

Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy?

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Climate change alters phenological relations between interacting species. We might expect the historical baseline, or starting-point, for such effects to be precise synchrony between the season at which a consumer most requires food and the time when its resources are most available. We synthesize evidence that synchrony was not the historical condition in two insect–plant interactions involving Edith’s checkerspot butterfly (*Euphydryas editha*), the winter moth (*Operophtera brumata*) and their host plants. Initial observations of phenological mismatch in both systems were made prior to the onset of anthropogenically driven climate change. Neither species can detect the phenology of its host plants with precision. In both species, evolution of life history has involved compromise between maximizing fecundity and minimizing mortality, with the outcome being superficially maladaptive strategies in which many, or even most, individuals die of starvation through poor synchrony with their host plants. Where phenological asynchrony or mismatch with resources forms the starting point for effects of anthropogenic global warming, consumers are particularly vulnerable to impacts that exacerbate the mismatch. This vulnerability likely contributed to extinction of a well-studied metapopulation of Edith’s checkerspot, and to the skewed geographical pattern of population extinctions underlying a northward and upward range shift in this species.

Keywords: climate change; phenological asynchrony; mismatch; life-history trade-off; winter moth; Edith’s checkerspot

1. INTRODUCTION

Since the Third Assessment Report of the IPCC in 2001, one of the major concerns about biological impacts of recent anthropogenically driven climate change is that they can alter interactions between species in ways which could cascade through communities or even ecosystems (Harrington *et al.* 1999; IPCC 2001, 2007; Visser *et al.* 2004; Cleland *et al.* 2007; Memmott *et al.* 2007; Both *et al.* 2009). One of the reasons for this concern is that recent climate-related trends have differed among functional groups and trophic levels (figure 1; Parmesan 2007; Thackeray *et al.* 2010). For example, Edwards & Richardson (2004) found strong advances in the timing of peak abundances of North Atlantic marine zooplankton but no net change in the dominant phytoplankton, diatoms. Within functional groups, members of the same community may respond differently (Forrest *et al.* 2010) and these differences may be systematic, leading to predictable changes in community composition. Examples are differences in population trends between community members differently positioned within their geographical ranges,

such as intertidal invertebrates off California (Sagarin *et al.* 1999) and birds in the UK (Thomas & Lennon 1999). Abundances of exotic and native species are responding differently, exemplified by plants in Thoreau’s woodland (Willis *et al.* 2008, 2010). Experimental warming caused early-blooming species to bloom earlier but late-blooming plants to bloom even later (Sherry *et al.* 2006). We also see systematic effects of life-history traits: e.g. diatoms with and without resting-phase spores differed in the magnitude of change in the timing of their peak abundances (Edwards & Richardson 2004).

There is particular interest in knowing whether climate responses differ between strongly interacting species, because such differences would have immediate impact on key ecological interactions, such as plant–pollinator, herbivore–plant, host–parasite/parasitoid and predator–prey (Visser & Both 2005). When evolved phenological synchrony between populations of interacting species is disrupted, detrimental effects can ramify through multiple interacting trophic levels (Both *et al.* 2009).

In order to consider this issue, we need to define ‘phenological synchrony’. First, consider mutualisms such as plant–pollinator interactions. When the peak timing of pollinator feeding coincides with peak requirement by the plant for pollinator visits, then we could sensibly describe the interaction as

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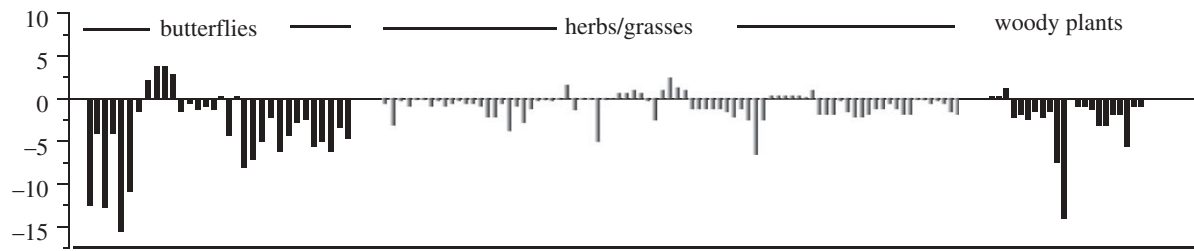


Figure 1. Diversity of rates of recent phenological change in butterflies, herbs and woody plants. Each bar shows change in days per decade for a single species. Data extracted from Parmesan (2007), which also included amphibians and birds. Mean rate of change in butterflies— 3.72 d d^{-1} , in herbs -1.05 , in woody plants -2.66 . Significance of differences by Fisher's PSLD: butterfly–herb 0.005; butterfly–woody plant 0.02. Note that Thackeray *et al.* (2010) present very different results using a large dataset from a restricted area (the UK).

phenologically synchronized (cf. van Asch & Visser 2007). In interactions that involve exploiter and victim, such as predator–prey or parasite–host, we can use a parallel definition of synchrony. If the life cycle of the exploiter is timed so that it can exploit the victim optimally and that of the victim is timed to be maximally exploited, then the life cycles of the two species are well-synchronized.

The basic biology of interacting species often generates strong expectation that their degree of synchrony should be affected by climate. For example, black, thermophilic caterpillars of the Finnish butterfly *Melitaea cinxia* bask in the sun, so that when the sun shines they can speed their development more than that of their immobile, white-cocooned specialist parasitoids (*Cotesia melitaearum*). By this means, the caterpillars can use cool, sunny conditions to generate adaptive phenological asynchrony with the parasitoids. In dull weather, they are not able to do this and suffer increased parasitoid attack as a result (Van Nouhuys & Lei 2004). In this situation, it seems clear that almost any change of climate would influence relative development time and, hence, the degree of butterfly–parasitoid synchrony, with consequences for the dynamics of their interaction.

An obvious metric to examine as an indicator of climate-change impacts on phenology is the temporal trend in relative timing of the life cycles of interacting species (Visser & Both 2005). To properly quantify impacts on species' interactions, one would need long time-series encompassing periods of natural climate variability as well as anthropogenic climate change (McCleery & Perrins 1998). Long-term, multi-taxon analyses are beginning to appear (Parmesan & Yohe 2003; Root *et al.* 2003; Menzel *et al.* 2006; Parmesan 2007; Thackeray *et al.* 2010). However, for species that are actually known to interact, the number of studies remains very small (reviews by Harrington *et al.* 1999; Stenseth & Mysterud 2002; Visser & Both 2005). In The Netherlands, peak abundance of tree-feeding caterpillars has advanced more than the breeding dates of tits, to the detriment of the birds (Visser *et al.* 1998, 2004, 2006; Both *et al.* 2009). Winder & Schindler (2004) show that the timing of diatom bloom in Lake Washington has advanced steadily since the 1960s, while among their potential consumers, *Daphnia* were phenologically

unchanged from 1977 to 2002. In contrast to these studies showing increasing asynchrony, the phenology of the orange-tip butterfly (*Anthocharis cardamines*) in the UK has fluctuated in precise synchrony with that of its crucifer host plant (Sparks & Yates 1997).

The vast majority of long-term data on phenology do not inform us about changes in the relationships between tightly interacting species. For example, we know how the timing of cherry blossom in Japan has changed over 600 years (Menzel & Dose 2005), but we cannot plot the relative timing of the cherry trees and their pollinators over the same period. Where long-term data are not available for both members of an interacting species' pair, conclusions about impacts of climate change on phenological synchrony tend to be drawn from current status and recent information, often gathered entirely during the period when impacts of anthropogenic climate change are already expected. For example, workers have used short-term datasets to develop models of the responses of phenology to annual climate variability (e.g. Dewar & Watt 1992). These models are then used to extrapolate phenology of target species to longer time series than those for which field data have been gathered (Memmott *et al.* 2007; Morin *et al.* 2009).

Extrapolation from short-term datasets may work well, provided that species' responses to varying climate (the 'reaction norms' of climate response) are not themselves in flux. However, in some systems these reaction norms are already changing (Visser *et al.* 2006; van Asch *et al.* in preparation), in which case models that assume a constant response are unlikely to either forecast or 'hindcast' a species' true response to long-term climate change. Rather than using models to estimate the baseline for effects of current change on relative timing of interacting species, there has been a tendency in the literature to assume that the baseline should be close to synchrony (e.g. Both *et al.* 2009). If the baseline were indeed precise synchrony between consumer and resource, change in any direction would be detrimental to the consumer. But is baseline synchrony the appropriate assumption?

Here, we develop the theme that the starting point for climate change impacts may often have been evolved asynchrony between consumer and resource. In such a circumstance, change that exacerbates

pre-existing mismatch has the potential to be extremely detrimental to the consumer, while change that diminishes it should be beneficial. If asynchrony frequently evolves as an adaptive strategy, this requires us to rethink our assumptions about how human-driven climate change is affecting species' interactions.

There are at least two avenues by which natural selection might lead to baseline asynchrony between interacting species, both with theoretical and empirical support. The first avenue is via coevolution. In mutualistic interactions, coevolution would tend to maximize synchrony, but in exploiter–victim interactions, coevolutionary ‘arms races’ would tend to generate asynchrony as the victim tends to evolve into ‘enemy-free time’.

The second avenue for evolution of adaptive asynchrony is via life-history trade-offs (Roff 1992; Reznick *et al.* 2000; Davidowitz *et al.* 2005; Roff & Fairbairn 2007), and this is the theme we explore in most detail in this paper. Consider the simplest situation in which a population living in a seasonal environment has one fixed generation per year with discrete, non-overlapping generations. When time is limited, individual members of that population may face certain death if they fail to fit their active life stages into the period when resources are available. At the same time, if they ‘waste’ time by failing to use that same period of resource availability in its entirety, they may suffer reduction in fecundity. If individuals can precisely detect or predict both the beginning and end of the period during which they can feed, then a population can evolve to the point where every member just fits its development into the available time and synchronizes its activity with resource availability. But if individuals cannot make this detection and/or prediction with accuracy, a life-history trade-off between fecundity and mortality emerges with phenological asynchrony as a potential outcome.

To understand this trade-off, one can envisage two possible outcomes, that are themselves two ends of a continuum of strategies:

- Timing and length of the life cycle evolve so that most individuals are able to fit their development into the available time and few die because of failure to achieve this fit. Because individuals cannot detect precisely when the ‘available time’ begins and ends, the corollary of this strategy is that most individuals also suffer reduced fecundity by failing to use the full time that the resource is available.
- Timing and length of the life cycle evolve so that most individuals die from failure to fit their development into the available time. However, the few that do survive are able to use almost all the available time and benefit from high fecundity.

This second strategy will appear as an apparent maladaptation, measured as a high degree of mortality as many (or even most) individuals in a population fail to fit their life cycles into the available time and die because of asynchrony with their resources.

Here, we explore two well-documented case studies: Edith's checkerspot butterfly (*Euphydryas editha*), on

which we ourselves have worked since 1967, and the winter moth (*Operophtera brumata*), that has been studied intensively by a diversity of researchers, not including ourselves. The life histories of these two species are quite different, yet in both cases a high frequency of asynchrony has been observed between the insect and its host plant at particular stages in their interaction. In each case, conspicuous mortality occurred when individual insects failed to synchronize a feeding stage in their life cycle with the availability of food from their host plant (Feeny 1970; Singer 1972; Holliday 1985; Weiss *et al.* 1988; Cushman *et al.* 1994; van Asch & Visser 2007). In each case, mortality caused by asynchrony was the likely cause of climate-driven population dynamic fluctuations (Singer 1971; Varley *et al.* 1973; Hunter *et al.* 1997; McLaughlin *et al.* 2002a; Hellmann *et al.* 2003). In the checkerspot, asynchrony has been implicated in population extinctions (Singer & Ehrlich 1979; Ehrlich *et al.* 1980; Singer & Thomas 1996; Thomas *et al.* 1996; McLaughlin *et al.* 2002a,b). The first observations of phenological mismatch in both systems were made more than 40 years ago, prior to the onset of major impacts of current anthropogenically driven climate change.

To the extent that species' interactions might have had an evolved asynchrony or mismatch as their starting point, assumptions of baseline synchrony would risk mis-detection, mis-estimation and mis-attribution of climate change impacts. If we can improve our understanding of the circumstances that might lead to the evolution of synchrony or asynchrony as a baseline, we can also improve our ability to interpret short-term data on species' relationships, which ultimately will improve our long-term projections of future climate-change impacts. Detailed examination of our two target species, that we undertake here, clarifies the need for better understanding of the role that life history plays in climate-change responses.

2. EVIDENCE FOR ASYNCHRONY AS A HISTORIC STABLE STATE

(a) Case study no. 1: the bay checkerspot and its ephemeral annual host plants

Our interest in phenological mismatches between herbivorous insects and their hosts originates in our studies of a subspecies of Edith's checkerspot, the bay checkerspot (*Euphydryas editha bayensis*). This is a Federally endangered butterfly living in coastal grassland in central California and endemic to serpentine soils. It feeds on two annual host genera, *Plantago* and *Castilleja*. Two metapopulations have been studied, one that is now extinct at the Stanford University Reserve at Jasper Ridge (Ehrlich 1961, 1965; Labine 1968; Singer 1972; Harrison *et al.* 1991; McLaughlin *et al.* 2002a,b) and a much larger, still extant metapopulation at Morgan Hill (Harrison *et al.* 1988; Weiss *et al.* 1988; Cushman *et al.* 1994; Hellmann 2002). At both sites, some habitat patches contained only *Plantago*, while others contained both hosts growing intermingled. *Plantago* was always the more abundant and the more predictable from year to year and received the higher number of eggs

(Labine 1968; Hellmann 2002). Larvae began feeding on mild or sunny days in December or January and often remained inactive through periods of cold, cloudy weather. From mid-March to early April, adult butterflies emerged (figure 2a). Females mated almost immediately and laid eggs within 1–2 days (Labine 1968; Boggs 1997) that hatched in another 2 weeks. Young larvae needed to feed for at least 10 days and reach mid-third instar before they could respond to host senescence by diapause. Even if they continued to find food, they entered obligate diapause at the beginning of fourth instar (occasionally fifth). Because individual larvae were forced by host senescence to diapause at slightly different stages, their sizes at diapause were diverse, and so were their starting sizes at break of diapause in winter. A sample of 70 diapausing larvae collected in the field ranged in size by an order of magnitude, from 1.5 mg to 16.5 mg, with a mode of 4 mg (Singer 1971).

Ovipositing adult bay checkerspot at the Jasper Ridge site did not accurately predict the timing of host senescence. Almost all clutches (40 of 41 observed by Singer 1971) were laid on or near host plants that were green and edible to larvae when the eggs were laid. However, most plants were no longer edible when eggs hatched. In the first two years of study (1968 and 1969), 77% and 80% of egg masses, respectively, hatched onto dried plants, and the larvae perished without feeding, even though many hundreds of edible host individuals were present in the habitat at the time of egg hatch (Singer 1972). Similar asynchrony between host senescence and egg hatch occurred in 1970 and 1971 (table 1; Singer 1971; Singer & Ehrlich 1979). In figure 2a, which is based on these early observations at Jasper Ridge, we place a bar below the *x*-axis to show seasonal progression of food availability, which began to decline as hosts senesced even before the very first eggs hatched. In subsequent studies in the 1980s and 1990s, researchers found similar negative consequences of host senescence (Dobkin *et al.* 1987; Cushman *et al.* 1994; but see Fleishman *et al.* 1997 as an exception). Cushman *et al.* (1994) calculated a probability of survival of zero for offspring of adults eclosing in the second half of the emergence season.

The suite of studies that found high mortality of neonate and pre-diapause larvae from asynchrony with their hosts documented three ways in which larvae could survive the critical period in April and early May when hosts were rapidly senescing.

- When slope aspect was diverse, larvae developed faster on south-facing slopes and hosts senesced later on north-facing slopes, allowing increased probability of survival when adults that developed on warm south-facing slopes oviposited in cooler sites (Singer 1971, 1972; Dobkin *et al.* 1987; Weiss *et al.* 1988).
- Mean senescence time of *Plantago* occurred earlier than that of *Castilleja*, and where both hosts occurred together, many larvae that survived did so by migrating from dying *Plantago* to still-edible *Castilleja* (Singer 1972; Hellmann 2002).

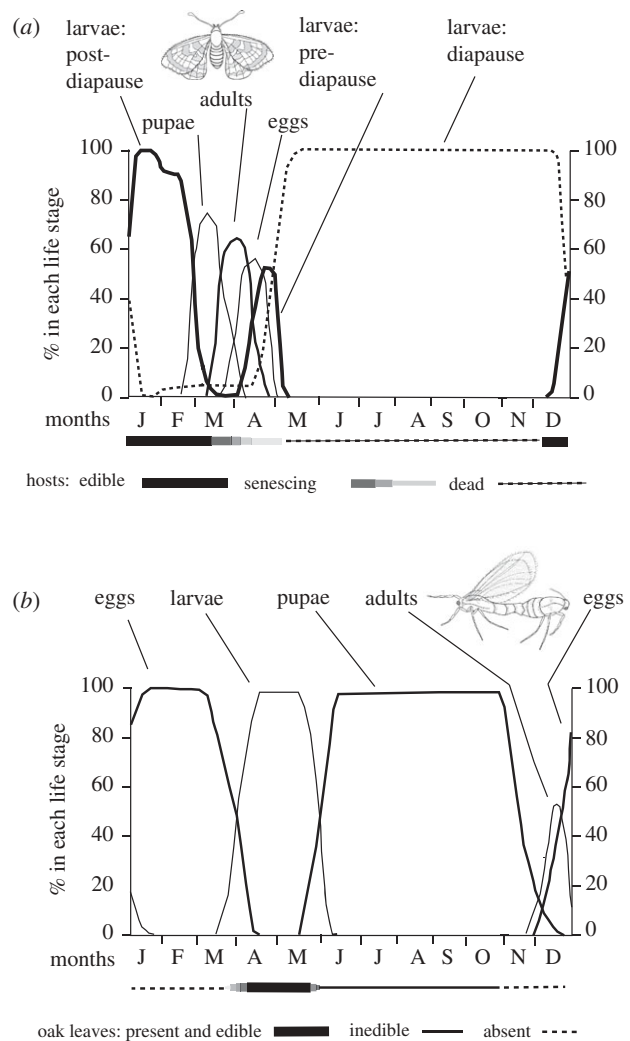


Figure 2. Life cycles of two lepidopteran species. (a) Bay checkerspot, showing the proportion of insects in each life-history stage through the seasons. All larvae break diapause and start to feed in December–January, so there is a brief period when the entire population comprises feeding larvae. However, very shortly some larvae (a different proportion each year) decide not to complete their development, return to diapause and try again the following year. This explains the presence of diapausing larvae for almost the entire year. Eggs, adults and pupae never comprise 100% of the population because each one overlaps in time with other stages. The bar below the *x*-axis shows changes in the availability of hosts. Black bar, both host species 100% edible. Decreasing shading in the bar indicates the progression of host senescence in the following categories: 70–99% edible; 50–69% edible; 10–49% edible; 1–9% edible. Dotted line: all hosts of both species dead. (b) Winter moth. The bar below the *x*-axis shows both availability and edibility of oak leaves. The bar strengthens in late March as budburst occurs at different times on different individual trees, then weakens in May as leaves lose their edibility.

- Feeding by gophers (*Thomomys bottae*) created small patches of fertilized soil on which *Plantago* senescence was delayed (Singer 1971, 1972; Hobbs & Mooney 1985).

The onset of winter rains caused both hosts to germinate and checkerspot larvae to break diapause, so at this stage there was no phenological mismatch between

Table 1. Calculated survival at egg hatch of *E. editha* at Jasper Ridge, 1970, for four different oviposition dates (adapted from Singer 1971).

| date | number of quadrats suitable for egg laying | number of quadrats suitable for hatchlings | 'survival' = % of eggs hatching in quadrats with food available |
|----------|--|--|---|
| 22 March | 181 | 132 | 73 |
| 29 March | 175 | 51 | 29 |
| 4 April | 98 | 25 | 26 |
| 16 April | 18 | 3 | 17 |

insect and host. One reason for the difference in phenological match of checkerspot with host birth (caused by rainfall) and with host death (senescence) might be that it is easier for a diapausing larva to tell how much rain is falling than for an ovipositing adult to make the crucial distinction between a green *Plantago* that has two weeks of remaining life and one that will survive for the three-and-a-half to four weeks that are necessary from the insect's perspective. The task faced by the larva to achieve synchrony is very different from the task faced by the adult, so it is unsurprising that they are not performed with equal precision.

(b) Case study no. 2: the winter moth and its oak tree host

Winter moth (*O. brumata*) is a typical member of the guild of temperate-zone/subarctic polyphagous lepidopterans specialized to feed in early spring on young, expanding leaves of woody plants (van Asch & Visser 2007). This guild can achieve high densities, cause substantial defoliation and achieve pest status (Hagen *et al.* 2007). Member species are typically time-constrained in feeding and have a lower number of generations per year (usually just one) when compared with guilds feeding on herbs (Cizek *et al.* 2006). Their populations fluctuate significantly more than those of insect guilds feeding on mature leaves of the same trees (Forkner *et al.* 2008).

Winter moth larvae grow quickly and in June form pupae that last through the summer and eclose in early winter (November/December). Males have wings and can fly feebly if there is no wind; whereas, wind or no wind, females are wingless and can only crawl feebly (figure 2b). Each female emerges from her subterranean pupa, finds a tree, climbs it, mates and lays all her eggs on the same tree. Eggs last through the remainder of winter and hatch in early spring (figure 2b).

Pedunculate oak, *Quercus robur*, is a favoured host of winter moth and in Wytham Wood (Oxford, UK), young leaves of oak provided a more suitable resource for larvae than any other host species (Feeny 1970; Wint 1983). Optimum timing of egg hatch on oak should coincide with budburst (van Asch & Visser 2007) but eggs cannot detect budburst directly (Buse & Good 1996). In Wytham in the 1960s, substantial mortality occurred when eggs hatched before the buds

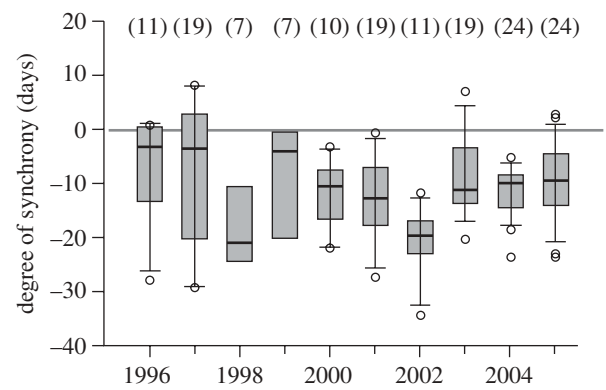


Figure 3. Recent asynchrony between winter moth and oak in The Netherlands. Zero line is median budburst, box-whiskers plots show distribution of hatch times with respect to the individual trees on which eggs were found. Numbers at the top of plot are numbers of trees censused. Adapted from van Asch & Visser (2007).

burst on their natal trees (Feeny 1970; Varley *et al.* 1973). Asynchrony at this same stage has been recently documented in The Netherlands (van Asch & Visser 2007; figure 3). Larval mortality caused by early egg hatch seems typical not only of winter moth on hosts other than oak (Holliday 1985), but also of other spring-feeding Lepidoptera on deciduous trees (DuMerle 1999; van Asch & Visser 2007). However, exceptions do exist: Holliday (1985) reported a range of neonate mortality from 6 to 85% in different studies, and Buse *et al.* (1999) reported relatively close synchrony between budburst and egg hatch at a study site in Wales.

A winter moth larva that hatches from its egg before budburst occurs on its own tree is not automatically doomed. It can live without food for 4–10 days, depending on temperature (Tikkanen & Julkunen-Tiitto 2003; van Asch *et al.* 2007) and can migrate short distances by spinning a silk thread and releasing its hold on the tree, taking off on the breeze in search of a tree with leaves. Entomologists refer to this as 'ballooning'. Because different tree species and even individual oak trees vary by as much as several weeks in their timing of budburst (Tikkanen & Julkunen-Tiitto 2003), some ballooning migrants can leave trees where budburst has not occurred and succeed in finding food. They do so with sufficient frequency that migration can have a clear impact on the distribution of larvae among trees (Holliday 1977). However, the overall rate of survival of neonate emigrants is likely to be low (Zalucki *et al.* 2002). Migration is undirected and risky, and cannot be undertaken many times, because silk is metabolically expensive. Better success is likely to attend migration by larvae that have fed for a while and have accumulated reserves. They are also able to balloon, provided they are still in first or second instar (Holliday 1977 and references therein), and this can be a means of emigration from trees on which synchronization of egg hatch and budburst has been favourable to the moths, with resulting defoliation (Hunter 1992).

The timing of mean budburst varies from year to year, but the relative timing is stable among oak trees;

an early tree is consistently an early tree. Thus, the early tree 'catches the worm'. Among oaks at Wytham studied by Varley & Gradwell, there was very clear association between timing of budburst and subsequent density of feeding larvae: the oaks that waited longest to burst their buds suffered the lowest rates of attack (Hunter *et al.* 1997). Because a wingless female winter moth is likely to climb the same tree from which she descended as a larva (Graf *et al.* 1995) and because the males do not move far (van Dongen *et al.* 1997), it is possible for the moths to evolve local adaptation, such that earlier egg-hatch occurs on earlier-leaving trees. There is evidence that this has indeed occurred both with respect to variation among individual oak trees with differing times of budburst (van Dongen *et al.* 1997) and among tree species (Tikkanen *et al.* 2006).

Adult emergence of winter moth is staggered (Holliday 1985). The phenological difference between early and late egg hatch is less than the difference between early and late adult emergence, hence less than the difference between early and late oviposition. Eggs that are laid late develop faster than those laid early (Buse *et al.* 1999). Despite the compression of egg hatch times relative to adult eclosion times, timing of egg hatch is still remarkably variable for a trait under strong selection. Buse & Good (1996) reported a range of 28 days between earliest and latest hatch in a sample of eggs kept under the same conditions. Modelling of tree and insect responses to climate by Visser & Holleman (2001) indicated that, in The Netherlands, climate warming should cause increasing asynchrony in the absence of evolution, but experimentally applied warming of 3°C to winter moth and oaks in Wales caused no change in synchrony (Buse & Good 1996; Buse *et al.* 1999).

3. FECUNDITY–MORTALITY TRADE-OFFS AS DRIVERS OF ASYNCHRONY

Selection tends to maximize geometric mean fitness rather than arithmetic mean fitness (Gillespie 1977), so that, all else being equal, strategies that minimize variance of success among individuals and among years should tend to evolve. However, at least superficially, this does not appear to be the case for our two study systems, both of which show high variability of successful reproduction among generations (Ehrlich 1965; Varley *et al.* 1973; Hunter *et al.* 1997; McLau-glin *et al.* 2002a; Hellmann *et al.* 2004; Forkner *et al.* 2008).

Life-history theory suggests that fecundity and survival are often subject to trade-offs, whereby either trait can only be maximized at the expense of the other (Roff 1992; Gotthard *et al.* 1994; Higgins 2000; Reznick *et al.* 2000; Roff & Fairbairn 2007). When this occurs, several different combinations of traits affecting fecundity and survival may confer approximately equal fitness, and may coexist, leading to surprising amounts of phenotypic variation in individual traits that strongly affect fitness. This reasoning may explain how winter moth maintains substantial heritable variation in the timing of egg hatch (Buse & Good 1996; van Asch *et al.* 2007).

How can we ask whether the very high mortality rates and high fecundities in our two case histories reflect adaptive strategies to balance conflicting pressures or maladaptive interactions with the particular hosts used in the studies, perhaps stemming from recent migration to a novel habitat in the case of the butterfly (Cushman *et al.* 1994) or from polyphagy in the case of the moth (Wint 1983; Hunter 1990, 1992)? One way to consider the problem would be to ask from a given starting date, what are the consequences for both fecundity and mortality of advancing or delaying insect phenology? In the next two sections, we explore what is known in both systems that would relate to this question.

(a) *The bay checkerspot*

Post-diapause larvae of the bay checkerspot that were programmed to mature earlier and take less risk of offspring mortality from host senescence would of necessity become smaller adults and suffer a fitness cost from reduced fecundity (Boggs 1997; Gotthard *et al.* 2007; Neve & Singer 2008; but see Reznick *et al.* 2000 for discussion of exceptions to this style of logic). Conversely, those programmed to grow large would prolong larval development and benefit from high fecundity at the cost of high risk of mortality for their offspring. In fact, bay checkerspot adults are heavily built and have near-record high fecundity for butterflies: Labine (1968) recorded a mean fecundity of 731 eggs with a likely upper limit around 1200. Cushman *et al.* (1994) measured the sizes of females in the field and calculated that they corresponded to fecundities ranging from 135 to 1680, with a mean around 500. Many females cannot fly well until they have lost weight by laying their first few egg clutches (Labine 1968). These insects appear to have evolved a strategy that maximizes fecundity at the cost of high offspring mortality caused by phenological mismatch with their hosts.

To properly assess the role of a fecundity–mortality trade-off in the evolution of bay checkerspot life history, we would need relevant empirical data for a series of dates in a series of years. Although we have information from several time periods (reviewed by Hellmann *et al.* 2004), data from different studies are not strictly comparable. However, we do have detailed observations on phenology and mortality from a single year, 1970 (Singer 1971), which can be combined with estimates of fecundity obtained from measures of larval growth rates in the field (Weiss *et al.* 1988) to develop a working hypothesis.

In 1970, 290 randomly chosen points at Jasper Ridge were marked with individual flags. Vegetation was censused within two circular quadrats, of radius 5 and 10 cm, centred on each flagged point. The presence of at least four green *Plantago* leaves within the 5 cm quadrat was used to classify the central point as suitable for oviposition and likely to receive eggs, should a searching butterfly alight there. This criterion was based on observed distributions of natural egg clutches. On four dates, starting at the date of earliest oviposition and encompassing the entire season during which butterflies were laying eggs, the small-sized

quadrats were assessed as oviposition sites. At each point judged suitable for oviposition, the larger quadrat was subsequently assessed, two weeks later, for the likely fates at hatching of neonate larvae. If any edible host material (either *Plantago* or *Castilleja*) was present within 10 cm of the flag, then the 'larvae' were classified as 'survived' at least into first instar (Singer 1971). Choice of this criterion for neonate survival was based on observed fates of naturally hatching clutches in the field. Its use underestimates total mortality owing to asynchrony, as host senescence at any time before a larva had reached mid-third instar was observed to result in starvation.

Of the 290 sites examined, 214 had sufficient quantity of *Plantago* for oviposition, but even at the beginning of the flight season on 22 March, the plants were already senescent at 33 of these, leaving 181 judged suitable for oviposition (table 1). The number of suitable quadrats dwindled with each census as senescence progressed, as shown in the first column of table 1. The second column shows the number of sites judged suitable for larvae at egg-hatching and the third, the same expressed as a percentage. For example, of the 175 sites suitable for oviposition on 29 March, 51 (or 29%) were suitable for larvae when eggs laid on 29 March would have hatched.

The temporal pattern of host senescence was not uniform, causing a rapid decrease of survival probability between laying dates of 22 March and 29 March, but a plateau in the middle of the flight season from 29 March to 4 April, and possibly up through 16 April, when the very last eggs were laid. In that year, we estimate that a female larva deciding how large to grow and when to pupate would have sacrificed only 3/29 (or about 10%) of her offsprings' survival by deferring her first oviposition from 29 March till 4 April. How much fecundity would she have gained by the same decision? We can make an educated guess by putting together the known mean weight of eggs (0.23 mg; Moore & Singer 1987) with the measured rates of weight gain by larvae in the field (Weiss *et al.* 1988, 1993). In late January, last instar larvae gained an average of 35 mg d⁻¹ on a 15° south-facing slope and 8 mg d⁻¹ on a 15° north-facing slope (Weiss *et al.* 1993). At 20 mg d⁻¹, one week's growth would add 140 mg to the weight of a female larva. If we assume that about a third of this weight gain would go towards egg production (cf. Gotthard *et al.* 2007); this would amount to around 200 additional eggs.

There is an additional source of variation in adult size/fecundity, as not all larvae are starting from the same size at the same time. Recall that bay checkerspot larvae diapaused at a diversity of sizes, from 1.5 to 16.5 mg. As a result, post-diapause larvae in the same habitat growing in early spring were not all at the same stage of development. Female *E. editha* larvae that find themselves developing late in the season relative to their sisters tend to shorten their development and sacrifice some of their growth, thereby regaining some but not all of the 'lost' time. As a result, the latest-eclosing females are smaller than the earliest ones (Neve & Singer 2008). In

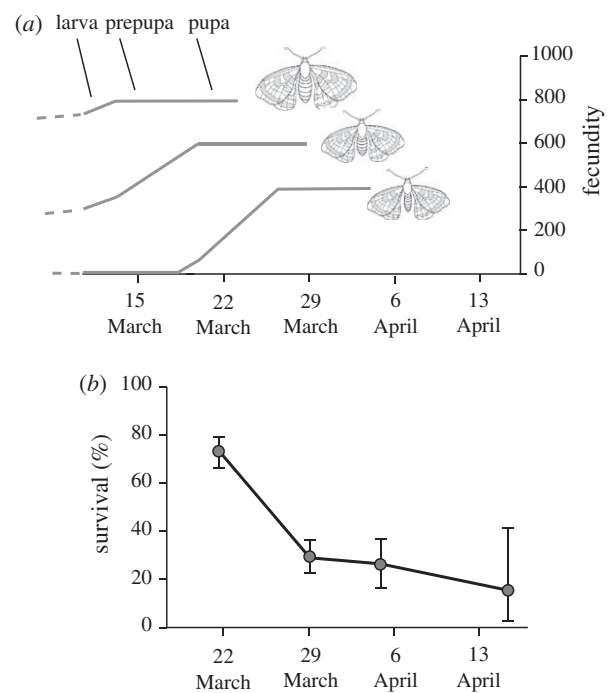


Figure 4. (a) Stylized depiction of bay checkerspot eclosion dates and fecundity gain with larval feeding. The three ascending lines show fecundity gains for female larvae that had broken diapause synchronously at a time earlier than that shown in the figure, at three different (arbitrary) sizes. No fecundity is gained until the larva reaches a size at which it could become adult, hence the smallest larva is feeding but still indicated with zero fecundity as it enters the time period of the graph. Each larva has the option to pupate at any point along its ascending growth curve, with consequent fecundity shown on the ordinate. The pupation times chosen by the insects depicted result in lower fecundity of later-emerging adults, despite the fact that each insect would gain higher fecundity by delaying maturity. The lines do not show weight gain, since insects lose weight when preparing to pupate (prepupa) and during the pupal stage. We have shown fecundity gain rates increasing and pupal durations decreasing as the weather gradually warms from March into April. (b) Estimated survival at hatch from bay checkerspot egg clutches laid on different dates in 1970. Data taken from table 1. Bars show 95% CI. For methods see text.

summary, we expect genetic covariance between size and timing to be positive (late = large) but the environmental covariance is negative (late = small). In *E. editha*, environmental covariance can be the dominant component of the observed phenotypic covariance (Cushman *et al.* 1994; Neve & Singer 2008; cf. Price *et al.* 1988).

We have illustrated these different possible growth trajectories in figure 4a, which shows larvae breaking diapause at three different sizes, with growth and ultimate fecundities estimated as detailed above. In drawing the fecundity curves, we have used Weiss *et al.* (1988) estimates of larval growth rates, but we have shown larvae growing slightly faster at later dates, as the air temperature warms and solar radiation, in which larvae bask, becomes stronger. Within each trajectory, the longer that maturity is delayed, the greater would be the fecundity; however, the larva that is largest when coming out of diapause has the shortest time needed to feed to reach

maximum observed fecundity. Conversely, the smallest post-diapause larva, even though it feeds for longer, is only able to achieve a fraction of this maximum potential. Thus, in our simulation, the earliest maturing female has a fecundity of 800 eggs (the end of the upper grey line) and the latest maturing female only 400 eggs.

Figure 4b shows the hatching survival estimates from table 1, with 95% confidence intervals added. These estimates made in 1970 are similar to direct observations of neonate mortality from the previous year (1969), in which 80 per cent of newly hatched larvae died immediately on hatching, owing to host senescence (Singer 1972). Jointly, figure 4a,b depicts the relationship between larval growth, female fecundity and neonate mortality (but recollect that additional mortality of larvae failing to reach mid-third instar, not shown, is also because of asynchrony). Figure 4b illustrates that the trade-off between fecundity and mortality may result in weak selection on phenology over a span of a week or more. Assuming constant starting larval size and microhabitat, the strategies leading to oviposition on 22 March or on 4 April may result in equally high fitness, for different reasons. High fitness for 22 March ovipositors would stem mainly from high offspring survival, and high fitness for 4 April ovipositors would stem mainly from the higher fecundity of an adult achieved from its prolonged larval feeding.

(b) *The winter moth*

The winter moth also faces a trade-off between fecundity and mortality, though in a very different manner from the checkerspot. Feeny (1970) delayed winter moth egg hatch by about 12 days by chilling them. He then fed groups of delayed fourth instar larvae on frozen leaves of two ages: leaves gathered on 16 May when fourth instar larvae were feeding naturally, and new leaves gathered on 28 May. Larvae fed on late-gathered leaves encountered the accumulation of host defences as those leaves matured and produced very small pupae that had zero survival to adulthood. Subsequent authors have studied changes of leaf quality over shorter time periods and confirmed that the rapid decline of host quality as leaves mature reduces the pupal weight of late-feeding insects (Wint 1983; Buse *et al.* 1999; Forkner *et al.* 2004; van Asch & Visser 2007). Small pupae pay a clear penalty in terms of fecundity (figure 5).

Eggs could play 'safe' in the mortality stakes by hatching late, but many of those that did so would miss the beginning of the time window when young, expanding host leaves were at peak edibility (peak quality for caterpillar growth). Therefore, late hatching reduces both neonate mortality risk and adult fecundity, while early hatching increases risk of neonate starvation but increases the fecundity of survivors. Individuals that hatched so early that they starved to death as neonates are not depicted in figure 5. The dramatic variability of fecundity among those that survived suggests that many eggs hatched too late to maximize fecundity, while a few individuals did indeed hatch very close to budburst. We suspect that

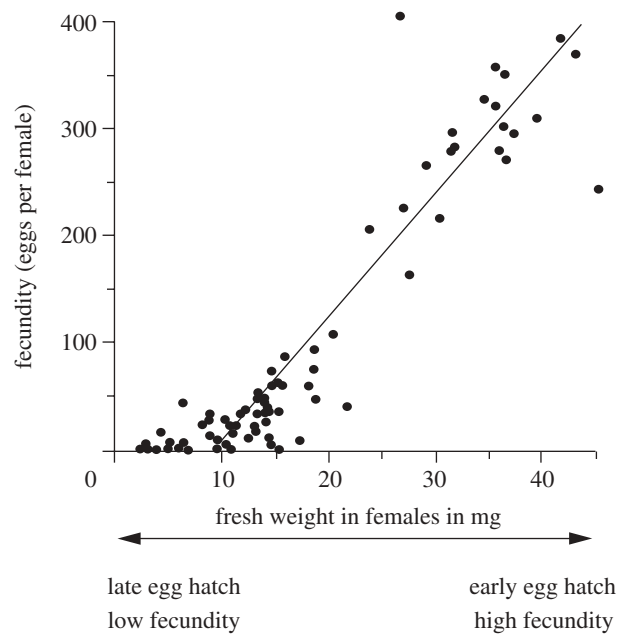


Figure 5. Diversity of body weight and fecundity in a sample of winter moth females collected in a single year in the same apple orchard. Adapted from Holliday (1985).

this is how the single individual with fecundity of over 400 achieved the US pronunciation of its name, the 'winner moth'.

van Asch *et al.* (2007) designed an experiment to estimate natural selection on phenology. They divided neonate larvae into three groups and fed each group leaves from a different tree: one tree with natural budburst 5 days prior to the start of the experiment, one with budburst precisely at the start of the experiment (the 'synchronous' treatment) and one bursting 5 days after the start. Larvae fed leaves from the late-budburst tree were therefore starved for 5 days before they could begin to feed. Larvae fed from the early-budburst tree ate leaves 5 days older than those fed to the 'synchronous' treatment. In contrast to Feeny's (1970) larvae that suffered high mortality when fed leaves 12 days more mature than 'normal', van Asch *et al.*'s larvae suffered no additional mortality when fed older leaves. However, their pupal weight was reduced when compared with the 'synchronous' treatment, from around 45 mg to 26 mg in one replicate and from 43 to 33 mg in a second replicate (fig. 2 of van Asch *et al.* 2007). Larvae fed from the late-budburst tree and starved for 5 days had poor survival, reduced from about 40 per cent in the synchronous treatment to 10 per cent in one replicate and from 60 to 5 per cent in the other. Those that did survive the late budburst treatment had higher pupal weights, probably because they were fed younger leaves than the synchronous treatment throughout their lives.

van Asch *et al.* (2007) calculated the fitness losses, compared with the synchronous treatment, of the 5-day early treatment and the 5-day late treatment. These losses were estimated as being exactly equal, generating a symmetrical fitness curve across different phenologies, with a fitness peak at exact synchrony of mean egg hatch with mean budburst. In consequence, van Asch and co-workers view the current asynchrony as maladaptive and their model predicts rapid

evolution starting from this point (figure 3) 'leading to a restoration of synchrony'. An exception to this prediction, they note, might be maintenance of asynchrony by evolutionary forces not incorporated in their model, such as larval migration between oaks and other tree species with earlier budburst.

Note that in both van Asch *et al.* (2007) and van Asch & Visser (2007), the concept of 'synchrony' is as a population-level trait, in which mean egg hatch coincides with mean budburst and many larvae hatch before budburst. This is only an optimal strategy if deviations from exact synchrony have equal effects in both directions, as calculated by van Asch *et al.* (2007). If, however, fitness curves for hatch time relative to budburst were not symmetrical, we would expect the optimal hatch date to differ from synchrony (cf. Martin & Huey 2008). For example, if fitness consequences of late egg hatch were more severe than those of early hatch, an asynchrony in the direction of early hatch, as is observed, would be predicted (cf. Ruel & Ayres 1999).

4. ASYNCHRONY DRIVEN BY CO-EVOLUTIONARY ARMS RACE?

Synchrony between exploiter and victim is adaptive from the perspective of the exploiter; however, optimal phenology from the victim's perspective might be very different. The victim would benefit from a phenology in which its most vulnerable life stages were concentrated in 'enemy-free time', when the exploiter is least active. To the extent that victims have some degree of success in evolving timing to escape exploiters, then a resulting coevolutionary arms race would generate asynchrony between the interacting species. Thus, as we hinted in §1, coevolutionary dynamics lead to an expectation for greater baseline synchrony between mutualists than in exploiter–victim interactions.

Consider the hypothesis that asynchrony between winter moth egg hatch and oak budburst is perpetuated by evolution of oaks, specifically by evolution of late budburst and early accumulation of chemical defences. Logically, we might expect the moth to win any coevolutionary arms race with the tree, since its generation time is much shorter. However, theory appears to be conflicting on this prediction (references in Hoeksema & Forde 2008) and empirical evidence fails to support the hypothesis that generation times are important in this context. Hoeksema & Forde (2008) defined 'locally adapted' parasites as those that performed better on their own host population than on other populations of the same host species in reciprocal transplant experiments. Applying this definition to a meta-analysis of 27 parasite–host systems, Hoeksema & Forde (2008) found no evidence that the relative generation times of parasite and host influenced the degree of local adaptation of a parasite population to its own host population. Instead, they found that relative rates of gene flow were most important, with parasites achieving better local adaptation when their rates of gene flow were greater than those of the host.

In most years, all oaks are attacked by winter moth to some extent. However, recall that trees with early

budburst supported higher populations of herbivores. Oaks in the same population were dramatically variable in the timing of budburst (Varley *et al.* 1973). As in the moth, when we see variability of a trait that strongly affects fitness, we suspect that a trade-off lurks close by. In the case of oaks, there is a trade-off between resistance to early-feeding caterpillars (not only the winter moth) and potential for growth in years of low herbivore density. The presence of trade-offs in both moth and tree helps illustrate why the outcome of any coevolutionary arms race is hard to predict. Evolution of timing of egg hatch involves the trade-off of fecundity and mortality in the moth, and evolution of budburst time involves the trade-off between growth and tissue loss from herbivores. These effects are unlikely to be symmetrical between the interacting species!

In the checkerspot–*Plantago* system, we have a lower expectation that host-evolved defence might affect phenological synchrony. The observed densities of insects and plants at Jasper Ridge (Singer 1971; Hobbs & Mooney 1985) did not allow for more than about one plant in a thousand to receive eggs and be vulnerable to attack by pre-diapause larvae. Further, by the time that eggs hatched, the plants that were still alive had matured the majority of their seeds and were beginning to senesce. But the hypothesis that plant defence is involved seems testable in this case, albeit with very low power. Most populations of *Plantago erecta* on serpentine soils have no recent history of attack by the butterflies; some, such as Jasper Ridge have been recently attacked and are now released, while the Morgan Hill population is currently attacked. If the butterflies are acting as selective agents to maintain early senescence of their hosts, common-garden experiments with these populations should show Morgan Hill plants to be the shortest lived.

5. ASYNCHRONY PERPETUATED BY GENETIC CONSTRAINTS ON SIZE OR PHENOLOGY?

Might asynchrony reflect genetic constraints on size or phenology independent of life-history trade-offs? In our two case study systems, there is little evidence for this mechanism being the main force driving observed asynchrony.

Edith's checkerspot has considerable interpopulation variation of adult size that is maintained in laboratory culture when insects are raised in a common environment and on a common host. The population-level mean mass of a newly eclosed female varied from 102 to 325 mg (Singer & Hanski 2004). The mean weight of newly eclosed females of the bay checkerspot is towards the high end of this range, in the order of 250 mg (Cushman *et al.* 1994). It seems unlikely, then, that a genetic constraint would prevent evolution to a smaller adult size with shorter lifespan, earlier eclosion and reduced offspring mortality.

In its capacity to affect phenological match/mismatch, the functional equivalent to adult size of the checkerspot is the timing of egg hatch of the winter moth. Is egg hatch timing subject to constraint or free to evolve a locally adaptive value? van Asch *et al.* (2007) showed that it is free to evolve by

demonstrating substantial heritable within-population variation. The response of moth eggs to temperature treatments depended not only on the identity of their mother but also on that of their father. Winter moth egg hatch also showed extensive heritable variation among study sites (Tikkanen *et al.* 2006) and among trees with differing phenology (van Dongen *et al.* 1997). Therefore, populations of the moth with high mortality do not seem to be under genetic constraints that prevent them from evolving later egg hatch and better synchrony with budburst... and, indeed, such evolution is occurring (van Asch *et al.* in preparation).

6. OBSERVED RESPONSES OF TARGET SPECIES TO CLIMATE CHANGE

Both of our two case study systems have been sensitive to the small levels of climate change that they have experienced during the past century, but have shown different types of response. The observed effects of climate change on the bay checkerspot have been dramatic impacts on population dynamics, causing extinction of a long-studied metapopulation (McLaughlin *et al.* 2002a). Evolutionary responses have not been investigated. Impacts on the winter moth involve significant evolution of egg hatch phenology (van Asch *et al.* in preparation) as well as population dynamic effects (Hunter *et al.* 1997).

(a) *Bay checkerspot*

As we have described, the baseline condition of bay checkerspot involved routinely high mortality caused by phenological mismatch with its host plants. If the degree of this asynchrony were to vary among years in response to climate, then the population dynamics of the butterfly would be highly climate-sensitive. We do indeed have a strong expectation that plants and insects should respond differently to climate, based on differences in their biology. Both plants and insects are time-limited and under selection to develop fast, although in caterpillars speed of development may suffer a trade-off with resistance to starvation (Gotthard *et al.* 1994). Checkerspot larvae are black, bask when the sun shines and develop faster when they can do so. Their host plants, in contrast, are not black and do not bask in the sense that a mobile animal can do. These annual plants live longer in years when the wet season is prolonged or when weather is cool (Hellmann *et al.* 2004, p. 49). Host developmental rates and eventual senescence are not expected to depend on climate in exactly the same way as larval growth. In fact, they did not. Weiss *et al.* (1988) found that small differences in air temperatures in the field (6°C on average between north- and south-facing slopes) were enough to alter the relative timing of butterfly egg-laying and host-plant senescence, such that the window for feeding by pre-diapause larvae could be as long as 17 days (for north-facing slopes) or could collapse to nothing, with the average egg mass being laid after host senescence, on south-facing slopes. Singer (1971) found that the time difference between peak oviposition and 50 per cent host senescence was not constant among years, varying by 6 days across 4 years of

study. It should vary more widely over longer time periods. We therefore expect the insects to have climate-sensitive population dynamics (Ehrlich 1965; McLaughlin *et al.* 2002a). Warming *per se* is not necessarily deleterious, however: in a greenhouse experiment using natural plots containing both host species, Hellmann (2002) found increased larvae survival when experimental radiative heat raised mean soil surface temperatures from 20°C to 30°C.

Early work showed that the year-to-year dynamic trend in the two larger Jasper Ridge populations, relative to each other, was significantly associated with spring rainfall in the first year of each pair of years (Singer 1971). Subsequent population fluctuations at Jasper Ridge were modelled against climate data by McLaughlin *et al.* (2002a), who showed that fluctuations of insect numbers in the topographically homogeneous patch were more tightly linked to climate than those in the patch with greater diversity of slope aspect. Using a long-term dataset from 1969 to 1998, they identified a strong role of climate in the overall population dynamics, and implicated increasing inter-annual variability of rainfall in the decline of the butterfly (McLaughlin *et al.* 2002b). The Jasper Ridge populations winked out one by one and the small three-patch metapopulation that Ehrlich had studied since the 1950s (Ehrlich 1961, 1965) became extinct in the early 2000s (McLaughlin *et al.* 2002a,b). As predicted (Singer 1971; Weiss *et al.* 1988), the population with the highest topographic diversity held out longest. In summary, McLaughlin *et al.* (2002a) wrote that 'the routes to extinction for *E. e. bayensis* in protected habitat were random walks driven by climatic variability'.

This insect was unlikely to be able to compensate for effects of changing climate on its density because its populations were only weakly regulated (Singer 1971, 1972; Singer & Ehrlich 1979; Harrison *et al.* 1991; McLaughlin *et al.* 2002a). Pre-diapause larvae died of starvation because their hosts senesced, not because hosts had been eaten by conspecific larvae. This source of mortality would not be alleviated in years of low butterfly density, yet mortality at this stage of the life cycle was so high in each year of the original study (1968–1971) that there was little latitude for population regulation to be generated from factors acting at other stages (Singer 1971; Singer & Ehrlich 1979). Among the various ecotypes of Edith's checkerspot, the bay checkerspot has been particularly vulnerable to yearly climate variability (Singer & Ehrlich 1979).

Climate-related population extinctions of Edith's checkerspot, caused by differing responses of plants and insects to drought, were first reported by Singer & Ehrlich (1979) and Ehrlich *et al.* (1980). Larvae can respond to drought conditions by feeding for a few days after breaking diapause and then re-entering diapause until the following year. However, they do need to find at least a small quantity of food to replenish their reserves. A suite of populations feeding on the annual *Collinsia tinctoria* became extinct when host seeds responded to the California drought of 1977–1978 by not germinating at all (Singer & Ehrlich 1979; Ehrlich *et al.* 1980). Taking these observations along with those of the asynchrony between bay

checkerspot and its two annual hosts, it is not surprising that populations of Edith's checkerspot adapted to perennial hosts (especially the genus *Pedicularis*) have been dynamically more stable and suffered significantly lower extinction rates than populations feeding on annual plants (Thomas *et al.* 1996; Boughton 1999).

The bay checkerspot's sensitivity to climate variability is paralleled in other Edith's checkerspot subspecies. Major fluctuations of populations in other ecotypes of *E. editha*, including population booms and extinctions, have been driven by extreme climate events and extreme climate years (reviewed by Parmesan 2003). Over the species' range as a whole, from Baja California to Alberta and from sea level to over 3000 m, patterns of population persistence and extinction led to statistically significant increases in mean latitude and mean altitude of extant *E. editha* populations over the latter part of the twentieth century (Parmesan 1996). Edith's checkerspot proved a harbinger of the general trends towards upward shifts in elevational ranges and poleward shifts in latitudinal ranges that are currently occurring under climate warming (Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006).

(b) Winter moth

Unlike the checkerspot, the winter moth has substantial density-dependent mortality, stemming from predation in the pupal stage (Varley *et al.* 1973; Hunter *et al.* 1997). Depending on the form of the density-dependence, the moth's population dynamics are likely to be buffered against effects of climate change that would exacerbate the mortality from asynchrony with hosts. Any increase in mortality of neonate larvae at egg hatch would tend to be mitigated by decreased mortality of pupae. Nonetheless, strong natural selection is associated with the degree of synchrony between moth and tree at each of two stages: first, asynchrony between egg hatch and budburst influences neonate mortality, and then later, asynchrony between late-instar feeding and leaf maturity affects fecundity. Because changing climatic conditions have been advancing the phenology of the moth more than that of the oaks, and because timing of egg hatch is heritable, we expect to see rapid evolution of moth phenology. Irrespective of whether the baseline relationship between moth and tree were synchronous or asynchronous, if that baseline were adaptive and has been changed, we expect to see it restored. This seems to be exactly what is happening. The reaction norm that describes the relationship between timing of egg hatch and winter temperature regimes has changed significantly between 2000 and 2005 (van Asch *et al.* in preparation), in the direction that would reduce the strength of moth–tree asynchrony. This result is reminiscent of the climate-induced evolution of response to photoperiod in pitcher-plant mosquitoes (Bradshaw & Holzapfel 2001).

7. INTERACTIONS BETWEEN VOLTINISM, GEOGRAPHY AND CLIMATIC STRESS

We have focused here on univoltine species, that is, species with a single generation per year. However,

many insects typically have different numbers of generations per year in different regions or even in nearby habitats with different mean temperatures (Friberg & Wiklund 2010). In consequence, the extent to which they are under climatic stress can vary in a complex geographic pattern. A species may be living at the limits of its ecological tolerance as bivoltine populations at one latitude, while a few kilometres closer to the pole, this same species may be univoltine (either facultatively or obligately). The switch to a single generation creates unused 'spare' time in the growing season, removes climatic stress stemming from phenology and frees populations to use resources on which development is slow (Nylin 1988; Scriber & Lederhouse 1992). As populations approach the poleward range boundary, a single generation may fill the available growing season (or development may take several years) and climatic stress may re-assert itself. Thus, the extent to which climate is a limiting factor, or exerts strong selection, can emerge from interactions between each population or ecotype and its resources, rather than simply increasing towards range boundaries. Further, the potential for plastic or evolutionary responses may differ among conspecific populations as it does between *Parus major* (great tit) in the UK and in The Netherlands (Charmantier *et al.* 2008).

8. CONCLUSIONS

Both of our focal lepidopteran species have evolved high-risk life-history strategies. While winter moth eggs gamble with their own lives by hatching early, bay checkerspot caterpillars gamble with the lives of their offspring by growing large and eclosing late as adults. In each case, the result is the evolution of populations in which large numbers of individuals die because they fail to fit their life cycles into the available timespan. Because such a population exists near the limits of its ecological tolerance, it is particularly vulnerable to impacts of climate change.

Regardless of the extent to which baseline starting points for global warming impacts involve synchrony or asynchrony, rapid changes in the degree of synchrony seem inevitable. Two species in baseline synchrony would clearly become less synchronous with climate change. In contrast, two species that begin in asynchrony, like our focal species, could either become better synchronized or even more mismatched with climate change.

It is this latter possibility that has dominated the literature on the implications of observed shifts in species' phenologies. One estimate is that 62 per cent of species (mostly Northern Hemisphere) have shifted their timing in response to warming trends of the past four decades (Parmesan & Yohe 2003), with different taxonomic groups and different trophic levels showing significantly different magnitudes of response (Parmesan 2007; Thackeray *et al.* 2010). If species that depend on each other are indeed showing different magnitudes (or even directions) of response, then the implications are both obvious and severe.

Ectotherms are particularly sensitive to climate (Huey & Kingsolver 1993; Kingsolver 2009), and

Lepidoptera are particularly sensitive ectotherms (Dennis 1993). The potential importance of climate change to climate-sensitive endangered species, such as the bay checkerspot is self-evident. In contrast, the winter moth is far from being an endangered species: it is a forest pest with frequent outbreaks (Cuming 1961; Hagen *et al.* 2007; Jepsen *et al.* 2009). However, as a typically abundant species, it is such an important link in the food chain that a decline in its abundance owing to reduced synchrony with oak would affect not only the moths but also the birds that depend on them to raise their chicks. The relationship between the birds and moths is in turn susceptible to effects of changing climate (Van Noordwijk *et al.* 1995; Cresswell & McCleery 2003; Gienapp *et al.* 2006; van Asch & Visser 2007; Both *et al.* 2009).

Here, we chose to explore two systems that are generally agreed to be well-studied, with multiple research groups publishing dozens of papers over more than 40 years. Yet, even then, we find it difficult to quantify what has happened to phenological synchrony and to predict what is likely to happen to it in the future. In these systems, one cannot argue that insufficient quantity of research, in a general sense, is the culprit. In both the bay checkerspot and the winter moth, difficulty in documenting long-term changes in phenological synchrony stems partly from successive groups of researchers having recorded information on phenologies, fitnesses, and so on in different ways that are not strictly comparable. In order to properly record both phenological change and the population dynamic responses emerging from it, we will need better standardization of observations (Visser & Both 2005; Miller-Rushing *et al.* 2010), as well as funding support for long-term monitoring of a suite of ecological measures on target species.

Projections of future impacts of climate change on biodiversity rely crucially on understanding current responses. With respect to species' interactions, impacts are often inferred from very few years of data. However, we argue that such short time series are inadequate to determine true impacts if their interpretation relies on assumptions about the historical nature of the interaction. Given the deficit of long-term datasets, we usually do not know the extent to which the starting points of species' interactions (prior to current anthropogenic change) involved synchrony or asynchrony. Therefore, we also do not know when findings of current asynchrony are, in fact, impacts of recent climate change, and when they are simply stable, complex adaptive strategies resulting from evolution of life histories or coevolutionary dynamics. The case studies here, coupled with a few other well-understood systems, clearly indicate that the ultimate impacts of climate change on wild species will depend in complex ways on existing life-history trade-offs, interactions among multiple trophic levels, adaptations to historical climatic stresses, and behavioural and physiological plasticity, as well as on evolutionary change (Hoffmann & Blows 1994; Carroll *et al.* 2001; Cresswell & McCleery 2003; Parmesan *et al.* 2005; Balanya *et al.* 2006; Chown *et al.* 2007; Charmentier *et al.* 2008; Both *et al.* 2009; Kingsolver 2009; Kirkpatrick 2009; van Asch *et al.* in preparation).

For the moment, our level of confidence is higher for achieving a qualitative understanding of species' responses than a quantitative one. To improve the state of the science, we need to develop generalizations about which classes of species' interactions in which types of environment will respond in particular ways. With climate change progressing rapidly, and scientific datasets severely historically limited, it behoves the scientific community to partner with individuals and organizations to incorporate non-traditional data sources into scientific assessments (Root & Schneider 2006). Amateur naturalists, both dead and living, are an under-used source of valuable information on species' biologies (cf. Miller-Rushing & Primack 2008). To improve our projections of climate change impacts on species and systems in time for that information to be useful in protecting these same species from the worst impacts of global warming, we need to combine the expertise of natural historians, community ecologists and evolutionary biologists working on behavioural and physiological responses to environment, including evolution of life-history strategies.

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