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Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming

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The climate-sensitive butterfly *Euphydryas editha* exhibited interpopulation variation in both phenology and egg placement, exposing individuals to diverse thermal environments. We measured ‘egg-space’ temperatures adjacent to natural egg clutches in populations distributed across a range of latitudes (36°8′–44°6′) and altitudes (213–3171 m). Eggs laid > 50 cm above the ground averaged 3.1°C cooler than ambient air at 1 m height, while eggs at < 1 cm height averaged 15.5°C hotter than ambient, ranging up to 47°C. Because of differences in egg height, eggs at 3171 m elevation and 20.6°C ambient air experienced mean egg-space temperatures 7°C hotter than those at 213 m elevation and ambient 33.3°C. Experimental eggs survived for one hour at 45°C but were killed by 48°C. Eggs laid low, by positively geotactic butterflies, risked thermal stress. However, at populations where eggs were laid lowest, higher oviposition would have incurred incidental predation from grazers.

Interpopulation variation in phenology influenced thermal environment and buffered exposure to thermal stress. At sites with hotter July temperatures, the single annual flight/oviposition period was advanced such that eggs were laid on earlier dates, with cooler ambient temperatures. The insects possessed two mechanisms for advancing egg phenology; they could advance timing of larval diapause-breaking and/or shorten the life cycle by becoming smaller adults. Mean weight of newly-eclosed females varied among populations from 92 to 285 mg, suggesting that variable adult size did influence phenology.

Possible options for in situ mitigation of thermal stress include further advancing phenology and raising egg height. We argue that these options exist, as evidenced by current variation in these traits and by failure of *E. editha* to conform to restrictive biogeographic constraints, such as the expectation that populations at equatorial and poleward range limits be confined to higher and lower elevations, respectively. This optimistic example shows how complex local adaptation can generate resilience to climate warming.

The magnitude of biological response to current climate change is extremely variable, even among species living in the same habitat (Parmesan et al. 1999, Willis et al. 2008, Thackeray et al. 2010, Yang et al. 2011, Ellwood et al. 2012, DeVactor et al. 2012). Camouflaged within observed mean global trends of shifts in range and phenology (Crick and Sparks 1999, Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006, Hickling et al. 2006, Chen et al. 2011, Poloczanska et al. 2013) are a substantial number of species showing no response at all and a minority showing changes in the opposite direction to those expected from regional warming (Gienapp et al. 2006, Parmesan 2007, Thackeray et al. 2010, Cook et al. 2012). Functional groups with strong interactions, such as plants, insects and birds, are responding differently to the same climate experiences (Parmesan 2007, Thackeray et al. 2010, Ellwood et al. 2012, DeVactor et al. 2012). Integrating the factors that underlie the current diversity of climate change response (Forrest and

Miller-Rushing 2010, Hoffmann and Sgro 2011, Diez et al. 2012) will improve our ability to predict responses to future climate warming and develop appropriate conservation strategies (Dawson et al. 2011, Pettorelli 2012).

One way to address this complexity is by seeking a mechanistic understanding of the traits involved in thermal adaptation of species representing particular functional groups (Buckley et al. 2011, Chown 2012, Sinclair et al. 2012). Physiological research will contribute part of this; however, for animals capable of changing their microclimates through behavior, understanding of thermal ecology will require a behavioral as well as a physiological component. For instance, it will be necessary to include habitat choice in predictions of climate change response, since this choice affects an organism’s experience of microclimate (Andrewartha and Birch 1954, Blondel 1985, Weiss et al. 1988, Thomas et al. 1999, 2001, Boughton 1999, Martin 2001, Ashton et al. 2009, Suggitt et al. 2011, 2012, Lawson et al. 2012).

No matter whether active behavioral choices or survival differences among microsites drive habitat associations, we expect thermally constrained organisms to occur in locally warmer microclimates towards higher latitudes or elevations. Field observations support this expectation. In Evolution Canyon in Israel, warm-adapted species and genotypes of bacteria, fungi, rodents, trees and fruit flies were distributed on south-facing slopes while cool-adapted forms occurred principally on the opposite canyon walls (reviewed by Nevo 2012). In the San Gabriel Mountains of southern California, two lizard species with nearly identical thermal physiologies adjusted their behavior with increasing elevation to achieve similar microhabitat temperatures: *Sceloporus occidentalis* was almost completely arboreal at low elevation, and *S. graciosus* was mainly ground-dwelling at high elevation; lizards of both species were partly arboreal, partly ground-dwelling at intermediate elevations (Adolph 1990). The butterfly *Aporia crataegi* changed its microhabitat choice with elevation, laying eggs on the cool north-facing sides of host plant bushes at low elevation and on the warm south-facing sides at higher altitudes, achieving the same egg temperatures at both elevations (Merrill et al. 2008). Another butterfly, *Hesperia comma*, was restricted to south-facing slopes with low vegetation height at its poleward range margin. This distribution buffered the influence of cool climate and was achieved partly by oviposition preference for warm hosts (Davies et al. 2006) and partly by thermally-biased local extinctions (Lawson et al. 2012). These examples suggest that we can help predict responses to climate change by understanding how variation in habitat utilization affects overall experience of climate.

The present work investigates thermal ecology and microclimate experience of the North American Nymphalid butterfly *Euphydryas editha*, with the aim of better understanding and predicting its responses to anthropogenic climate change.

Study system

Euphydryas editha is a non-migratory species that ranges through the western United States, western Canada, and northwestern Baja California (Parmesan 1996, Ehrlich and Hanski 2004). Within our current study area, across California and southern Oregon, *E. editha* occurs widely scattered in isolated populations and metapopulations, in climates ranging from the fringe of the Mojave desert (at Walker Pass, Inyo County, California) to continuously-waterlogged fen (Deer Creek, Josephine County, Oregon, Table 1) and at elevations ranging from sea cliffs through coniferous forest around 2000 m (Rabbit Meadow and Tamarack Ridge, Table 1) to arctic-alpine tundra at over 3000 m (Dunderberg Peak, Table 1).

Euphydryas editha is always univoltine, with a single generation per year and a ‘flight season’ lasting three to five weeks when adults are active and eggs are laid. Eggs hatch after about two weeks and larvae must feed for two more weeks before they enter an obligate diapause lasting seven to ten months. Choice of oviposition site is critical to egg and larval survival; neonate larvae do not travel far from the oviposition site and normally begin feeding on the plant chosen by their mother or on a nearby plant. As pre-diapause larvae develop, their ability to search and find hosts increases rapidly (Hellmann 2002), while post-diapause larvae normally wander in search of food, often feeding on seedlings rather than on the individual plant chosen by their mother.

Principal host plants of the butterfly belong to the families Plantaginaceae (*Collinsia*, *Plantago*, *Penstemon*) and Orobanchaceae (*Pedicularis*, *Castilleja*). Butterflies in our study area oviposit on their principal host plant genera in a complex spatial mosaic (Singer and Wee 2005, Singer and McBride 2012, Mikheyev et al. 2013). This variation in host affiliation is driven principally by heritable differences among populations in oviposition preference (Singer and Parmesan 1993, Singer and McBride 2012). Similar interpopulation variation occurs in other heritable traits, including adult

Table 1. Population and site data. Column 2–4 give geographical information. ‘Peak flight season month’ is the month of peak oviposition in most years (month of peak oviposition in typical years given, with occasional earlier/later months shown within parentheses). ‘Flight season temp’ is the mean maximum temperature, from PRISM, in the most frequent month of peak oviposition. ‘Mean daily max July’ is the mean maximum temperature in July, normally the hottest month. ‘Phenological mitigation’ is an estimate of the cooling achieved by advancing the flight season earlier than July. It is obtained by simply subtracting flight season temp from the July mean maximum.

Population name	Elevation (m)	Longitude	Latitude	Peak flight season month	Flight season temp (°C)	Mean daily max July (°C)	Phenological mitigation (°C)
San Diego	198	116°91′	32°63′	March (April)	19.9	33.2	13.3
Pozo	533	120°48′	35°30′	(May) June	28.9	31.9	3.0
Piute Mt	2465	118°42′	35°45′	June	24.6	27.1	2.5
Big Mdws	2382	118°39′	35°89′	June	18.2	22.0	3.7
Rabbit Mdw	2383	118°87′	36°75′	(June) July	23.0	23.0	0
Yucca Point	1250	118°89′	36°83′	(April) May	20.4	30.1	9.8
Tamarack	2309	119°23′	37°16′	June	20.2	24.1	3.9
Dunderberg	3171	119°31′	38°07′	July	17.9	17.9	0
Bircham Flat	1900	119°45′	38°45′	(April) May	17.6	27.2	9.6
Leek Spring	2200	120°25′	38°64′	June (July)	19.3	23.0	3.7
Mt Tallac	2400	120°10′	38°89′	July	19.7	19.8	0
Gold Lake	2073	120°67′	39°67′	July	24.2	24.2	0
Illinois River Rd	457	123°68′	42°28′	April	16.6	30.3	13.7
Deer Creek	450	123°68′	42°28′	July	30.3	30.3	0
Cardwell Hill	213	123°36′	44°59′	May	18.2	25.3	7.1

size (Singer et al. 1995), clutch size (Singer and McBride 2010), and the height above the ground at which eggs are laid (McBride and Singer 2010).

Climate sensitivity of *E. editha*

Euphydryas editha populations vary dramatically in phenology (Table 1). Peak flight, when most eggs are laid, can be in any month from March to July. At least some of this phenological variation is forced upon the insects, since montane habitats are still under snow in March when butterflies are flying at some low-elevation sites (cf Gutierrez Illan et al. 2012). In most montane habitats larvae diapause through late summer, fall and winter, finally breaking diapause at the melting of winter snowpack. Adults emerge about a month after snowmelt and females start laying eggs 2–3 days after eclosion. In contrast, larvae at many low elevation sites diapause through summer, break diapause in winter, and produce adults in March or April (Singer and Parmesan 2010). However, exceptions occur: at some low-elevation sites, represented in our study by Deer Creek and Pozo (Table 1), larvae prolong their diapause through winter and most of spring, refraining from feeding as soon as food becomes available and producing butterflies in June/July rather than March/April.

Past observations indicate that at least some populations of *E. editha* have been highly climate-sensitive (reviewed by Singer and Parmesan 2010) and subject to climate-induced population extinctions (Ehrlich et al. 1980, Thomas et al. 1996, McLaughlin et al. 2002). Patterns of population extinction and persistence, obtained by comparing distribution in the early 1990s with prior data, showed significant latitudinal and elevational shifts in the species' center of abundance that matched predictions from warming climate (Parmesan 1996).

The extensive variation of habitat type, habitat location, and phenology among populations of *E. editha* should expose individuals to very different thermal environments. Documented variation among populations in egg placement by adults resulted in very different egg heights above the ground (Singer and McBride 2010) and also seemed likely to affect thermal environments for eggs and neonate larvae, life stages that are potentially vulnerable to heat stress because of their immobility. Here, we concentrated on the egg stage in order to assess the current range of thermal environments encountered by *E. editha* in different habitats and the potential for insect response to future climate warming. We did not investigate the possibility that physiological tolerance of eggs to high temperature might evolve, and our study assumed the absence of such evolution.

Relationships between thermal ecology and climate change resilience

At the population level, resilience depends on the ability of the insects to minimize effects of climate warming on eggspace temperatures by placing eggs in cooler microsites. To assess this ability, we first ask whether populations in the hottest environments have already evolved to place eggs in the coolest microsites or whether alternate microsites might

exist, on current hosts or on alternative potential hosts, that would allow cooler eggspace temperatures. Next, we ask whether our study populations might modify their phenology to allow oviposition in cooler months. One way to modify oviposition phenology would be to retain the same life cycle length but to shift larval feeding into currently-unused time periods in which hosts are available; accordingly, we ask whether such unused time periods exist. Another way to modify oviposition phenology would be to shorten the life cycle to produce smaller adult insects at earlier dates; to assess this possibility, we examine current variability of adult size.

At the species level, we hypothesize that, if our study species lacked climate resilience, it would follow biogeographic patterns reflecting climate constraints. For example, thermally-constrained populations in lower latitudes should be forced to higher elevations and those at high latitudes should be forced to lower elevations. Insects in hotter climates should be forced to lay eggs on earlier dates and in cooler microsites. We ask to what extent the observed biogeographic patterns of *E. editha* imply these potential constraints.

Questions addressed

We posed the following sets of questions:

1) *Questions about phenology*

How does phenology of flight season (and hence of oviposition) vary among our study sites? What are the consequences of this variation for ambient air temperatures during the period of egg development and for potential exposure of eggs to thermal stress?

2) *Questions about egg placement*

Given the ambient air temperatures that result from each population's phenology, how does among-population variation in egg placement (specifically egg height above the ground) affect 'eggspace' temperatures, the temperatures to which eggs are actually exposed? Might egg placement expose eggs to potentially lethal temperatures, and does this possibility imply climate-caused natural selection on egg height? If so, can predator-mediated natural selection on the same trait, egg height, complement or oppose the climate-caused selection?

3) *Questions about resilience to future climate warming*

At the level of the population, what options do our study insects have for in situ adaptation to warming climate? At the species level, to what extent do overall biogeographic patterns imply climate-imposed constraints that predict future resilience, or lack of it?

Methods

Phenology and its thermal consequences

Using a combination of our own observations and museum records accumulated by Parmesan (1996), we recorded the identity of the month of peak flight (and hence peak oviposition) in 15 *Euphydryas editha* populations (Table 1)

distributed across a wide range of latitudes (11°9' degrees) and altitudes (from less than 200 m to greater than 3000 m elevation).

We obtained climate data for each site from the PRISM climate mapping system (PRISM Climate Group 2004). PRISM is an acronym for Parameter-elevation Regressions on Independent Slopes Model, created by PRISM Climate Group, Oregon State University, <<http://prism.oregonstate.edu>>. PRISM is a continuously-updated, knowledge-based system utilizing point data, a digital elevation model, and expert knowledge of complex climatic extremes, including rain shadows, coastal effects, and temperature inversions. Each PRISM value was taken from an 800 × 800 m grid cell (the smallest size available) centered on the target butterfly population. For each site, we obtained mean daily maximum temperatures, averaged over the period 1970–2000 (a standard timeframe used in climate analyses), for two months: the month of July and the month of peak flight. For sites in which flight and oviposition could occur with equal probability in two months, we used the temperature for the hotter of those months. Hereafter, we abbreviate the mean daily maximum for the month of peak flight as ‘flight-season-temp’ (Table 1).

We defined two new population-level variables and conducted two different analyses to investigate how population-level traits affect thermal environments experienced by the egg stage. First, in order to estimate the effect of climate on local phenology of the insects we calculated ‘phenological advance’ as the number of months between July and the month of peak flight at each site (Table 1). For example, phenological advance would be two months at a site with peak flight in May and zero at a site with peak flight in July. We then used a Spearman’s rank correlation test to seek an association between phenological advance at each site and the mean daily July maxima. This analysis asks whether the insects advanced their phenology more at sites where July temperatures were hotter.

Second, in order to estimate how phenological advance might affect thermal experience of the insects, we subtracted flight-season-temp from the mean daily site maxima for the month of July. For brevity, we refer to the value obtained from this subtraction as ‘phenological mitigation’, since it should be related to the mitigation of thermal stress that the insects achieve through phenological advance at each site (Table 1). We tested for an effect of overall climate on phenological mitigation, again using a Spearman’s rank correlation to seek an association between phenological mitigation and the mean July maximum temperature. This second analysis entails a potential autocorrelation; if July temperatures were hotter at sites with a steeper gradient of temperature increase in spring, we would tend to find a relationship between July temperatures and our measure of phenological mitigation, independently of any response to climate by the insects. We include the analysis nonetheless, since it does estimate the extent to which phenological advance actually causes the insects to operate in lower ambient temperatures. We should not assume that phenological mitigation can be simply deduced from phenological advance, since the rate of warming from spring to summer is variable among sites and faster at sites that are farther from the coast.

Finally, we also used Spearman’s rank correlation to analyze associations between flight-season-temp and egg height, site elevation, and site latitude. All statistical testing was conducted in R ver. 3.0.2 (<www.R-project.org/>).

Egg heights, eggspace temperatures and thermal tolerance

We visited eight of our 15 study sites during the seasons when eggs were present, and we searched host plants for natural egg clusters. We measured the height above the ground of each egg clutch. At five sites, we also measured the maximum height of each host plant bearing eggs. During the hottest part of the day (between 11:00 a.m. and 3:00 p.m.) we used a fine, low-thermal-capacity thermocouple to make instantaneous measurements of ‘eggspace temperatures’, i.e. air temperatures within 1–2 mm of each egg clutch. Immediately after each recording, we measured ambient air temperatures directly above the eggs at one-meter height, shielded from direct sunlight. In one population (Deer Creek), eggs were often laid at heights of around one meter, in which case we measured ambient air temperature at one-meter height, laterally displaced from the position of the eggs by around 0.3 m. We used a Spearman’s rank correlation to test whether the temperature differences between eggspace and ambient temperature were significantly correlated with egg height on the plants.

Thermal tolerance

Field data indicated that temperatures up to 47°C occurred in the immediate environments of eggs in the field. Using this value as a starting point, we measured survival rates of eggs exposed for one hour to 45°C, 46°C, 47°C, 48°C and 50°C. Eggs were obtained as ‘families’ (i.e. groups of siblings) when clutches were laid by butterflies captured in the field in June 2012 at two sites, Tamarack Ridge and Piute Mountain, both of which featured in the egg temperature recordings. We used twelve families from Tamarack and four from Piute. For each trial we placed four to six sibling eggs into a small, thin-walled glass vial with a 5 mm square of *Plantago lanceolata* leaf to maintain humidity. We placed the vials in an incubator already at the chosen temperature for the trial. We waited for the temperature to return to the set value and exposed the vials containing eggs to the set temperature for an hour. We then opened the incubator, allowed the vials to cool and measured egg survival from the eventual hatching of larvae. Due to equipment failure, we were only able to complete the 45°C, 48°C and 50°C trials.

Incidental predation by grazers

At several sites, grazers started eating the top of a *Pedicularis semibarbata* plant and reduced its height by removing the upper portions of leaves; sometimes just a small portion, sometimes the entire leaf (Supplementary material Appendix 1 Fig. 1). Prior observations indicated that grazing did not normally commence prior to the checkerspot flight season. Therefore, we assumed that cumulative grazing damage, recorded at a time when most eggs had hatched, approximated the exposure of eggs to grazing. At two sites where *P. semibarbata* was abundant and used by *E. editha*, we censused randomly located quadrats and recorded the

numbers of plants shortened by grazers and the numbers of plants left intact. Likewise, we recorded the proportion of *Collinsia torreyi* plants clipped short by grazers at three sites. At one of the sites, Rabbit, we recorded grazing on both hosts, including censuses on *C. torreyi* in both 1999 and 2006. Rapid evolution of butterfly diet has occurred at this site (Singer et al. 1993), as a result of which *C. torreyi* was a host of the insects in 1999 but not in 2006.

We compressed each host, year and site combination into a single data point and used a Mann–Whitney rank test to determine whether the proportion of grazed *P. semibarbata* was significantly different from the proportion of grazed *C. torreyi*. An earlier census in which plants were marked and followed through the season had shown that a small proportion of plants of both species were completely removed by herbivores. Such removal is irrelevant to our current considerations, since natural selection on egg height should be unaffected by it.

Options that could increase resilience to climate change

To explore potential options for each population to adapt in situ to near-term anthropogenic climate change, we conducted a series of measures. One potential option could be to adjust adult size. To illustrate the range of variation of adult butterfly sizes existing in nature, we weighed newly-eclosed female *E. editha* from two of our current study sites (Rabbit Meadow and Cardwell Hill), a third site (Gardisky Lake) lying within 3 km of our study site at Dunderberg, and a fourth site (Morgan Hill) representing the Bay Checkerspot, a much-studied low-elevation ecotype of *E. editha* (Ehrlich and Hanski 2004). This suggests that the potential for advancing phenology by reducing adult size at any particular site might be estimated from the difference between current mean adult size at the target site and the smallest mean size observed across our study populations.

Next, to ask what unused phenological options may be open to the insects, we recorded the presence and absence of apparently-usable time periods outside those in which larvae were observed to be active. By ‘apparently-usable’, we mean time periods with temperatures warm enough to permit insect activity in which hosts were present with foliage of an age that larvae normally consume. In some cases, phenological changes might require host shifts to plants that were not used currently by the insects at the focal site but served as principal hosts of *E. editha* at other sites. In order to describe this situation we classified such plants as ‘potential hosts’. We then recorded whether actual or potential hosts were present and available at times when the insects did not use them. Actual or potential hosts available before larvae had emerged from diapause were classified as ‘early hosts’. Conversely, ‘late hosts’ were hosts still phenologically available after young larvae had ceased feeding and entered diapause.

Third, in order to ask whether unused physical space might provide refuge from thermal stress, we asked whether eggs in each population could have been laid at cooler microsites (i.e. higher than they were) on the same plants. At five populations, we measured the total heights of plants bearing eggs, as well as the heights of the eggs on the same plants.

Finally, we used a Spearman’s rank correlation test to test the relationship between elevation and latitude that is expected from constraints imposed by climate (i.e. we expect

insects to occupy low elevations at high latitude and high elevations at low latitude). In addition to our study sites (which were mostly situated close to the range center), we also recorded the elevations and latitudes of the ten sites closest to the known poleward and equatorial species’ range limits.

Results

Phenology and its consequences

The month of peak flight varied among our study sites between March and July (Table 1). Phenological advance, the displacement of peak flight month from July, was positively correlated with July mean maximum temperatures (Fig. 1a; Spearman’s rank correlation: $\rho(13) = 0.609$, $p = 0.016$). However, when we removed two sites at which later oviposition was impossible because hosts were unavailable (Bircham Flat and Illinois River Rd, Table 2), this correlation fell short of statistical significance (Spearman’s rank correlation: $\rho(11) = 0.548$, $p = 0.053$).

As a result of the association between July temperatures and phenological advance, we also found a significant association between the July mean daily maxima and phenological mitigation, the extent to which the insects reduced exposure to high egg temperatures by early flight (Fig. 1b; Spearman’s rank correlation: $\rho(13) = 0.535$, $p = 0.040$). However, this relationship also lost significance when data from Bircham Flat and Illinois River Rd were excluded (Spearman’s rank correlation: $\rho(11) = 0.452$, $p = 0.12$).

Among the fifteen core study populations, we found no significant association between flight-season-temp and either latitude (Fig. 2) or altitude (Fig. 3) (Spearman’s rank correlation: $\rho(13) = -0.315$, $p = 0.25$ for latitude, $\rho(13) = -0.021$, $p = 0.94$ for altitude).

Egg heights, eggspace temperatures, and thermal tolerance

Irrespective of the host genus used, eggspace temperatures decreased with increasing height, with hotter temperatures near the ground. Temperature difference between eggspace and ambient was significantly correlated with egg height on the plant (Fig. 4, Table 3; Spearman’s rank correlation: $\rho(130) = -0.850$, $p < 0.001$). The majority of eggs naturally laid close to the ground existed in eggspaces with temperatures ranging from 12–20°C above ambient, achieving levels in excess of 40°C when ambient temperatures were in the 20s. Our highest individual eggspace readings were 44.4°C and 47.1°C at the Rabbit Meadow site.

We plotted flight-season-temp against egg placement and observed a slight trend for eggs to be laid higher (i.e. in cooler microhabitats) when they were exposed to hotter climates (Fig. 5). However, this trend fell well short of statistical significance (Spearman’s rank correlation: $\rho(13) = 0.318$, $p = 0.25$).

Thermal tolerance

Regardless of their population of origin (from either Piute or Tamarack) all eggs ($n = 16$ families) survived an hour’s exposure to 45°C and all were killed at both 48°C and 50°C.

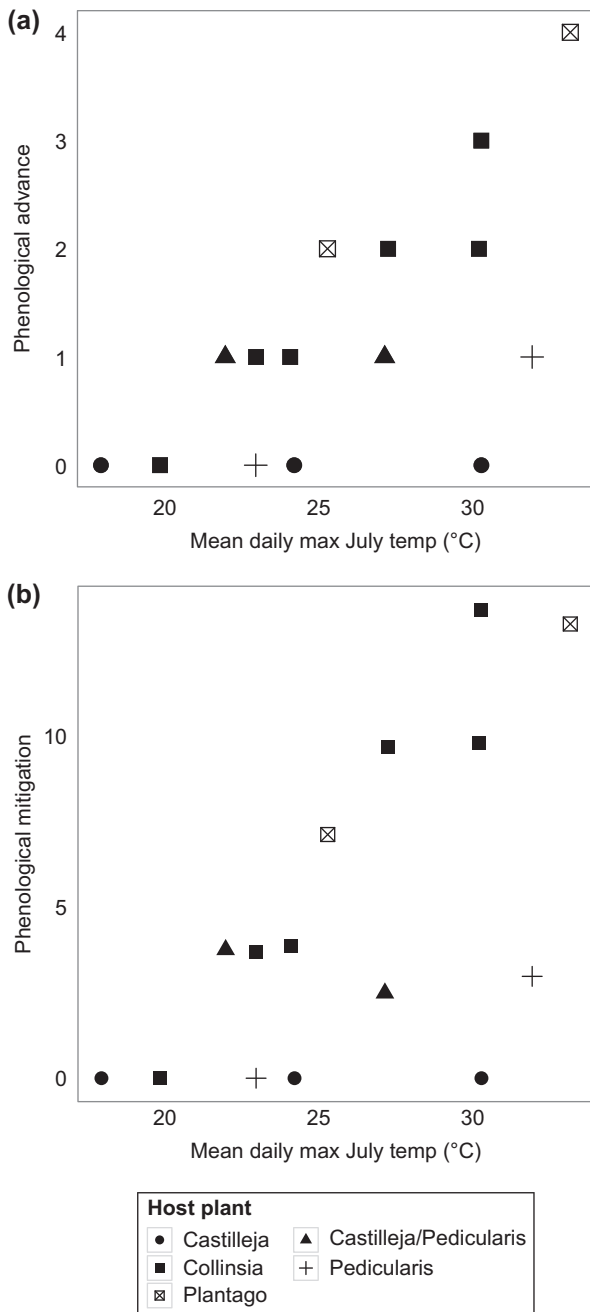


Figure 1. (a) ‘Phenological advance’, i.e. the difference, measured in months, between July and the peak flight month (higher numbers = earlier flight) plotted against mean daily maximum temperature in July. The relationship is significant using all data ($p = 0.016$); but non-significant when two populations with no options for later host use were removed ($p = 0.053$). (b) ‘Phenological mitigation’, the difference between mean daily maximum temperature in July and mean daily maximum in the month of peak oviposition, plotted against July mean maximum temperatures.

Incidental predation by grazers

Pooling data from all observations (Table 4), we found 44% of 460 *Pedicularis semibarbata* plants were shortened by grazers that clipped the tops of the plants. Only 0.4% of 739 *Collinsia torreyi* plants were similarly damaged. The difference between hosts was highly statistically significant

Table 2. Phenological fitting of *E. editha* into the season of host availability.

Population name	Early host	Actual host	Late host
San Diego	NONE	<i>Plantago</i>	<i>Cordylanthus/Antirrhinum</i>
Pozo	<i>Pedicularis, Plantago</i>	<i>Pedicularis</i>	<i>Pedicularis</i>
Piute Mt	NONE	<i>Cast/Pedic</i>	<i>Castilleja/Pedicularis</i>
Big Mdws	NONE	<i>Cast/Pedic</i>	<i>Castilleja/Pedicularis</i>
Rabbit Mdw	NONE	<i>Pedicularis</i>	<i>Pedicularis</i>
Yucca Point	NONE	<i>Collinsia</i>	<i>Castilleja</i>
Tamarack	NONE	<i>Collinsia</i>	<i>Castilleja/Pedicularis</i>
Dunderberg	NONE	<i>Castilleja</i>	<i>Castilleja</i> ²
Bircham Flat	NONE	<i>Collinsia</i>	NONE
Leek Spring	NONE	<i>Collinsia</i>	<i>Castilleja/Pedicularis</i>
Mt Tallac	NONE ¹	<i>Cast/Pedic</i>	<i>Castilleja/Pedicularis</i> ²
Gold Lake	<i>Castilleja/Collinsia/Pedicularis</i>	<i>Castilleja</i>	<i>Castilleja/Pedicularis</i> ²
Illinois River Rd	NONE	<i>Collinsia</i>	NONE
Deer Creek	<i>Castilleja</i>	<i>Castilleja</i>	<i>Castilleja</i>
Cardwell Hill	<i>Plantago</i>	<i>Plantago</i>	<i>Plantago</i>

¹At this site we have not directly observed that larvae break diapause as soon as weather and host availability permit, we deduce it from the combination of snow records, north-facing aspect of the slope and the flight season.

²At these three sites the hosts indicated are available in most years after larvae have entered diapause; however, in two years during the period 1978–2014, late flight season caused by spring snowmelt may have reduced late host availability to near zero or less than zero, causing local extinctions.

(Mann–Whitney rank test on proportion of plants grazed by host for each site/year combination: $Z = 2.76$, two-tailed $p < 0.006$). When we restricted analysis to plants censused at the same site and in the same year, we found that the same strong differences between the two hosts that appeared in the overall data appeared at Rabbit Meadow in 1999 and again in 2006 (Table 5).

Options available to increase resilience to climate change

Mean weights of newly-eclosed female *E. editha* were variable among populations, ranging from around 92 to around 285 mg (Table 6).

Actual or potential hosts present and available before larvae emerged from diapause (‘early hosts’) and those present after all larvae had entered diapause (‘late hosts’) are recorded in Table 2. Where the ‘early host’ or ‘late host’ is the same as the ‘actual host’, a phenological shift could be achieved without a host shift; where the early or late hosts do not include the actual host, a host shift would be necessary for the insects to utilize the early or late time periods. Where Table 3 has an entry stating NONE, this indicates that no host would be available and that a phenological shift into the early or late time period would not be possible.

At Deer Creek, eggs were laid on inflorescences of *Castilleja* close to the highest points of the plants. At the

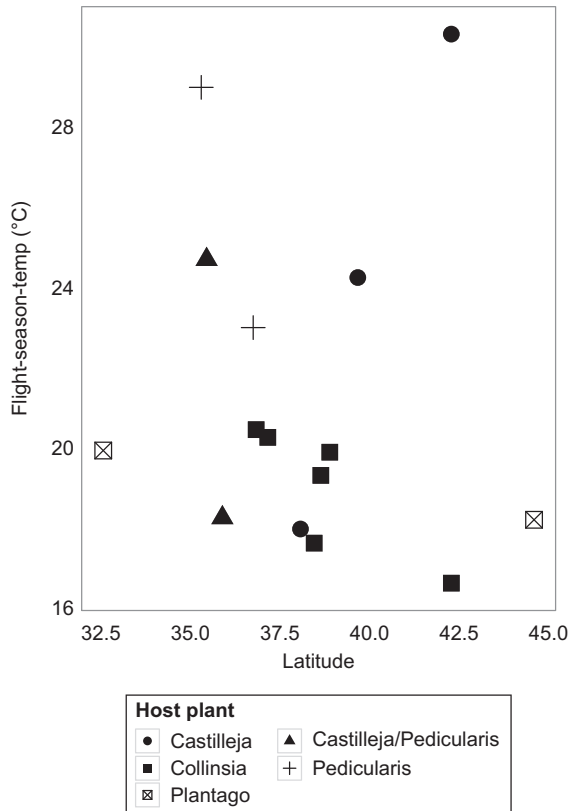


Figure 2. ‘Flight-season-temp’, the mean daily maximum temperature at each site during the month of peak flight, plotted against latitude. Relationship is non-significant at $p = 0.25$.

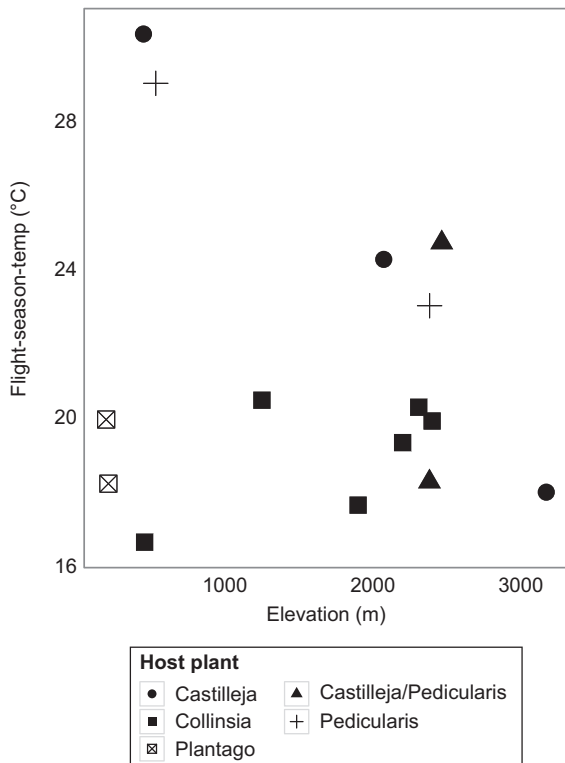


Figure 3. ‘Flight-season-temp’, the mean daily maximum temperature at each site during the month of peak flight, plotted against altitude. Relationship is non-significant at $p = 0.94$.

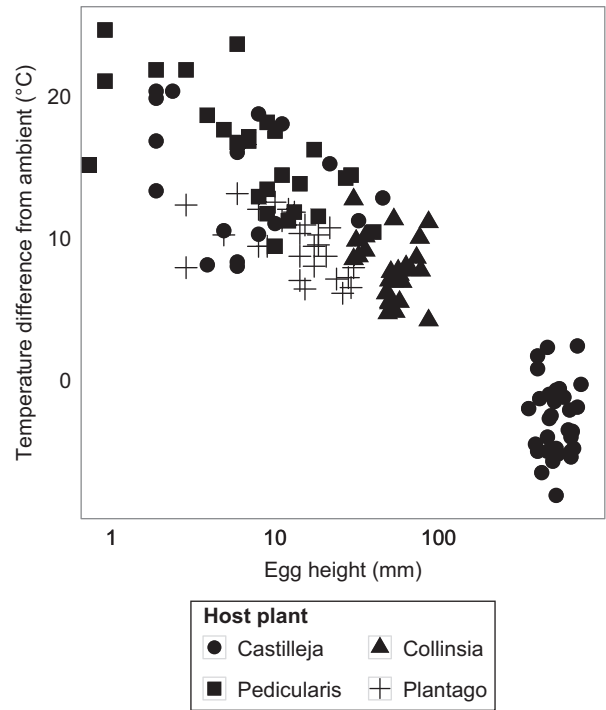


Figure 4. Temperature differences between ambient, measured at 1m height above the ground, and ‘egg-space temperatures’ measured within 1 mm of natural egg clutches, plotted against egg height above the ground (mm). Data gathered from the eight study sites for which egg-space temperatures are listed in Table 4. Study sites are not distinguished in the plot: symbols indicate plant genera on which egg-space temperatures were measured. Separate clusters for the host genus *Castilleja* reflect populations with different oviposition heights. The x-axis is presented in log base 10 scale. Relationship is significant at $p < 0.001$.

other fourteen sites oviposition would be physically possible higher up on the plants. At seven of those sites eggs were laid at mean heights below 10 mm (Table 3), with the insects tucking their eggs under leaves as close as possible to the ground. At the remaining six sites the eggs were laid part-way up the plants, with the possibility for them to be higher still. Table 6 shows mean egg heights and mean values of plant height minus egg height for individual egg clutches at five sites. To illustrate the difference in egg placement on similar plants, we include photographs of typical natural egg clutches laid low on *Castilleja* at Gold Lake and high on *Castilleja* at Deer Creek. (Supplementary material Appendix 1 Fig. A2).

Neither latitude nor altitude was significantly correlated with mean egg-space temperatures (Spearman’s rank correlation: $\rho(6) = -0.643$, $p = 0.096$ for latitude, $\rho(6) = 0.643$, $p = 0.096$ for altitude). The identity of results from these two analyses is neither an error of calculation nor an error of typography; it is a genuine coincidence. In the larger dataset of 34 populations, augmented with those at range limits, there was a significant positive correlation between site latitude and elevation (Fig. 6: Spearman’s rank correlation $\rho(32) = 0.4932$, $p = 0.003$). This result is in the opposite direction from the expected trend for populations to occupy higher elevations at lower latitudes.

Table 3. Mean egg heights, eggspace temperatures and differences between eggspace temperatures and ambient air. \pm indicates 95% confidence intervals for the means. Sample sizes (n) for ambient-eggspace differences are the same as for eggspace temperatures. Populations are listed from south to north.

Population name	Host genus	Mean egg height (mm) \pm 95% CI	Egg Ht n	Mean eggspace temp. ($^{\circ}$ C) \pm 95% CI	Eggspace temp. N	Mean ambient temp. ($^{\circ}$ C)	Mean difference ambient/ eggspace temp. ($^{\circ}$ C)
San Diego	<i>Plantago</i>	3.2 \pm 1.0	6				
Pozo	<i>Pedicularis</i>	50 \pm 22	6				
Piute Mt	<i>Cast/Pedic</i>	7.0 \pm 4.2	23	38.0 \pm 2.37	23	23.7	14.3 \pm 2.32
Big Mdws	<i>Cast/Pedic</i>	5.8 \pm 2.6	8				
Rabbit Mdw	<i>Cast/Pedic</i>	8.2 \pm 2.7	42	40.0 \pm 1.68	23	23.4	16.3 \pm 1.81
Yucca Point	<i>Collinsia</i>	260 \pm 140	5				
Tamarack	<i>Collinsia</i>	49 \pm 5.5	35	32.1 \pm 1.08	13	23.9	8.24 \pm 1.31
Dunderberg	<i>Castilleja</i>	2.5 \pm 1.3	6	37.4 \pm 5.35	6	20.6	16.8 \pm 4.34
Bircham Flat	<i>Collinsia</i>	4.9 \pm 3.3	7				
Leek Spring	<i>Collinsia</i>	52 \pm 6.8	28	32.0 \pm 1.23	14	24.7	7.29 \pm 1.22
Mt Tallac	<i>Cast/Pedic</i>	43 \pm 43	5				
Gold Lake	<i>Castilleja</i>	9.9 \pm 7.3	8	34.8 \pm 3.10	8	23.4	11.4 \pm 3.28
Illinois River	<i>Collinsia</i>	65 \pm 15	9				
Deer Creek	<i>Castilleja</i>	450 \pm 31	34	30.5 \pm 0.84	34	33.3	-2.76 \pm 0.889
Cardwell Hill	<i>Plantago</i>	15 \pm 2.9	27	34.2 \pm 1.13	27	24.8	9.50 \pm 0.820

Discussion

Potential for alteration of microhabitat as responses to climate warming

Populations and species may buffer climate warming by altering their use of resources or habitats. Species previously classified as habitat specialists have colonized novel habitat

types as they extended their ranges polewards with warming (Thomas et al. 2001, Yang et al. 2011, Pateman et al. 2012). Others have disappeared from the hottest microhabitat patches, becoming restricted to “climate microrefugia” around cooler microhabitats (Wilson et al. 2007, McLaughlin and Zavaleta 2012). Like these species, *Euphydryas editha* occupies a diversity of habitats, most of which contain several potential host plants (Singer and Wee 2005, Mikheyev et al. 2013). Here, we have shown that some of these hosts could be used in alternate ways that would dramatically change the thermal experience of the insects. A clear example is the diversity of egg placement that we observed on both *Castilleja* and *Collinsia* (Table 3, Supplementary material Appendix 1 Fig. A2). The existence of diversity among populations in both egg placement and phenology suggests that *E. editha* living in warming habitats may have multiple options for climate responses besides the range shift documented by Parmesan (1996). They may be able to counter effects of warming by remaining in situ and altering their phenology, their choice of host species, and/or their oviposition microsites (with or

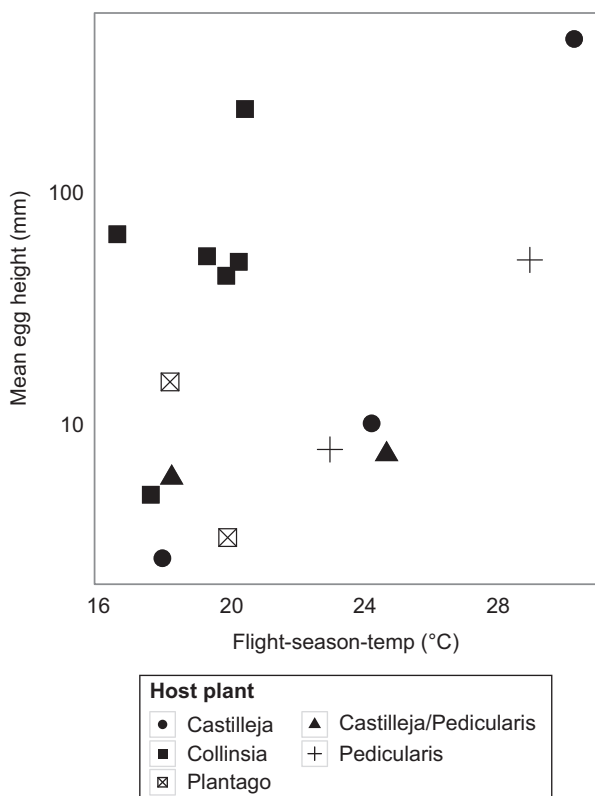


Figure 5. Mean egg height (mm) in each population plotted against ‘flight-season-temp’, the mean daily maximum temperature at each site during the month of peak flight. The y-axis is presented in log base 10 scale. Relationship is non-significant at $p = 0.25$.

Table 4. Observations of natural grazing on hosts. Grazers are primarily deer that bite off the top portions of the plants, causing reductions in total plant height. Any eggs laid on the plant parts thereby removed would be incidentally killed. The proportion of plants grazed is significantly higher on *Pedicularis* than on *Collinsia* at $p < 0.006$.

Site	Year	Host	No. plants inspected	No. plants grazed
Rabbit	1988	<i>Pedicularis</i>	27	10
Rabbit	1999	<i>Pedicularis</i>	164	105
Rabbit	2006	<i>Pedicularis</i>	229	70
Rabbit	2009	<i>Pedicularis</i>	7	7
Colony	2009	<i>Pedicularis</i>	33	9
Rabbit	1999	<i>Collinsia</i>	88	0
Rabbit	2006	<i>Collinsia</i>	323	1
Tamarack	2009	<i>Collinsia</i>	64	0
Tamarack	2010	<i>Collinsia</i>	30	0
Leek	2006	<i>Collinsia</i>	15	0
Leek	2009	<i>Collinsia</i>	83	0
Leek	2010	<i>Collinsia</i>	136	2

Table 5. Weights of newly-enclosed female *E. editha*.

Site	Sample size	Mean weight (mg) \pm 95% CI
Rabbit Meadow	153	131 \pm 3.13
Gardisky Lake (near Dunderberg)	9	92.1 \pm 3.24
Cardwell Hill	16	190 \pm 15.5
Morgan Hill	15	285 \pm 26.6

without a host shift). Below, we discuss the extent to which the biology of *E. editha* generates such options and thereby promotes resilience to anthropogenic climate change.

Phenology and its consequences for *E. editha*

Our study populations' peak flight and oviposition times occurred in any month from March to July (Table 1). Flight-season-temp, the mean daily maximum in the month of peak flight, was not significantly associated with either latitude or altitude. This suggests that the phenological variation among populations resulted in similar flight season temperatures across the range of conditions encompassed in our study. Some of this phenological variation was forced on the insects. Larvae at montane sites must wait until snowmelt to begin feeding, and sites 2000 m and higher are still under snow in March. These sites were forced into a relatively late phenology. Likewise, populations feeding on ephemeral spring annual hosts are forced into early phenology when later hosts are not available. However, only two of our fifteen study sites, Bircham Flat Road and Illinois River Road, lacked availability of 'late hosts', with the other 13 sites having the possibility of later flight seasons (Table 2).

A simple analysis, including all sites, shows that higher July temperatures are associated both with the extent of phenological advance into early flight seasons and with the degree to which phenological advance mitigates exposure to high ambient temperatures. However, if we are to use these analyses to test the hypothesis that the insects have evolved early phenology in response to thermal stress at hot sites, we should exclude the Bircham Flat and Illinois River Road sites that are forced to early phenology by host availability and do not have later phenological options available. Once this is done, both trends, though still suggestive, fall short of statistical significance.

Egg heights, eggspace temperatures, thermal tolerance and grazing

Singer and McBride (2010) observed egg height to be host-associated. Insects in populations using *Pedicularis semi-barbata* laid eggs at a mean height of around 4 mm, while those using *Collinsia torreyi* laid at a mean height of 50 mm, although both heights were available on both plant species (Singer and McBride 2010). Here, by studying a larger sample of populations than Singer and McBride, distributed over a greater diversity of habitats, we observed that egg height was even more variable than in the prior study but less tied to host affiliation. We documented striking differences in egg height among populations using very similar hosts (Table 3). For example, eggs laid at Deer Creek on *Castilleja*

Table 6. Available space for eggs to be laid in cooler microsites on the same hosts that are currently used. The last column represents the mean and range of the distance from each egg clutch to the top of the plant on which it was laid.

Site	Host plant	Sample size	Mean egg height (mm)	Mean (range) plant top-egg height (mm)
San Diego	<i>Plantago</i>	6	3.17	20.0 (14–30)
Rabbit Meadow	<i>Pedicularis</i>	10	7.60	66.1 (27–98)
Tamarack	<i>Collinsia</i>	14	47.2	36.93 (7–71)
Leek Springs	<i>Collinsia</i>	12	57.83	28.17 (12–44)
Dunderberg	<i>Castilleja</i>	3	2.17	56.16 (38–78)

miniata (ssp. *elata*) were placed on the flower heads almost as high on the plants as was physically possible (mean height 454 mm, Supplementary material Appendix 1 Fig. A2). In contrast, eggs laid on *C. miniata* at Gold Lake were tucked under leaves close the ground (mean height 9.88 mm, Supplementary material Appendix 1 Fig. A2). We also observed variable egg heights among *Collinsia*-feeding sites: eggs were laid high at three such sites and low at a fourth (Table 3).

We avoided working in unusually hot weather and recorded mean ambient temperatures below 25°C at all sites except Deer Creek. Nonetheless, at sites where the ground was mostly bare (i.e. all sites except Deer Creek and Cardwell), the soils reached temperatures above 60°C. These high ground temperatures caused eggspace temperatures to increase strongly with decreasing egg height (Fig. 4, Table 3), with the result that low-laid eggs experienced temperatures approaching 20°C above ambient. We made individual observations of eggspace temperatures above 40°C at all four sites where eggs were laid low. In contrast, eggs laid high on *Castilleja* flowers (at Deer Creek) averaged a few degrees cooler than the 'ambient' measures, presumably due to transpirational cooling, which is known to play a role in climate buffering of insect eggs. Potter et al. (2009) found that transpiration by *Datura* leaves cooled eggs of the moth *Manduca sexta* by around 6°C, protecting them from the otherwise lethal ambient temperatures of 46°C. To appreciate the dramatic effect of egg height, consider that mean eggspace temperature around eggs laid low in 20.6°C ambient temperature at Dunderberg (3171 m elevation) was 7°C

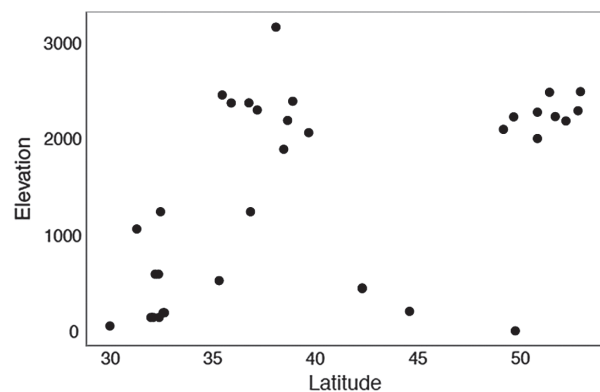


Figure 6. Elevation plotted against latitude of current study sites and sites near range limits. Positive association is significant at $p = 0.003$.

hotter than that of eggs laid high in 33.3°C ambient at Deer Creek (213 m elevation).

Observations of oviposition behavior in *E. editha* (videos attached to McBride and Singer 2010) suggest that egg heights resulted from decisions made by ovipositing females either to lay eggs at the site of alighting, as in populations where *Collinsia torreyi* was used, or to drop down and seek oviposition sites close to the ground, as in populations where *Pedicularis semibarbata* was used.

Eggs in our thermal tolerance experiment all survived at 45°C but were killed by an hour's exposure to 48°C. Comparing these laboratory experiments with our field observations, we infer that eggs must, at least occasionally, die from thermal stress in the field, although we did not observe this.

We combined recordings of incidental predation on host plants across four separate years during the season when eggs were present. More than 40% of *P. semibarbata* plants were shortened by grazers, while fewer than 1% of *C. torreyi* were so affected (Table 4). Eggs laid low on *P. semibarbata* would have been protected against incidental predation by grazers, while those on *C. torreyi* would have had no need of such protection. Prior work has shown that eggs laid high on *C. torreyi* benefitted from higher food quality for the neonate larvae (McBride and Singer 2010), and low egg placement on *P. semibarbata* speeded both egg and larval development (McBride and Singer 2010). It is not surprising, then, that in the set of populations studied by Singer and McBride (2010) eggs were consistently laid higher on *C. torreyi* than on *P. semibarbata*.

The egg is not the only immobile life stage that may need protection from ground-level temperatures; while we have found diapausing larvae of *E. editha bayensis*, the bay checkerspot, under small rocks at ground level in central California, diapausers of the southernmost *E. editha* subspecies, the endangered Quino checkerspot, were found off the ground, on shrubs that were not host plants of the butterfly (Pratt and Emmel 2010). The species' survival in its southern distribution may require habitat structure that permits escape from ground level during their midsummer inactive period.

Resilience to climate change

Across all of our measures (size, phenology, egg height and host plant choice), we found considerable variation among populations. This existing variation gives nearly every population in our study multiple options for adapting in situ to anthropogenic climate change.

Body size options

Mean weight of newly-eclosed females varied among sites by more than a factor of three (Table 5). When *E. editha* in the laboratory were fed the same hosts and kept at the same temperatures, they maintained size variation typical of their populations of origin (Singer et al. 1995). Therefore, we suspect that at least some of the size variation is heritable and could evolve in response to changing conditions (Singer and Parmesan 2010). The smallest mean size of newly-eclosed females that we observed was 92 mg at Gardisky Lake (Table 5). If size is indeed free to evolve, then populations with mean size greater than 92 mg should have the potential to evolve smaller sizes and thereby advance their phe-

nologies to oviposit on earlier, cooler dates, with earlier entry into their heat-resistant diapause phase. Anecdotally, we observe that this should apply to all of our study sites except Dunderberg, where the butterflies closely resembled those at Gardisky.

Phenological shift options

In twelve of the fifteen populations, larvae broke diapause as early in the year as it was possible for them to feed (Table 2). At these sites, any advance in phenology would likely happen at the expense of adult size and female fecundity. At the remaining three sites, larvae did not break diapause as soon as food was available (Table 2); they waited and produced adults relatively late (Table 1). These three sites had the potential for evolving earlier phenology without reducing adult size and without a host shift. However, it is possible that temporal activity patterns of natural enemies currently exclude larvae from feeding on earlier dates and would oppose evolution of earlier phenology.

Egg height options

Table 6 shows measured available space above natural egg clutches at five sites. Overall, we observed that eggs at seven of the 15 sites were laid as low as possible, and there was only one population (Deer Creek) where all eggs were laid almost as high above the ground as was possible on their hosts (Supplementary material Appendix 1 Fig. A2). At all sites but Deer Creek, space existed to oviposit in cooler microsites without a host shift. However, at our Rabbit Meadow site the principal host, *Pedicularis*, was clipped from the leaf-tips by grazers and eggs laid higher on the plants faced greater risk of incidental predation. A photograph (Supplementary material Appendix 1 Fig. A1) illustrates the drastic effect that this natural grazing would have on eggs laid close to the leaf tips.

Lack of biogeographic constraints

The only way in which the butterflies met biogeographic expectations was to advance phenology more at hotter sites (Fig. 1a–b) and even this relationship fell short of statistical significance when analyzed without populations where 'late hosts' were not available. Despite lacking statistical significance, this trend was strong enough to quash any association between geographical location (latitude or altitude) and mean egg-space temperature. Also, we might expect the insects to choose cooler microsites when ovipositing in hotter conditions but there was only a slight trend in this direction, driven by high egg clutches at the two hottest sites, Deer Creek and Pozo (Fig. 5). However, at the three next hottest sites (Piute, Gold Lake and Rabbit Meadow) eggs were laid close to the ground, so the expected trend fell well below significance.

The butterflies failed to occupy high elevations at lower latitudes and lower elevations at high latitudes (Fig. 6). The most equatorial known site for *E. editha* was at sea level and the most poleward site was around 2200 m; this clearly runs counter to expectation for a thermally-constrained organism. However, we find the statistically significant positive correlation between site latitude and elevation (Fig. 6) inconsequential. It results partly from lack of high elevation sites

(or lack of knowledge of them) in Mexico, partly from a bias towards higher elevations in our choice of mid-latitude sites for study and partly from the degradation by humans of low-elevation sites in British Columbia.

The high elevations of the most poleward populations suggest that the poleward range limit is not climate-constrained. Across all latitudes, the highest elevations recorded for *E. editha* are around Yosemite Park and in northern Inyo County, California (Parmesan 1996, Wee 2004), represented in our study by the population at Dunderberg Peak at 3171 m elevation. In this region, we observed the butterflies at elevations as high as vegetation occurred, suggesting that habitat availability rather than climate set the elevational limit of the species. In sum, among the various possible combinations of elevation and latitude that might form range limits only one, the equatorial range boundary at low elevation, may be set by climate. We note that the range shift documented by Parmesan (1996) was a significant northward and upward shift in the proportion of currently suitable *E. editha* habitats with extant populations, rather than a shift in range boundaries.

Conclusions

We provide two types of evidence suggesting that *E. editha* has a considerable arsenal at its disposal to respond to warming climate. The first class of evidence stems from direct observations of our study populations. Many of them appear to retain options for reducing thermal stress on eggs. Some have the option of shifting to an earlier date with cooler ambient temperature, either by earlier breaking of diapause and/or by reducing adult size. Except for Deer Creek, all populations could increase egg height without a host shift. However, at one site, Rabbit Meadow, raising egg height would increase vulnerability to grazers.

The second category of evidence for resilience derives from the weakness of expected biogeographical trends. Overall, the weak relationships between flight season temperature and latitude/altitude, plus the failure of the insects to consistently choose the coolest microsites in the hottest climates (Fig. 5) suggest that options for in situ adaptation to warming climate exist. The more climate-constrained the insects become, the more we expect them to conform to these expected patterns.

Despite known climate sensitivity of *E. editha* and observed climate-caused population extinctions and range shifts, we expect that this species' potential for rapid evolution (Singer et al. 1993) and ecotypic variation (Singer and McBride 2010) will enable it to persist across most of its range as climate warms. However, particular ecotypes may prove extremely vulnerable. A prime example is the federally endangered bay checkerspot *Euphydryas editha bayensis*. Although it is located near the center of the species' latitudinal range, the bay checkerspot operates close to the limits of its ecological tolerance (Singer 1972, Weiss et al. 1988, McLaughlin et al. 2002, Singer and Parmesan 2010). It evolved to those limits by trading adult fecundity against offspring mortality (Singer and Parmesan 2010), resulting in phenological asynchrony with its ephemeral hosts and high larval mortality from host senescence; most populations are extinct, and those remaining are sensitive to climatic fluctuations (Weiss et al. 1988, McLaughlin et al. 2002; Hellmann 2002).

How can we reconcile known climate-sensitivity with our developing view of the species as a whole as climate-change-resilient? The answer may lie in the mosaic nature of the insects' ecotypic variation that affects their experience of climate. Climate-sensitive populations adapted to ephemeral annuals exist interdigitated with populations using perennial hosts that are less sensitive to year-to-year climate fluctuations (Singer and McBride 2012). Instead of the expected geographical and elevational trends in the way climate is experienced by individual populations, our study illustrates a geographic mosaic of microclimate and thermal stress produced by diverse phenology, diverse microhabitats, diverse resources, and diverse behaviors involved in resource utilization. The ecological and evolutionary sources of this mosaic imply that *E. editha* has many options for responding to climate warming, and should have higher resilience than expected of such a climate-sensitive species.

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Supplementary material (available online as Appendix oik.01490 at <www.oikosjournal.org/readers/appendix>). Appendix 1.