The effects of experimental warming on the timing of a plant–insect herbivore interaction

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Summary

1. The phenology of many species is shifting in response to climatic changes, and these shifts are occurring at varying rates across species. This can potentially affect species' interactions and individual fitness. However, few studies have experimentally tested the influence of warming on the timing of species interactions. This is an important gap in the literature given the potential for different direct and indirect effects of temperature via phenological change.

2. Our aim was to test the effects of warming on the western tent caterpillar (*Malacosoma californicum pluviale*). In addition to the direct effects of warming, we considered the two primary indirect effects mediated by warming-driven changes in its host plant, red alder (*Alnus rubra*): changes in resource availability due to phenological mismatch (i.e. changes in the relative timing of the interaction), and changes in resource quality associated with leaf maturation.

3. We experimentally warmed egg masses and larvae of the western tent caterpillar placed on branches of red alder in the field.

4. Warming advanced the timing of larval but not leaf emergence. This led to varying degrees of phenological mismatch, with larvae emerging as much as 25 days before to 10 days after the emergence of leaves. Even the earliest-emerging larvae, however, had high survival in the absence of leaves for up to 3 weeks, and they were surprisingly resistant to starvation. In addition, although warming created phenological mismatch that initially slowed the development of larvae that emerged before leaf emergence, it accelerated larval development once leaves were available. Therefore, warming had no net effect on our measures of insect performance.

5. Our results demonstrate that the indirect effects of warming, in creating phenological mismatch, are as important to consider as the direct effects on insect performance. Although future climatic warming might influence plants and insects in different ways, some insects may be well adapted to variation in the timing of their interactions.

Key-words: budburst, climate change, cuttings, leaf quality, moth, phenology, spring, synchrony, temperature, tree

Introduction

Climate change is causing phenological shifts at highly variable rates across species in different functional groups and trophic levels (e.g. Parmesan 2007; Thackeray *et al.* 2010). Such species-specific variation in response to climate has often led to changes in the relative timing of key activities (phenological synchrony) among strongly interacting species (e.g. Visser & Holleman 2001; Post & Forchhammer 2008; McKinney *et al.* 2012) but not always (e.g. Bauer *et al.* 2010; De Vries *et al.* 2011; Iler *et al.* 2013). Altered timing of ecological interactions, such as plant–herbivore, or predator–prey, can influence species' abundances, food web structure and ecosystem-level properties such as primary productivity (e.g. Edwards & Richardson 2004; Liu *et al.* 2011).

Determining the implications of changes in phenological synchrony is critical for predicting how ecological communities will respond to climate change. In seasonal

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environments, phenology is thought to be under strong selection (Futuyma 1998; van Asch & Visser 2007). For example, initiating growth or reproduction too early or too late in the season can reduce fitness via stressful abiotic conditions, reduced resource availability or quality, or from increases in top-down pressures (e.g. herbivory or predation). For example, premature larval emergence of early-spring-feeding insect herbivores might increase the risk of mortality due to severe weather or from lack of food (Hunter 1990), whereas late emergence could reduce fecundity via reduced foliage quality (Feeny 1970). Alternatively, delaying emergence has also been shown to improve synchrony with budburst (Baltensweiler 1993) and improve survival by reducing the rate of parasitoid attacks (Hunter & Elkinton 2000). Other experimental evidence of phenological shifts altering the timing of interactions between insect herbivores and their host plants (e.g. Hunter 1990; Martel *et al.* 2001) has found that such shifts do not always have important fitness consequences (e.g. Kerslake & Hartley 1997; Durant *et al.* 2005). Our understanding of the issue remains rudimentary in the context of climate change, however, given few direct, experimental tests quantifying the effects of changes in phenological synchrony on fitness due to changes in temperature (Klapwijk *et al.* 2010; Liu *et al.* 2011).

Temperature may influence fitness not only via direct effects (e.g. temperature-dependent physiological processes), but also via indirect effects through altered interactions with other species (e.g. phenological mismatch; Barton, Beckerman & Schmitz 2009; Harmon, Moran & Ives 2009). Indirect effects can, in fact, be stronger than the direct effects of temperature, and the two may interact, either amplifying or countering one another (e.g. Suttle, Thomsen & Power 2007; Barton, Beckerman & Schmitz 2009). For example, the net effect of warming on plant productivity can be due largely to a warming-induced increase in herbivory rather than direct effects on plant growth (Barton, Beckerman & Schmitz 2009; O'Connor 2009). To our knowledge, no study has compared the direct effects of warming on consumer fitness to those effects mediated by warming-driven phenological shifts, even though this is essential to predicting the net impact of climate change on ecological communities. Note that, following many previous studies (e.g. Suttle, Thomsen & Power 2007; Gilman *et al.* 2010; Harley 2011), we use the term 'indirect effect' to mean an effect of climate on some biotic response (e.g. insect fitness) that is mediated by a third variable (e.g. plant phenology), rather than to mean the effect of one species on another mediated by a third species (Strauss 1991).

We experimentally manipulated spring temperature around egg masses and larvae of the western tent caterpillar [*Malacosoma californicum pluviale* Dyar (Lepidoptera: Lasiocampidae)], an early-spring-feeding insect herbivore, placed on the branches of its host plant, the red alder [*Alnus rubra* Bongard (Betulaceae)] in the field. Our aim was to test the influence of warming on the phenology of the

two species and on insect performance (i.e. growth, development). In addition to the direct effects of warming on insect performance, warming could also lead to two primary effects mediated by changes in the host plant: changes in resource availability via phenological mismatch, and changes in resource quality. Other indirect effects of warming on insect performance could include changes in top-down pressures (e.g. predators, pathogens, parasitoids), but we do not measure those effects here. For measures of insect performance, we used larval development time, larval weight at the fourth instar and family survival [western tent caterpillar females lay 100–250 eggs in a single egg mass (referred to henceforth as a 'family')].

We tested a series of predictions concerning the main effects of warming on insect performance. First, based on the temperature–body size rule, warming should directly reduce development time and decrease final body size (Atkinson 1994), while having little or no effect on survival, provided that the temperature remains below the species' upper threshold for viability (Amarasekare & Sifuentes 2012). Secondly, the effects of warming via leaf quality on insect performance should be negative, given that warming is expected to accelerate leaf maturation and that more mature leaves are a lower quality resource (e.g. Buse *et al.* 1998). Finally, the effect of mismatch should depend on how warming changes the relative timing of larval and leaf emergence, and on the measure of performance. In this system, there are likely to be two possibilities: warming could cause larvae to emerge in advance of leaf emergence (negative mismatch), or it could cause larvae to emerge closer to the time of optimal food quality (positive mismatch, i.e. fewer days between leaf and larval emergence than in control treatments). If warming leads to a negative mismatch, then development time should increase, as larvae will not have food available upon emergence, countering the direct effect of warming. Alternatively, if warming leads to a positive mismatch, development time should be faster as food will be available to larvae sooner, and they will develop more quickly at warmer temperatures. Opposite effects of the two mismatch scenarios are predicted for larval weight and family survival (i.e. both should decrease with a negative mismatch and increase with a positive mismatch).

Materials and methods

STUDY SYSTEM

Western tent caterpillars occur in the Pacific Northwest of North America (our study region) where they feed on a variety of tree species including red alder (Myers 2000). They are univoltine, and larvae emerge from eggs in the early spring at roughly the same time as budburst, generally in late March or early April. Five instars of gregarious larvae feed for 6–8 weeks and form conspicuous silken tents on which they congregate on or in between bouts of feeding. Pupation occurs in June, and adults emerge after 2 weeks and mate. Adults do not feed and only survive for 1–4 days. Once mated, females deposit a single egg mass.

A few weeks later, embryogenesis begins and larvae develop and remain within the eggs until the following spring.

Red alder is a native deciduous tree and is widely distributed in lowlands throughout the Pacific Northwest (Harrington, Zasada & Allen 1994).

STUDY DESIGN OVERVIEW

Experiments were carried out at two sites on the University of British Columbia (UBC, Vancouver, British Columbia; 49°15′ 42·72N, 123°14′ 56·78W) campus: Totem Field (a mowed field research site) and UBC Farm (an experimental farm and forest research site). At both sites, we used the south-facing side of 15 trees adjacent to open fields. In 2010, we conducted a pilot experiment at Totem Field to (i) test the effect of our proposed warming method (polyethylene bags as 'greenhouses') on branch-level temperature, (ii) provide an initial assessment of warming effects on early phenology of both species (but not the full life cycle) and (iii) verify the presence of sufficient variation in temperature and mismatch among branches within treatments to permit statistical tests of direct vs. indirect effects (via the host plant) of temperature on performance. On March 10, 2010, single egg masses were placed on two branches of each of 15 trees with one branch serving as a control and the other warmed. For the warmed treatment, clear polyethylene bags (35 × 55 cm) with 8–10 holes (5 × 5 cm) for ventilation and water drainage were attached over the egg masses near the tips of the branches and fastened with a tie.

A criticism of this approach is that the entire physiological unit (i.e. whole tree) has not been exposed to the warming treatment. However, warming only branches has advanced vegetative phenology in other tree species (Barton & Jarvis 1999), and other studies have found temperature-related shifts in budburst using severed branches in controlled environments (Pop, Oberbauer & Starr 2000; Jepsen *et al.* 2011). Moreover, the timing of budburst has been shown to be similar between cuttings and donor trees (Vitasse & Basler 2014), suggesting little whole-tree influence on bud development in the spring. Nevertheless, to test for potential differences between warming the entire tree and only the terminal end (~50 cm) of a branch, in 2011, we compared the date of budburst on branches that were cut (i.e. physiologically separated from the tree) to ones that remained attached. Our prediction was that if the control of budburst on branches was independent from the tree, buds on cut and uncut branches would burst at the same time. For this experiment, we used a 2 × 2 factorial systematic block design where we had four treatments (cut and attached, warming and control) per tree on 15 trees at Totem Field. Cut and attached branches were paired and placed as close together as possible on the tree to minimize microclimate variation. Branches were cut after bags were added and then attached back to the same branch with zip ties. To maintain a water supply to the cut branches, we attached water spikes to the end of the cut branches that were refilled with water semi-daily and a thin slice was cut from the branches once a week to optimize water uptake. The experiment was started in conjunction with the main experiment, and budburst was observed daily.

The main experiment began on 27–28 January 2011, when single egg masses were deployed to warmed and control branches of each of 15 trees in each of the two sites (i.e. 30 pairs). At Totem Field, a second warming replicate per tree was added. Therefore, in total across the two sites, there were 30 control and 45 warmed branches. Warming treatments were identical to those used in the pilot experiment.

To determine whether warming affects insect performance through changes in leaf quality, we conducted a bioassay in a controlled environment in 2011 in which larvae were either fed leaves from warmed or control treatments from Totem Field. Larvae for this experiment were from 20 egg masses placed on trees at Totem Field at the same time the main experiment was started (four egg masses on each of five trees). Ten bags were added to branches (without egg masses) on each of the five trees to provide a 'warmed' food supply for the experiment.

WARMING EXPERIMENTS

Branches varied in the amount of direct sunlight they received given their position and height from the ground. While the terminal ends of branches were used, some branches were less exposed than others (e.g. found mid-way to the main trunk or under other branches). Branch height ranged from ground level to around 4 m. Egg masses were randomly assigned to each branch. Egg masses in 2010 were taken from an apple orchard on Saturna Island (*c.* 50 km from UBC, across the Strait of Georgia) on 17 February 2010 and kept outdoors until they were attached to branches. Egg masses used at Totem Field in 2011 were from moths reared from the 2010 pilot study (Appendix S1, Supporting information). Egg masses used at UBC Farm in 2011 were collected along Trueworthy Road on Saturna Island on 11 January 2011 and kept outdoors until they were attached to branches. In 2011, egg masses were split by site to avoid potential viral contamination from the Saturna Island population, where a nucleopolyhedrovirus (Myers 2000) was thought to potentially be prevalent that particular year.

Small temperature loggers (iButtons®; Maxim Integrated Products Inc., Sunnyvale, CA, USA) were placed next to all egg masses to record the temperature every hour throughout the main experiment. Two iButtons at each location recorded relative humidity (on a control and warmed branch). Only minor differences in relative humidity existed between treatments over the span of the whole experiment (mean and maximum daily maximum relative humidity of the warming treatments was 2·34 (%RH) and 1·26 (%RH) greater than ambient conditions, respectively).

Branches were checked every 1–2 days for budburst, leaf emergence, larval emergence and larval instars. For all phenological events, the first observation per branch or family was used for analysis given that it was difficult to capture the date when the entire family or branch reached a stage. Budburst was defined when the bud scale was broken and leaf tissue visible. Leaf emergence was defined as a leaf fully separated from the bud (but not yet expanded). Phenological mismatch was defined as the number of days between larval emergence and first leaf emergence (negative values indicate larvae emerged before leaves, and vice versa). Starting at third instar, 10 different randomly chosen larvae from each family were weighed every 4 days (or sooner if they had reached another instar). The field experiment was terminated beyond early fourth instar because warmed families had to be moved to other branches to replenish the leaf supply, thereby changing leaf quality. However, until that point (after leaf emergence) larvae were never foliage limited (i.e. we ensured that bags initially included enough buds).

We used three measures of performance for each family: larval development time (from larval emergence to fourth instar), final larval weight (based on the first weight measurement after moulting to fourth instar) and family survival (number of larvae still living when we terminated the experiment). Faster development is

beneficial for insects as it reduces the time that larvae are vulnerable to disease and natural enemies (e.g. predators, pathogens) (Benrey & Denno 1997) and larval weight is strongly correlated with fecundity in insects (Honěk 1993; but see Leather 1988). The latter relationship is expected to be strong for the western tent caterpillar because they do not consume food during the adult stage. Given the gregarious behaviour of larvae and large family size, we could not measure the survival of individual larvae; however, we were still able to estimate family survival. The complete disappearance of larvae precluded some developmental, weight and survival measurements on some families (Table S1, Supporting information).

LEAF QUALITY EXPERIMENT

Larvae raised for the leaf quality experiment were kept on the trees under natural conditions until they reached late second instar, when they were brought into the laboratory and maintained in a controlled environmental chamber (day: 22 °C, night: 18 °C). The first two families to reach late second instar on each tree were used. In the laboratory, families were initially kept together because young larvae depend on their siblings. They were fed control leaves from their host tree until they reached the late third instar. Twenty-five larvae were then randomly chosen from each family, individually weighed (day 0) and placed randomly into plastic cups (one larva per cup) with mature leaves (>5 cm length) from either warming or control treatments. Leaves were replaced every 24 h (i.e. larvae were never food limited) in approximately the same amount between treatments. Larvae were weighed every 5 days. For performance, we used survival (from third instar onwards), female pupal weight and time to reach pupation.

STATISTICAL ANALYSIS

The analysis was divided into four sections (see Appendices S1 and S2 for statistical details, Supporting information) and performed using ʀ 2.14.1 (R Development Core Team 2012). First, to test the effect of warming a branch on budburst, rather than a tree, we compared differences in budburst between cut and attached treatments. We also tested for the sensitivity of budburst to temperature within treatments. Secondly, to determine whether warming affected the early phenology of the two species, we examined treatment differences in phenology from 2010 to 2011. We also tested for treatment differences in insect performance from 2011. We did not examine treatment differences in family survival given the substantial treatment effects (e.g. bags prevented dispersal) in addition to warming. Thirdly, we used a confirmatory path analysis to test for the relative effects of treatment, branch-level temperature and mismatch on insect performance. Given the low sample sizes, we did not perform a path analysis for family survival for Totem Field. Finally, to test the effects of warming via leaf quality on insect performance, we compared insect performance between treatments in the leaf quality experiment.

As both environmental conditions and the source of egg masses differed between Totem Field and UBC Farm, we treated these sites as two experiments rather than two treatments of an experimental factor. Consequently, all analyses were conducted separately for Totem Field and UBC Farm. We used linear mixed-effects models and generalized linear models (library 'nlme' in ʀ, R Development Core Team 2012) for all analyses.

Path Analysis

To test for the relative effects of treatment, temperature and mismatch (the latter two varied within treatments) on insect performance, we performed a confirmatory path analysis, which identifies the most likely causal links among correlated variables (Shipley 2009). We tested for possible causal links between treatment, temperature, mismatch and performance. Temperature might directly influence performance and mismatch with no causal link between mismatch and performance. Alternatively, temperature could influence mismatch, which in turn affects performance, with no direct link between temperature and performance. Moreover, overall treatment differences (in addition to temperature) could also directly influence mismatch and performance. We tested eight possible cause–effect linkage models for each measure of performance at each site (Table S2; Fig. S2, Supporting information). We tested the conditional independence (statistical independence after accounting for other variables) of treatment on mismatch and performance, and temperature on performance (Table S2, Supporting information). See the Appendix S2 (Supporting information) for details on the path analysis approach we used.

We also explored within-treatment relationships between each measure of performance and mismatch and temperature (Appendix S2, Supporting information) because preliminary analyses showed different relationships within treatments. To assess the relative importance of direct and indirect effects (via the host plant) of temperature on performance, we compared standardized regression coefficients. As the main temperature variable, we used mean daily maximum temperature calculated up to May 25 (the average date across all families to reach the fourth instar), which was found to be the best predictor of larval performance (Appendix S2, Supporting information).

Results

TREATMENT TEMPERATURE EFFECTS

Throughout the pilot warming experiment in 2010, warming treatments were 2·93 °C (0·18SE) warmer than ambient conditions based on mean daytime temperature. In 2011, mean daytime temperature in warming treatments over the duration of the main experiment was 2·97 °C (0·22SE) and 1·97 °C (0·23SE) warmer than ambient conditions at Totem Field and UBC Farm, respectively. Overall, Totem Field was warmer than UBC Farm with mean daytime temperatures being 1·45 °C (0·36SE) higher for warmed branches and 0·45 °C (0·14SE) higher for controls.

TESTING THE EFFECT OF BRANCH-LEVEL WARMING ON BUDBURST

Control and warmed branches had the same budburst timing regardless of whether they were attached to the tree. This shows that budburst on branches can respond independently from the whole tree to warming. Buds of branches cut from trees did not differ in the date of budburst compared to attached branches ($\chi^2_{3,2} = 0.0007$,

$P = 0.98$), nor was there any difference between only control ($\chi^2_{3,2} = 0.0008$, $P = 0.98$) or warming ($\chi^2_{3,2} = 0.0053$, $P = 0.94$) branches (Fig. S1, Supporting information).

Analysis of the relationship of budburst to the measured within-treatment temperature variation (among both cut and attached branches) showed that budburst was earlier on warmer replicates for the Totem Field warming treatment (-3.45 days per °C (1.38SE), $LRT_{4,3} = 5.24$, $P = 0.022$) but no relationship existed for any other within-treatment-site combination (Totem control: $LRT_{3,2} = 0.50$, $P = 0.48$; Farm control: $LRT_{3,2} = 1.62$, $P = 0.20$; Farm warming: $LRT_{4,3} = 1.66$, $P = 0.20$). This suggests that short-term changes in temperature at the branch level can elicit a response in phenology.

TREATMENT DIFFERENCES IN PHENOLOGY AND PERFORMANCE

In both years, warming treatments led to substantial shifts in larval but not leaf phenology (Table 1, Fig. 1). In 2010, larval emergence was significantly advanced in warming treatments compared to control treatments by an average of 18.1 days (1.19SE) ($LRT_{4,3} = 65.44$, $P < 0.0001$). However, there was no treatment difference in budburst ($LRT_{4,3} = 0.54$, $P = 0.46$). As a result, a significant difference in the degree of mismatch between treatments occurred; on average, warmed larvae emerged 17.75 days (1.19SE) after budburst ($LRT_{4,3} = 67.72$, $P < 0.0001$).

In 2011, larval emergence was significantly advanced in warming treatments compared to controls by an average of 24.0 days (2.39SE) at Totem Field ($LRT_{4,3} = 50.62$, $P < 0.0001$) and 22.5 days (1.72SE) at UBC Farm ($LRT_{4,3} = 58.78$, $P < 0.0001$; Fig. 1). Warming treatments had no significant effect on the timing of budburst or leaf emergence at either site (Table 1). Consequently, there was a significant treatment effect on the degree of mismatch at both sites (Totem: $LRT_{4,3} = 44.33$, $P < 0.0001$, Farm: $LRT_{4,3} = 49.03$, $P < 0.0001$). At Totem Field, warming treatments caused a substantial negative mismatch: larval emergence preceded the emergence of leaves in warmed families by as much as 25 days (Fig. 1a). While warming also had a substantial effect on mismatch at UBC Farm, almost all larvae emerged after leaf emergence (i.e. there was no negative mismatch, Fig. 1b).

Warming had no net influence on insect performance. Neither development time nor final larval weight differed significantly between treatments at either site (Table 1). In other words, warmed families significantly advanced their entire larval phase (all having gotten to the fourth instar by May 30 (Totem) vs. June 10 (Farm); Totem: $LRT_{4,3} = 34.31$, $P < 0.0001$; Farm: $LRT_{4,3} = 43.16$, $P < 0.0001$; Table 1), but they required the same number of days as control families to develop to the fourth instar (Table 1, Fig. 1).

PATH ANALYSIS

The path analysis revealed that temperature and phenological mismatch had varying effects on insect performance (Fig. 2). A single model best fits the data for development time but not for larval weight or family survival. Therefore, the underlying causal structure influencing larval weight and family survival is not clear given our data. At Totem Field, development time was influenced by mismatch and temperature. Comparatively, at UBC Farm, development time was only weakly influenced by treatment. Mismatch and temperature had weaker effects on larval weight and survival. Mismatch did not influence larval weight or survival. After accounting for treatment, temperature had weak, opposing and inconsistent effects

Table 1. Differences in phenology and insect performance between warming and control treatments at Totem Field and University of British Columbia (UBC) Farm. 'Difference' is the mean difference between warming and control treatments, where a negative difference indicates that warmed families were earlier, faster or smaller than control families, and vice versa. Model fit was based on likelihood ratio tests (LRT)

Type of response	Response	Site	Difference (SE)	d.f.	LRT	*P* value
Phenology	Date of larval emergence (days)	Totem	−24.00 (2.39)	4,3	50.62	**< 0.0001**
		Farm	−22.47 (1.72)	4,3	58.78	**< 0.0001**
	Date of fourth instar (days)	Totem	−24.15 (2.88)	4,3	34.31	**< 0.0001**
		Farm	−25.07 (2.33)	4,3	43.16	**< 0.0001**
	Date of budburst (days)	Totem	2.70 (1.45)	4,3	3.40	0.065
		Farm	−1.27 (1.71)	4,3	0.58	0.45
	Date of leaf emergence (days)	Totem	−0.50 (0.65)	4,3	0.61	0.44
		Farm	−1.93 (1.035)	4,3	3.34	0.068
	Degree of mismatch (days)	Totem	−23.50 (2.67)	4,3	44.33	**< 0.0001**
		Farm	−20.53 (1.70)	4,3	49.03	**< 0.0001**
Larval performance	Development time (days)	Totem	−0.68 (2.63)	4,3	0.070	0.79
		Farm	−2.60 (2.91)	4,3	0.84	0.36
	Weight (g)	Totem	−0.20 (0.11)	5,4	3.17	0.075
		Farm	0.0680 (0.043)	5,4	2.44	0.12

Significant *P* values (<0.05) are in bold.
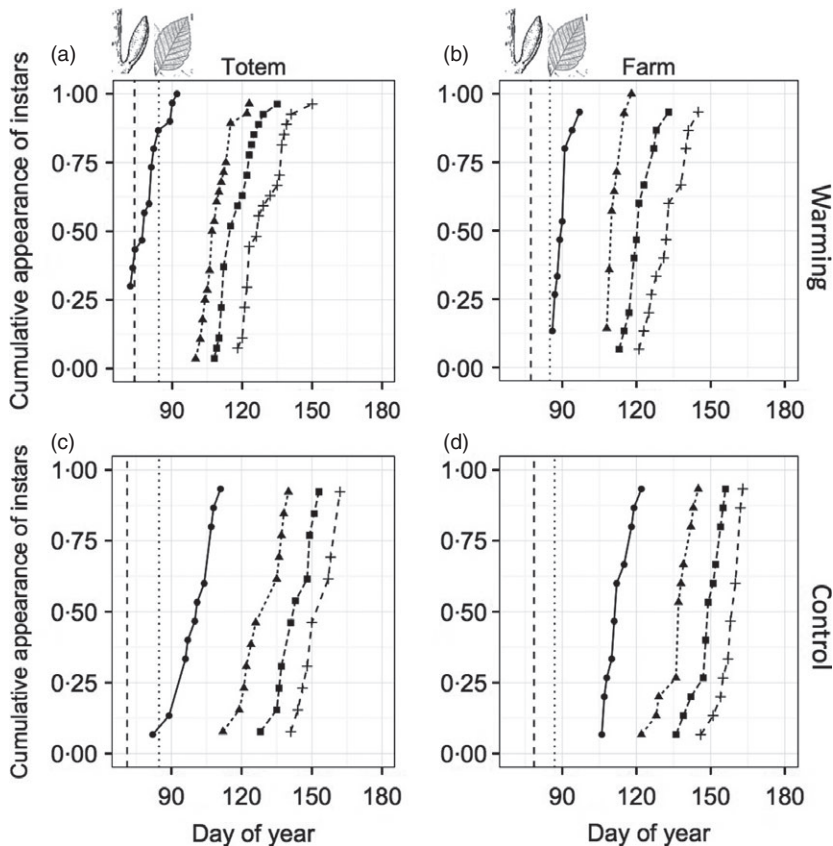
Fig. 1. Development of western tent caterpillar larvae at Totem Field (a, c) and University of British Columbia Farm (b, d) represented by the cumulative appearance of each instar across trees for families from warmed (a, b) and control treatments (c, d). Each cumulative curve represents a different instar, denoted by a different line type, from left to right: larval emergence, second, third and fourth instars. Vertical dashed lines represent the mean date of budburst and mean date of leaf emergence (from left to right) of each treatment.

on larval weight. As expected, temperature had no effect on survival (Fig. 2).

WITHIN-TREATMENT RELATIONSHIPS

Within treatments, warmer temperatures shortened development times (Table 2, Fig. 3). For both treatments at both sites, the slope of development time on temperature was negative (Table 2; Fig. 3c,d), although only significantly so for warmed families at Totem Field (-2.92 days per °C (0.39SE), $LRT_{5,4} = 16.37$, $P < 0.0001$). This was the treatment-site combination with the widest temperature range (8.19 °C compared to 1.66–5.38 °C for the other three treatment-site combinations; Fig. 3c,d). Although the development time–temperature relationship differs by treatment (a single line does not fit both sets of points), which suggests that another factor(s) is contributing to the relationship, temperature is likely to be an important cause of variation in development time as it remains significant after accounting for treatment at Totem Field ($LRT_{6,5} = 7.0$, $P = 0.0082$; Fig. 2).

Temperature-driven phenological mismatch influenced development time. The first families to emerge within each treatment took longest to develop, with stronger development–mismatch relationships for warming than control treatments (Table 2; Fig. 3a,b). Mismatch had a larger effect on development time than temperature for all treatment-site combinations (standardized coefficients; Table 2). Families in the warming treatment had shorter development

times than one would have predicted by extrapolating from the development–mismatch relationship for control families (i.e. warmed families fall below the control-group regression line; Fig. 3a,b). This suggests that the direct effect of warming opposes that of mismatch, resulting in no overall treatment differences in development time (Table 1). Indeed, development time was significantly shorter for the warmed families compared to the controls at Totem Field once leaves were present (8.32 days (2.44SE), $LRT_{4,3} = 9.21$; $P = 0.0024$). The effect of mismatch on development time remained significant after accounting for temperature (Totem warming: $LRT_{5,4} = 5.46$; $P = 0.020$; Farm warming: $LRT_{4,3} = 3.54$, $P = 0.06$). Therefore, at Totem Field, families developed the fastest if they emerged simultaneously with leaves and experienced relatively warm temperatures over their larval phase (Fig. 1a,c).

Temperature and mismatch had weaker effects on fourth instar larval weight and family survival (Table 2). The only clearly significant trend was that in control treatments at UBC Farm: the later the larvae emerged after leaf emergence, the greater the number of larvae that survived to the end of the experiment (6.13 larvae (2.36SE), $LRT_{5,4} = 7.24$, $P = 0.0071$). This suggests that later emergence improved larval survival, albeit only slightly.

LEAF QUALITY EXPERIMENT

The sources of leaves (warmed vs. control treatments) had varying effects on insect performance. Pupal weight of
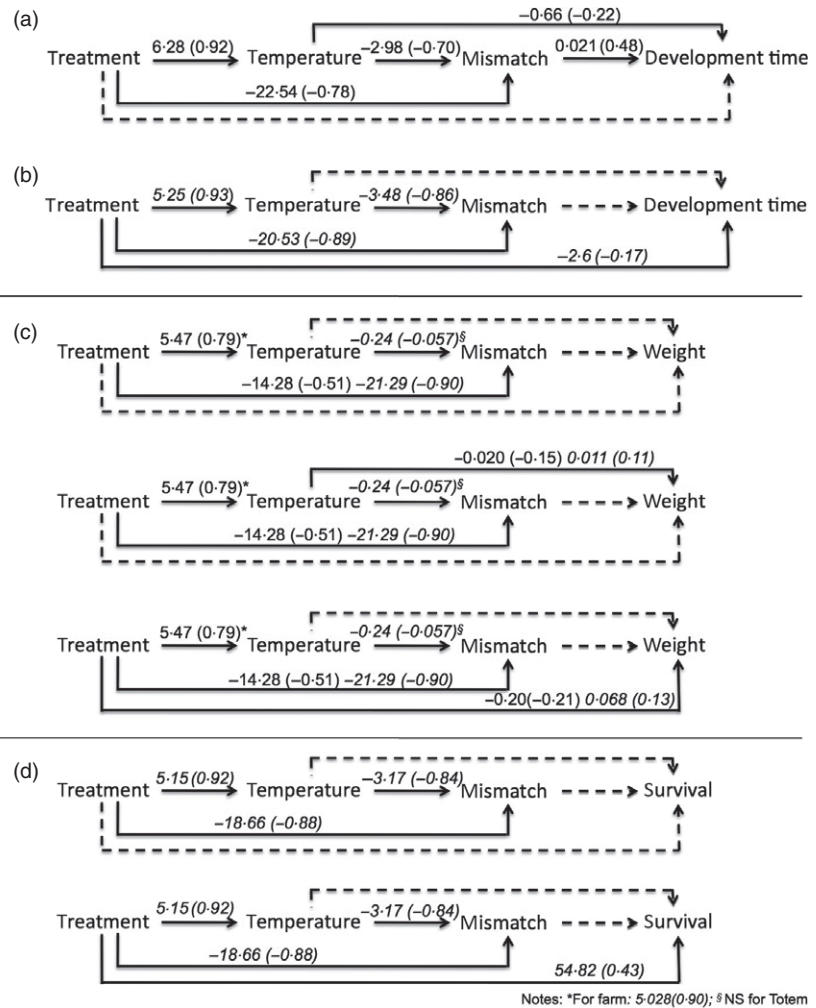
Fig. 2. Path models testing the relative effects of treatment, temperature and mismatch on insect performance. Shown are models that have the most support for development time at Totem Field (a; MODEL 6) and University of British Columbia (UBC) Farm (b; MODEL 7), larval weight (c; MODELS 3, 6, 7) and survival (d; MODELS 3, 7) (Table S3, Supporting information). The best model for larval weight (c) and survival (d) could not be distinguished among multiple models. Solid lines indicate significant causal paths ($P < 0.05$), and dashed lines indicate non-significant paths. Values are path coefficients and in parentheses are standardized coefficients. The path coefficients for UBC Farm are italicized. Path coefficients with LRT and P values are in Table S4 (Supporting information).

females fed warmed leaves was significantly lower than those fed control leaves (-0.035 g (0.014SE), $LRT_{5,4} = 4.44$, $P = 0.035$). However, neither survival ($LRT_{4,3} = 0.28$, $P = 0.095$) nor the amount of time taken to reach pupation ($LRT_{5,4} = 3.44$, $P = 0.064$) varied between treatments under these laboratory conditions.

Discussion

Recent climatic changes have led to changes in phenological synchrony for many (e.g. Visser & Holleman 2001; Post & Forchhammer 2008; McKinney *et al.* 2012) but not all (e.g. Iler *et al.* 2013) interacting species. However, surprisingly few studies have quantified the fitness or demographic consequences of such shifts (e.g. Both *et al.* 2006; Post & Forchhammer 2008). Our study contributes three main findings. First, experimental warming advanced the timing of larval emergence and the majority of the life cycle of the western tent caterpillar, one type of recent phenological shift that has been observed (Cara-Donna, Iler & Inouye 2014), but it did not significantly influence the early vegetative phenophases of the red alder. This led to varying degrees of phenological mismatch from -20 to $+10$ days, with larvae emerging before

and after the emergence of leaves (Fig. 3c,d). Greater temperature sensitivity of consumer phenology relative to that of its resource is consistent with some studies (e.g. Visser & Holleman 2001; Parmesan 2007) but not others (e.g. Both *et al.* 2009; Thackeray *et al.* 2010). Therefore, it remains difficult to predict trophic differences in phenological sensitivity to temperature.

Secondly, we found that experimental warming had no net effect on insect performance. This was likely as a result of opposing direct and indirect effects (via the host plant) of warming. Temperature-driven phenological mismatch increased insect development time by prolonging the first instar (Fig. 3a,b), while warming shortened development times (Fig. 3c,d), especially once leaves were present (Fig. 1). Therefore, larvae that emerged with leaf emergence and higher temperatures were able to develop most quickly (Fig. 3). We also found that warming-driven changes in leaf quality reduced pupal weight of females and therefore most likely fecundity, whereas warming increased final larval weight, albeit weakly. Together, these results suggest that the indirect effects of warming via the host plant countered the direct effects resulting in no net influence of warming on insect performance. This finding reinforces the importance of considering the

Table 2. Within-treatment relationships of insect performance with mean daily maximum temperature and degree of mismatch (indirect effect of temperature) at both sites. Larval weight was log-transformed for all treatments, and family survival was square-root transformed for the Totem Field warming treatment. Model fit was based on likelihood ratio tests (LRT). Significant and marginally significant P values (<0·06) are in bold

Performance	Predictor variable	Site	Treatment	Coefficient (SE)	Standardized coefficient	d.f.	LRT	P value
Development time (days)	Temperature (°C)	Totem	Warming	−2·92 (0·39)	−0·42	5,4	16·37	**< 0·0001**
			Control	−1·14 (2·60)	−0·15	3,2	0·22	0·64
		Farm	Warming	−1·56 (1·65)	−0·27	3,2	1·04	0·31
			Control	−0·66 (3·12)	−0·059	3,2	0·052	0·82
	Mismatch	Totem	Warming	−1·10 (0·21)	−0·81	5,4	13·44	**< 0·0001**
			Control	−0·13 (0·14)	−0·28	4,3	0·96	0·33
		Farm	Warming	−0·86 (0·44)	−0·47	3,2	3·76	**0·053**
			Control	−0·36 (0·22)	−0·37	4,3	2·90	0·089
Larval weight (g)	Temperature (°C)	Totem	Warming	0·018 (0·028)	0·078	5,4	0·42	0·52
			Control	0·72 (0·35)	0·48	4,3	3·60	**0·058**
		Farm	Warming	−0·041 (0·025)	−0·23	4,3	2·48	0·12
			Control	−0·10 (0·069)	−0·26	4,3	2·13	0·14
	Mismatch	Totem	Warming	0·0066 (0·0058)	0·13	5,4	1·26	0·26
			Control	−0·0070 (0·014)	−0·14	4,3	0·25	0·62
		Farm	Warming	−0·0037 (0·0086)	−0·065	4,3	0·19	0·6
			Control	0·0045 (0·0089)	0·094	4,3	0·26	0·61
Family survival (number of larvae)	Temperature (°C)	Totem	Warming	0·80 (0·42)	0·35	6,5	3·66	**0·056**
			Control	NA	NA	NA	NA	NA
		Farm	Warming	9·43 (11·41)	0·33	5,4	0·98	0·32
			Control	−27·56 (23·44)	−0·30	5,4	1·81	0·18
	Mismatch	Totem	Warming	1·21 (1·39)	0·33	6,5	0·92	0·34
			Control	NA	NA	NA	NA	NA
		Farm	Warming	1·30 (3·67)	0·13	5,4	0·19	0·67
			Control	6·13 (2·36)	0·49	5,4	7·24	**0·0071**

Significant and marginally significant *P* values (<0·06) are in bold.

indirect effects of climate change on species' responses through interspecific interactions (e.g. Suttle, Thomsen & Power 2007; Harmon, Moran & Ives 2009) and demonstrates that the net effects of climate change may be difficult to predict given the uncertainty of predicting the nature of indirect effects (McCann 2007).

Thirdly, we found that early-emerging larvae were surprisingly resistant to starvation. Larvae from some warmed families at Totem Field were without food for 3 weeks, and while we could not estimate individual larval survival, the degree of mismatch did not influence final family size for warming treatments. This suggests that emerging early did not lead to mass mortality. The observed starvation tolerance is substantially greater than what has been measured in controlled environments for most other early-spring-feeding Lepidoptera larvae (Smith & Raske 1968; Wint 1983; Hunter 1993; but see Hunter 1990). This particularly high degree of starvation resistance has been interpreted as an adaptation to variable budburst across years (Parry, Spence & Volney 1998) where the strategy of neonate larvae is to manage absent or poor quality foliage by 'persisting' rather than 'escaping' (e.g. wind-assisted dispersal). The success of this 'persistence' strategy is likely to be related to the amount of yolk remaining in their guts in the spring (Fitzgerald 1995). Given that this species is an early-season herbivore, it could also be an adaptation for increased plasticity to interannual variation in weather conditions

(Myers 1992; Fitzgerald 1995; Myers & Cory 2013), such as cold temperatures or frost in some areas (i.e. Boggs & Inouye 2012), rather than to budburst *per se*. This strategy would be consistent with the hypothesis that this interaction was phenologically mismatched historically (i.e. before climate change) to maximize overall fitness (Singer & Parmesan 2010). Nevertheless, these results suggest that the western tent caterpillar is likely to be quite resistant to warming-driven changes in phenological synchrony. Furthermore, these findings imply that starvation tolerance is an important trait to consider when predicting the severity of fitness consequences of phenological shifts for spring-feeding insects.

The early vegetative phenophases of the red alder were insensitive to our warming treatments. Temperature is thought to be the primary cue that triggers budburst in most plant species, especially for early-developing species such as the red alder (Pau *et al.* 2011). Indeed, we found advancement in budburst at our warmer site (Totem Field) relative to our cooler site (UBC Farm, Appendix S1, Supporting information), and with warmer temperatures within one of our treatments. We have also made qualitative observations of predictable interannual variation in budburst. Moreover, recent work has shown that budburst of the red alder was earlier with warmer microclimates (sun exposed vs. shaded branches; Sarfraz, Kharouba & Myers 2013) and that the phenophases of sister taxa have been sensitive to temporal variation in
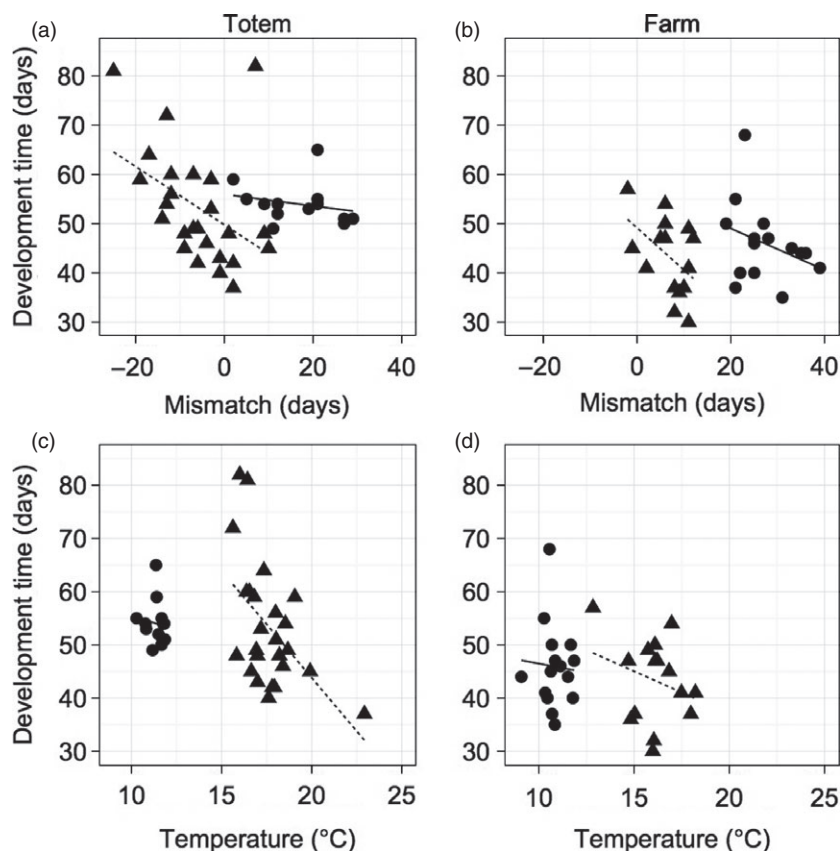
Fig. 3. Bivariate relationships of development time (larval emergence to fourth instar) with mismatch (a, b) and mean daily maximum temperature (c, d) for Totem Field (a, c) and University of British Columbia (UBC) Farm (b, d). Triangles represent warming treatments and circles represent control treatments. Negative (<0) and positive (>0) mismatch indicates that larvae emerged before and after leaf emergence, respectively. Dashed (warming) and solid (control) lines represent a best-fit line from simple linear regression models.

temperature (Miller-Rushing & Primack 2008; Sparks *et al*. 2011). This supports the likelihood that the early-season phenophases of the red alder are sensitive to temperature.

Given that we warmed the terminal end of branches rather than the entire physiological unit (i.e. whole tree), it could be that our results underestimate the sensitivity of early-season alder phenophases to warming. The molecular and genetic mechanisms underlying dormancy release are still poorly understood (Cooke, Eriksson & Junttila 2012; Vitasse & Basler 2014; Yordanov *et al*. 2014). For example, the origin of hormones responsible for dormancy release is a controversial topic, and hormones could be transported to buds from distant tissues (Rohde & Bhalerao 2007; Cooke, Eriksson & Junttila 2012; Vitasse & Basler 2014). Consequently, the relative importance of warming a branch vs. an entire tree is unclear. However, the timing of budburst in cuttings has been shown to be similar to mature trees, suggesting that buds do respond autonomously to temperature (Arias & Crabbé 1975; Couvillon *et al*. 1975; Vitasse & Basler 2014). While red alder populations can have high dormancy stability (i.e. prevention of premature budburst) and suffer delayed budburst due to a chilling deficit (having not experienced a threshold period of low temperatures; Hamann, Namkoong & Koshy 2001), chilling requirements for other tree species are normally met by the end of December in this region (R. Guy, pers. comm.). Therefore, it is unlikely that we interfered with

its chilling requirements. Instead, we suspect that alder is simply not as sensitive to spring temperature as western tent caterpillar pharate larvae, suggesting that our results are indicative of the mismatch – qualitative if not quantitative – likely to be created by climate change in this system. The passive warming of the bags during the first weeks of the experiment was rather modest – enough to accelerate larval emergence but not enough to advance budburst significantly (mean temperature treatment difference up to the beginning of budburst was 0·92 °C ± 0·023SE at Totem and 0·43 °C ± 0·18SE at the Farm). While further work is needed to understand how warming will affect alder phenology, our results illustrate a worst-case scenario for the western tent caterpillar, one in which there is no shift in early vegetative phenology of its main host plant but a marked shift in the timing of larval emergence.

As for virtually all field-warming experiments [e.g. open-top chambers which passively warm ground-level temperatures (Marion *et al*. 1997)], our warming treatments likely altered environmental variables besides temperature (Wolkovich *et al*. 2012), including CO_2 concentrations and UV-B radiation, possibly confounding the effects of temperature on insect performance, particularly development time (Fig. 3c,d). However, several lines of reasoning suggest minimal non-temperature-related effects of our treatments. Our bags likely reduced CO_2 to some extent when the leaves were fully developed and airflow was more limited (during late third and fourth

instars), and this could potentially affect larval performance (Buse *et al.* 1998; Robinson, Ryan & Newman 2012) and leaf quality (Robinson, Ryan & Newman 2012). However, given regular wind blowing through the bags, it is unlikely that CO_2 differed significantly among treatments, and because leaves grew faster in the warming treatments than control treatments (Appendix S1, Supporting information), it is unlikely that the bags limited photosynthetic rates. Later in the season when overall UV-B exposure was greater, some aspects, but not all, of larval performance and leaf quality may have been affected by reduced UV-B (Buck & Callaghan 1999; Rousseaux *et al.* 2004). Therefore, it remains unclear what the net effect of reduced UV-B on insect performance might have been. Despite the potential effects of abiotic factors such as CO_2 and UV-B on insect performance, they are considered to be less important overall than temperature (Scriber & Slansky 1981). Moreover, leaf quality is likely to have the greatest effect on early instars (Scriber & Slansky 1981) when changes in CO_2 and UV-B were likely to be minimal. Finally, before the emergence of leaves, the treatment difference in temperature is likely the only factor that could have influenced the emergence of larvae from their egg mass.

To our knowledge, this is the first study to demonstrate that warming-driven changes in phenological synchrony are as important to consider as the direct effects of warming on consumer performance. Our results revealed that experimental warming, of a magnitude consistent with predicted climate change effects for the study region over the next century, led to significant phenological mismatch between the western tent caterpillar and the red alder and advanced the insect's life cycle. While warming-driven phenological shifts may also influence other factors such as exposure to natural enemies (important determinants of fitness in natural populations (Myers 2000), we see clear evidence of opposing direct and indirect effects (through phenological mismatch and leaf quality) on insect performance. By not explicitly accounting for the indirect effects of warming, especially when they counter the direct effects, predictions about the consequences of climate change for a particular species could be misleading. Combined with their high starvation tolerance, these results suggest that the western tent caterpillar may be surprisingly resistant to the effects of climate change.

Acknowledgements

Data accessibility

All data associated with this paper can be found in Appendix S2 (Supporting information).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Additional methods, statistical analyses and results.

Appendix S2. Description of main statistical analyses.

Table S1. Sample size for each performance measure and treatment.

Table S2. Possible cause-effect linkage models used to test for the relative effects of treatment, temperature and mismatch on insect performance.

Table S3. Model fit of seven competing path models for three different response variables at Totem field and UBC Farm.

Table S4. Path coefficients for causal links associated with the models in Fig. 2.

Table S5. Model comparison of different temperature variables and performance (development time and larval weight) at each site.

Table S6. Treatment, phenological, larval performance, and temperature data for main analysis.

Table S7. Larval weight (g) data from fourth instar.

Fig. S1. Comparison of the timing of budburst on branches that were cut to ones that remained attached for both control and warmed treatments.

Fig. S2. Possible cause-effect linkage models used to test for the relative effects of treatment, temperature and mismatch on insect performance.