to the number of days between median hatching date and median death date ($n_{DC} = 11$ colonies, $n_{GA} = 15$ colonies; mean \pm SE)

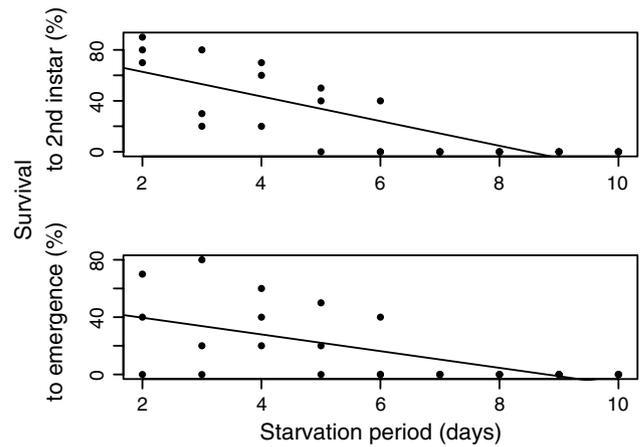


Fig. 4 Linear regressions showing the relationship between starvation period length and survival to: **a** second instar, **b** emergence, $n = 27$ colonies, three per starvation treatment

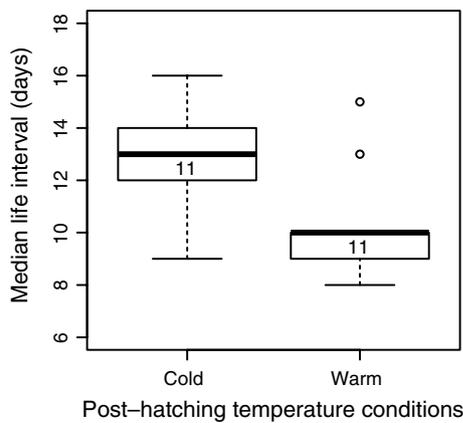


Fig. 3 Median life interval of wild egg masses from DC overwintering at ambient conditions and kept under a cold or warm post-hatching temperature regime. Numbers in boxes indicate sample size

Caterpillar colonies from GA survived starvation for periods 30 % longer than colonies from DC (GA = 12.07 ± 0.46 days, $n = 60$; DC = 8.41 ± 0.29 days, $n = 44$; overall model: $F_{3,100} = 13.35$, $P > 0.0001$; Table 3). However, median life intervals did not differ significantly among temperature treatments (Table 3; Fig. 2).

Effect of post-hatching temperature regime on caterpillar performance

Colony size of DC egg masses overwintering at ambient conditions averaged 125 ± 6 caterpillars. Spring temperature regimes significantly affected their starvation endurance, since colonies experiencing a cold post-hatching spring regime had a life interval 25 % longer than colonies kept under warm conditions (cold spring

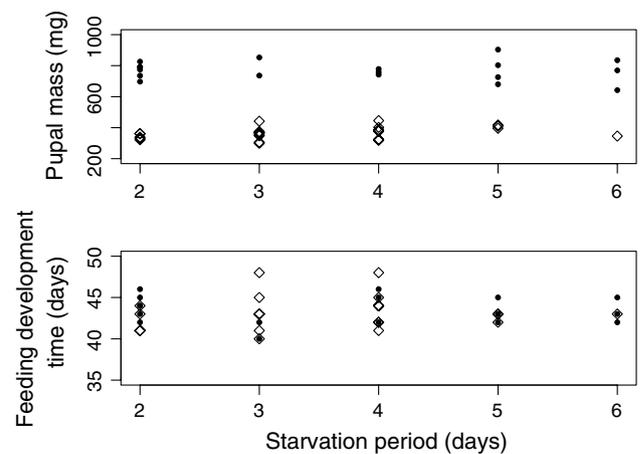


Fig. 5 The length of the starvation period endured by *M. americana* individuals before first feeding did not explain variation in either pupal mass or feeding development time. Filled circles females, open squares males; $n = 79$, 26 males, 18 females

12.73 ± 0.70 days, $n = 11$; warm spring 10.27 ± 0.60 days, $n = 11$; $Z = 2.1649$, $P = 0.02913$, Fig. 3).

Egg mass morphometrics

Egg masses from DC were 11 % longer than GA egg masses (DC 17.23 ± 0.45 mm, $n = 12$; GA 15.24 ± 0.31 mm, $n = 14$; $Z = 2.96$, $P < 0.0021$). However, egg mass length did not predict the number of caterpillars hatching (DC: $F_{1,10} = 0.07$, $P = 0.79$; GA: $F_{1,12} = 1.45$, $P = 0.25$) and the total number of eggs per egg mass did not differ significantly between populations ($t = 1.25$, $df = 22.98$, $P = 0.22$; GA 268.1 ± 20.11 eggs; DC 302 ± 18.12). Similarly, the proportion of eggs that hatched was not different

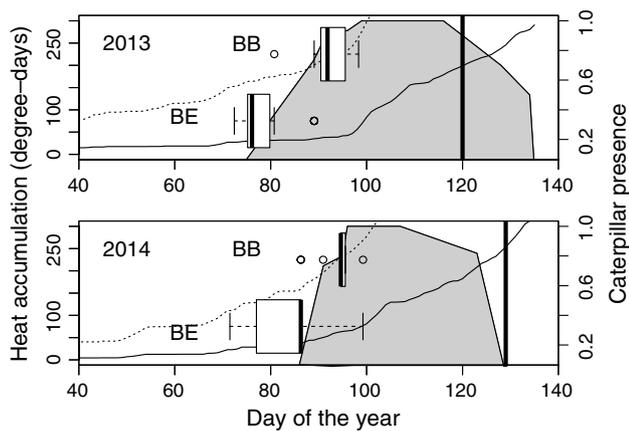


Fig. 6 Spring phenological events during 2013 and 2014. Lines indicate heat accumulation, dotted line degree-day accumulation base 4 °C and straight line degree-day accumulation at base 10 °C. Vertical lines indicate the date when all study trees had 90 % of their foliage fully mature (not suitable for caterpillar consumption) and boxes the moment of bud elongation (BE) and bud burst (BB). Shaded area denotes the presence of caterpillars in feeding stage

among populations ($t = 1.25$, $df = 22.98$, $P = 0.22$), with about two-thirds of the eggs from egg masses of both populations hatching (DC 0.62 ± 0.07 ; GA 0.67 ± 0.07).

Long-term effects of early starvation

Only 65 out of the total 270 starved caterpillars (24 %) survived to the second instar, and, of these, only 44 (16 %) successfully emerged as adult moths. No caterpillars recovered after enduring starvation periods of 6–10 days (Fig. 4). The length of the starvation period significantly affected survival to second instar ($R_{adj}^2 = 0.63$, $F_{1,25} = 45.55$, $P < 0.0001$, $n = 27$ colonies) and to emergence ($R_{adj}^2 = 0.35$, $F_{1,25} = 15.15$, $P = 0.0007$, $n = 27$ colonies). The slopes of these regressions did not differ significantly ($t = 0.88$, $df = 50$, $P = 0.38$). Moreover, we did not find a significant effect of starvation period on feeding development time (43.25 ± 0.27 days, $F_{1,42} = 0.16$, $P = 0.69$) or on the pupal mass of the survivors (males 364.32 ± 7.73 mg, $F_{1,24} = 3.33$, $P = 0.0804$; females 769.15 ± 15.01 mg, $F_{1,16} = 0.1116$, $P = 0.74$; Fig. 5).

Relative timing of caterpillar and foliage spring development

Maximum spring temperatures did not differ significantly among years ($t = 1.35$, $df = 149.55$, $P = 0.18$; 2013: 8.69 °C ± 0.60 ; 2014: 7.38 °C ± 0.77), but minimum spring temperatures were significantly lower in 2014 ($t = 4.06$, $df = 144.658$, $P < 0.0001$; 2013: 0.7 °C ± 0.42 ; 2014: -2.18 °C ± 0.57). In both years, black cherry trees

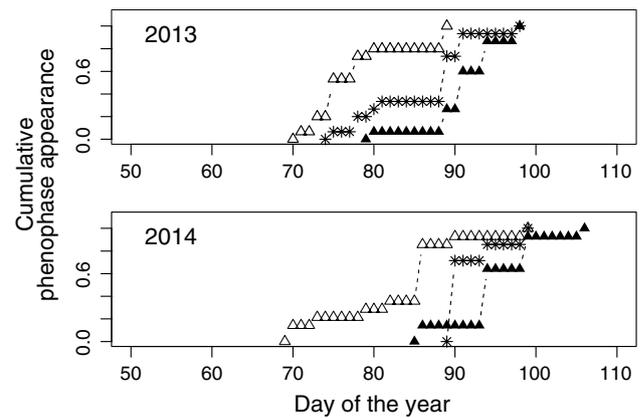


Fig. 7 Cumulative appearance of phenophases in Rock Creek Park, Washington, DC. Open triangles correspond to bud elongation, stars to caterpillar hatching and filled triangles to bud burst

started elongating their buds around March 12th, but actual budburst occurred a week later in the colder year, 2014. Similarly, caterpillars started hatching on March 18th in 2013 and 10 days later in 2014 (Fig. 6). For most plants, edible foliage (including swollen buds) was available before caterpillar hatching (Fig. 7); however, individual variation in spring development resulted in two egg masses hatching before bud expansion, and most egg masses hatching before full budburst (at least 50 % of open buds, Fig. 7). Asynchrony levels with respect to bud elongation (Q) ranged from -8 to 24 days and did not differ significantly among years ($Z = -0.63$, $P = 0.54$; median $Q_{2013} = 11$, median $Q_{2014} = 4$). In both 2013 and 2014, asynchrony levels did not differ significantly between Q and Q_i (2013: $Z = -0.23$ $P = 0.83$; 2014: $Z = -0.11$ $P = 0.92$). Caterpillar feeding season (from first hatchling record to last 5th instar record) was 26 % longer in 2013 than in 2014, and caterpillars had to feed on suboptimal foliage (when over 90 % of the leaves were mature) for up to 20 days in 2013 but only up to 7 days in 2014 (Fig. 6).

The role of foliage cues for caterpillar hatching

Caterpillars included in assay one (volatiles vs. control 1) hatched after almost 2 weeks of being transferred to spring conditions ($\bar{x}_{control\ 1} = 13.33 \pm 0.63$ days, $\bar{x}_{volatiles} = 13.5 \pm 0.84$ days) and median hatching time did not differ between treatments ($t = -0.15$, $df = 11$, $P = 0.88$, $n = 12$). The length of the hatching period was 8 ± 0.43 days for control and 7.33 ± 0.73 days for egg masses exposed to volatiles and did not differ significantly among treatments (paired t test $t = 1.10$, $df = 11$, $P = 0.29$). Assay two had similar outcomes, with neither time to median hatch (median_{control 2} = 11.00 days, median_{volatiles} = 11.5 days, $Z = 1.07$, $P = 0.28$ $n = 12$ pairs),

nor hatching period length (mean_{control 2} = 8.25 ± 0.8 days, mean_{volatiles} 7.75 ± 0.33 days; $t = 0.65$, $df = 11$, $P = 0.53$) differing significantly among treatments.

Discussion

Combining field observations and laboratory manipulations allowed us to forecast the phenological responses that eastern tent caterpillars are likely to exhibit as a result of warmer winter and spring temperatures, as well as the selective pressures they are likely to face under altered temperature regimes. In addition, our results highlight the importance of considering population-level variation in insect traits relevant to seasonality. The phenological responses we observed of *M. americanum* under controlled conditions suggest that warmer temperature regimes are likely to advance caterpillar hatching time and reduce their starvation endurance, resulting in an increased vulnerability of hatchlings to harsh weather. A 3 °C difference in overwintering temperature during 1 month resulted in a 2-day advance in caterpillar hatching. This advance is smaller than that observed by Schwartzberg et al. (2014) in *Malacosoma disstria*, in which a 3.4 °C difference throughout the experimental period triggered a hatching advance of ~4 days. We kept egg masses from both overwintering treatments under a uniform temperature regime during the period of caterpillar hatching (Table 2). Therefore, the smaller phenological advance we recorded is consistent with a shorter exposure to warmer temperatures.

In the local DC area, early season asynchrony index values (Q) were positive, indicating that caterpillars from most egg masses hatched when foliage was already available. Our relocation of egg masses to facilitate observation did not affect our estimations of budburst and hatching synchrony, since Q did not differ significantly from Q_i (the asynchrony levels egg masses would have had if they had stayed on their original tree) in either year. Other species of spring caterpillars feeding on expanding leaves hatch only after edible foliage is already available (Ivashov et al. 2002; Butt et al. 2010; Sarfraz et al. 2013). In the western tent caterpillar, *Malacosoma pluviale*, Sarfraz et al. (2013) found that caterpillars hatched after budburst of their host plant, red alder (*Alnus rubra*). Similarly, Ivashov et al. (2002) found that tortricids feeding on oaks hatched in synchrony with budburst, in a study including data from seven seasons. These early spring feeders are probably following the same environmental cues as their food plants, or have similar temperature-dependent physiological constraints, since studies in which both caterpillars and food plants are subjected to warmer temperature regimes showed that both advanced their spring development without resulting in asynchrony (Buse and Good 1996; Vries et al. 2011; but

see Schwartzberg et al. 2014 for a counter example). However, hatching in synchrony with budburst does not necessarily translate into a zero starvation risk, because caterpillars require not only available food but must also attain body temperatures warm enough to digest it, so cold and cloudy spring periods when caterpillars cannot bask can lead to starvation even in the presence of edible foliage (Fitzgerald 1995).

Contrary to our expectations, warmer spring temperatures diminished the starvation endurance only of caterpillars overwintering at ambient conditions and not of those kept at constant temperature regimes in the laboratory. Egg masses in the field experience periods of below freezing temperatures, so a possible explanation is that overwintering at stable (but relatively high) temperatures in the laboratory is stressful and masks the effects of post-hatching warming. This is consistent with field caterpillars from DC surviving starvation for slightly longer periods of time than their peers under controlled winter conditions; however, further experiments explicitly comparing temperature variation among treatments would be required to corroborate this finding.

Previous studies have shown that warm spring temperatures reduced larval starvation endurance; for example, *Tortrix viridana* and *O. brumata* caterpillars kept at 5 °C survived starvation for longer periods than caterpillars kept at 20 °C (Hunter 1990). Similarly, Butt et al. (2010) showed that *Lambdina fiscellaria* caterpillars kept at 10 °C survived starvation for 4 days, which was twice as long as caterpillars kept at 22 °C. These experiments are informative, corroborating that caterpillars kept at higher temperatures have higher respiration rates and energy use; however, they depict an unrealistic scenario, since caterpillars kept at ~20 °C would probably already have food available and would have body temperatures warm enough to digest it. We found that *M. americanum* can survive starvation periods of up to 13 days. This is an intermediate value considering that *O. brumata*, *Lymantria dispar* and *L. fiscellaria* can survive up to 4 days, *T. viridana* 12 days and *T. processionea*, which hatches before budburst, up to 3 weeks. Consistent with previous data (Ivashov et al. 2002), we showed that caterpillars can compensate for early starvation. Only 24 % of the caterpillars subjected to a starvation period survived; however, those survivors seemed to have fully recovered, since they did not show detectable effects on pupal mass or development time.

We found population-level variation in starvation endurance with caterpillar colonies from GA surviving for longer periods than colonies from DC. Variation among caterpillar colonies in starvation endurance has been observed before in *T. processionea* (Wagenhoff et al. 2013), and Stockhoff and Url (1991) found that larger gypsy moth caterpillars survived starvation for longer periods than smaller

individuals. In antlions, starvation endurance follows Bergmann's rule, with larvae from the north, where food is scarce, being larger and enduring starvation for longer periods than larvae from the south, where food is more abundant (Arnett and Gotelli 2003). We found a contrasting pattern, since southern GA caterpillars endured starvation for longer periods than northern DC caterpillars. This could indicate that spring conditions in GA are less reliable than in DC, therefore selecting for enhanced starvation endurance. Conversely, this result is also consistent with a counter-gradient pattern, which occurs when individual size is limited by food availability despite selection to attain a larger size (Conover and Schultz 1995). If this were the case, then individuals from GA would be better nourished and therefore able to provide their offspring with larger energy reserves. Our finding that egg masses from DC were larger seems to be contradictory with this scenario; however, these measurements were taken without removing the spumaline, so this could just indicate that DC egg masses have a thicker spumaline cover than GA egg masses. Further studies measuring hatchling size would be needed to clarify this issue.

As a by-product of our experimental design (which utilized a single photoperiod based on DC conditions), we subjected GA egg masses to a slightly shorter photoperiod than they would have experienced in their native range (1.67 % shorter). In addition, we forced them to hatch at a DC schedule, at a slightly older age than they would normally. While other studies have found significant interactions of temperature and photoperiod in systems experiencing differences in day length of several hours (Bradshaw et al. 2004), we consider that this small reduction in the amount of light hours that GA egg masses experienced during the experimental period had a negligible effect on their phenological responses. In this case, the effect of age on starvation endurance could have played a more important role. Egg masses from different populations differed in age because moths in the south are active earlier in the year (~May in GA) than moths in north (~June in DC). Southern egg masses are older and have been in diapause for longer periods than northern egg masses. Therefore GA caterpillars hatching in their natural range may be able to endure starvation for longer periods than the ~12 days shown in our experiment. As a result, we might be underestimating the difference in starvation endurance between DC and GA populations.

Early *M. americanum* and *P. serotina* phenological patterns were similar in 2013 and 2014, with caterpillars hatching after bud elongation and before budburst in both years; however, budburst and hatching occurred about a week earlier in 2013, the warmer year. During this year, caterpillars also experienced a longer period feeding on

low quality foliage at the end of the season than in 2014. Pre-hatching temperatures were overall higher in 2013 than in 2014; however, heat accumulation was slower. In 2014, heat accumulation maintained a steadier slope, which probably increased caterpillar metabolic rates, allowing them to complete development before foliage reached maturity. These patterns suggest that the intensity of selective pressures favoring fast development in eastern tent caterpillars varies across years, and it is likely to intensify as local temperatures increase. If the scenario depicted in 2013 becomes more common, it could exert a selective pressure for faster developmental rates in caterpillars or for the incorporation of low quality foliage (fully developed leaves) into their diet. However, data from more years and an experimental approach would be required to establish a relationship between late season asynchrony and heat accumulation patterns. Late season asynchrony as depicted in this system is a phenomenon that is difficult to characterize and measure. The main reason is that foliage quality depends on leaf development and therefore has continuous values, as opposed to the presence or absence of foliage at the beginning of the season, which facilitates the calculation of asynchrony indices such as Q .

Field observations showed that *P. serotina* buds are active and elongating before caterpillar hatching; however, we found no evidence that caterpillars can detect this activity and hatch accordingly. We feel confident that volatile cues are unlikely to be used by *M. americanum*, because our study likely exposed the egg masses to higher concentrations of plant volatiles than they would experience in the wild, as they were confined in a Petri dish with limited air flow, and twig detachment has been shown in previous studies to increase volatile organic compound emissions (Vuorinen et al. 2005). Košťál (1992) found that fly hatchlings can detect volatile compounds from their food plants and use them for orientation; however, to our knowledge, there are no studies showing that pre-hatching caterpillars can detect or use foliage cues to hatch.

Eastern tent caterpillar hatching time is likely to advance as winter and spring temperatures rise, independently of foliage availability. We expect that irregular springs will exert a higher selective pressure for increased starvation endurance, while warm springs will exert a pressure for faster developmental rates or for the tolerance of a low quality diet. Warmer spring temperatures triggered by climate change have the potential to diminish individual caterpillar's ability to endure starvation; however, the acceleration of foliage quality decline could prove to be a more important selective pressure in this system. In addition, we showed that distant populations differ in their ability to cope with environmental unreliability and therefore are likely to exhibit differential responses to climate change.

Author contribution statement MA and JTL conceived and designed the experiments. MA performed the experiments and analyzed the data. MA wrote and JTL edited the manuscript.

Acknowledgments Funding was generously provided by the Washington Biologist's Field Club, The Harlan Trust Fund, a PhD fellowship from CONACyT (Mexico) and a George Melendez Wright Climate Change Fellowship, National Park Service (USA) to MA. We thank, E. Sigmon, A. Ashwati, M. Sliwinski, C. Indech and E. Bethke for their research assistance and S. Powell and two anonymous reviewers for comments on a previous version of this manuscript. All experiments were performed in compliance with the laws of the United States.

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