

Phenological synchrony between a plant and a specialised herbivore

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Received 5 December 2013; accepted 21 May 2014
Available online 29 May 2014



Abstract

Global anthropogenic climate change is altering the phenology of many species, with implications for interacting species. If species use different cues or respond at different rates, this could result in asynchrony between hosts and herbivores. The larval stage of the endemic critically endangered Sinai Baton Blue butterfly (*Pseudophilotes sinaicus*) feeds exclusively on the buds and flowers of an endangered near-endemic plant, the Sinai Thyme (*Thymus decussatus*), with a narrow window in time when both larvae and flowers are present. We test for synchrony in time and space between the flowering phenology of the host plant and the associated timings and abundances of the Sinai Baton Blue. Together with significant spatial variation amongst patches, there were large inter-annual variations in flowering period, up to two weeks between years, indicating phenotypic plasticity in response to abiotic conditions. The butterfly flight period was approximately synchronised to the flowering of its host plant, but there was no evidence of any detailed spatial or temporal correlations in phenology. The dramatic annual population changes, possibly cycles, in the butterfly, may partly be driven by differences in the responses between plant and herbivore to climate that cause varying degrees of synchrony between years.

Zusammenfassung

Der globale anthropogene Klimawandel verändert die Phänologie vieler Arten, was Auswirkungen auf interagierende Arten hat. Wenn Arten unterschiedliche Signale nutzen oder mit unterschiedlicher Geschwindigkeit reagieren, kann dies zu Asynchronität zwischen Wirten und Herbivoren führen. Die Larven des endemischen, vom Aussterben bedrohten Sinai-Bläulings (*Pseudophilotes sinaicus*) fressen ausschließlich an den Knospen und Blüten einer gefährdeten, fast endemischen Pflanzenart, des Sinai-Thymians (*Thymus decussatus*), wobei es ein enges Zeitfenster gibt, während dessen sowohl Larven als auch Blüten vorhanden sind. Wir prüften die Synchronität in Raum und Zeit zwischen der Blühphänologie der Wirtspflanze und dem zugehörigen zeitlichen Auftreten und der Abundanz des Sinai-Bläulings. Zusammen mit signifikanter räumlicher Variation unter den patches gab es große Schwankungen zwischen den Jahren bei der Blühperiode (bis zu zwei Wochen), was auf phänotypische Plastizität in der Reaktion auf abiotische Bedingungen hinweist. Die Flugperiode des Bläulings war ungefähr mit der Blüte der Wirtspflanze synchronisiert, aber es gab keinen Beleg für eine detaillierte räumliche oder zeitliche Korrelation bei der Phänologie. Die dramatischen jährlichen Populationsschwankungen, möglicherweise Populationszyklen, des Bläulings könnten zum

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Teil durch Unterschiede zwischen Pflanze und Herbivor hinsichtlich ihrer Reaktion auf das Klima bestimmt werden, wodurch sich unterschiedliche Grade der Synchronität in einzelnen Jahren ergeben.
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Keywords: Phenology; Phenotypic plasticity; Mismatch; Population cycle; Host plant; Butterfly; Egypt

Introduction

Climate change, particularly global warming, poses a serious threat to many species, with habitats expected to become drier accompanied with a rise in average temperatures (Giannakopoulos et al. 2009). Species dependent on environmental cues face problems if climatic patterns change, especially for herbivorous insects where ecological success is correlated to synchrony with host plants (Powell & Logan 2005). Some interacting species will use the same cues and show similar magnitudes of response, but not all species will respond in the same way (Phillimore et al. 2012). Such differences in species response to cues could result in increasing levels of asynchrony between interacting species, with the potential for a complete mismatch leading to extinction (Visser & Holleman 2001). Short-lived species are particularly vulnerable because consecutive years of sub-optimal resources (both in terms of quantity and quality) could lead to rapid declines in numbers and the possibility of local extinction. Synchrony can have vital consequences for the whole set of interacting species, affecting their population dynamics through bottom-up forces (Miller-Rushing et al. 2010).

Spring temperatures play a dominant role in determining plant phenology, with advancing phenologies associated with rising spring temperatures (Cook et al. 2012). The phenology of many plants in the Northern hemisphere is affected by spring temperatures (Doi and Katano 2008; Ovaskainen et al. 2013), but by no means all, since flowering can be influenced by other abiotic cues, particularly photoperiod, but also soil moisture and winter temperatures (Anderson et al. 2012; Cook et al. 2012). A study of 500 plant species in Concord (Massachusetts, USA) since 1852 showed that flowering has advanced 3.3 days earlier in the year per 1 °C rise in mean monthly temperatures for January, April and May (the last two being the two months preceding flowering) (Miller-Rushing & Primack 2008). The pattern of extinctions observed in Concord indicates that susceptibility is linked to climate response: species whose phenology did not follow the rising temperatures were much more likely to become locally extinct (Willis et al. 2008). Spatial variation in the phenology of host plants leads to pressure for their associated herbivores to be phenologically synchronised appropriately, otherwise there might be detrimental consequences for their population dynamics and abundance (Phillimore et al. 2012). For butterflies that can move, however, spatial variation in host–plant phenology could act as an insurance mechanism against temporal variation in their phenology (Weiss et al. 1988).

Insect herbivores also respond to rising average temperatures, usually by a shift in the flight season: adult emergence in many insect species varies with temperature and other environmental cues (Van Asch & Visser 2007; Robinet & Roques 2010). In general, insect phenologies seem to be changing at a steeper rate than plant phenology. This could lead to the adult insects appearing earlier when there are fewer resources, reducing survival and reproduction (Gordo & Sanz 2005; Mattila et al. 2006). Climate change seems also to be altering population cycles, disrupting mutually beneficial ecological interactions, particularly in insects whose life cycles are climate-dependent (Ims et al. 2008; Memmott et al. 2007).

There is a lack of long-term observational data that establish the extent of asynchrony and mismatches across multiple systems (Miller-Rushing et al. 2010). Where there have been long-term studies, such as the phenological timings of the plants in Concord, there are no recordings of their interactions with insects (e.g. pollinators), so it is impossible to investigate changing levels of synchrony (Miller-Rushing & Primack 2008; Singer & Parmesan 2010). In most cases we do not know what the ‘normal’ levels of asynchrony are, making it impossible to say whether detrimental effects of asynchrony are being exaggerated (Singer & Parmesan 2010).

Here we study the critically endangered Sinai Baton Blue butterfly and its exclusive larval host plant, the Sinai Thyme, an endangered plant growing in the arid mountains of the St Katherine Protectorate in South Sinai in Egypt, the most arid country in the world (FAO 2012, www.fao.org/ last accessed 10/03/2013). We study spatio-temporal variation in the timings of butterfly flight period and host plant phenology among ten patches.

Materials and methods

The study system

The Sinai Baton Blue butterfly (*Pseudophilotes sinaicus* Nakamura, 1975: Lycaenidae) is critically endangered, one of two endemic butterfly species in the St Katherine Protectorate, South Sinai, Egypt and a flagship species for the area (Thompson & Gilbert 2013). The larvae feed exclusively upon the buds and flowers of the host plant, Sinai Thyme (*Thymus decussatus* Benth, 1834: Lamiaceae), restricting the butterfly’s distribution to a network of patches on the mountaintops above 1800 m (James 2006c; Thompson & Gilbert 2014). The host plant only grows in well-defined soils

in open farshes (plateaus) or gullies separated by arid steep slopes. There is a narrow time frame of just a few weeks when the plant is flowering and larvae are present before they pupate and overwinter as a pupa. This increases the importance of flower availability in spring, intensifying the seriousness of mismatches and hence making the butterfly very sensitive to any shift in thyme phenology or changes to its own flight season (James 2006c). Over at least the past two decades there have been severe fluctuations in precipitation in the hyper-arid landscape. The extent to which these variations are normal for the area is uncertain because of incomplete meteorological records, and so we are dependent on local Bedouin knowledge.

The fieldwork was carried out upon the Mount Sinai massif above the town of St Katherine, where there are ten patches of thyme varying in size from 37 to the 659 thyme plants of Farsh Shoeib (see Appendix A: Table 1), previously (James et al. 2003) found to hold one of the largest butterfly populations (see Fig. 1). Farsh Shoeib is the only patch where thyme phenology has been recorded in the past (in 2002). In contrast, its butterfly population has been surveyed each year since 2002, and these data suggest that the patch population undergoes cycles with an apparent three-year period (Gilbert et al. 2010), involving large increases in population size and crashes to very low numbers. The underlying drivers of this cycle are unknown. Fieldwork was carried out in Farsh Shoeib in spring 2010, and across all the patches of the massif in spring 2011 and 2012.

Monitoring phenological timings

To compare the flowering phenology with 2002, plants were scored according to the same phenological scale created by James (2006b). The plants vary in size from 10 cm in width to several metres, and there is often significant variation in the phenology among parts of a single plant. Once a week, from the first weekend in April, five inflorescences were randomly selected from the most advanced area of flowering on the plant and scored phenologically on a scale of 0–7 (see Appendix A: Table 2): the average of the five scores represented the weekly phenological state of plant. In 2010, 642 plants were surveyed weekly in Farsh Shoeib, whilst in 2011 and 2012, 100 plants were randomly selected and scored from Farsh Shoeib. To compare the phenological synchrony amongst patches in 2011 and 2012, 50 plants from each of the remaining patches were randomly selected and scored, apart from Safsafa which had less than 50 plants so we scored every plant, per year.

Monitoring the status of the Sinai Baton Blue

In order to monitor the synchrony of the flight season and the relative population abundance, a transect was walked the length of every patch twice a week between 10 am and 2 pm – the peak time of adult flight activity – to count the numbers.

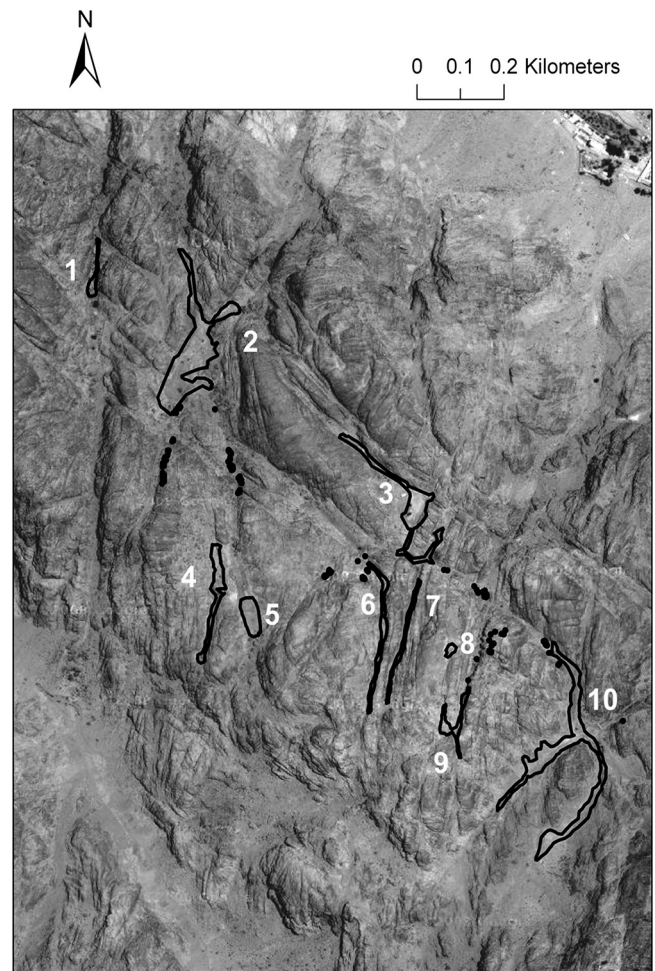


Fig. 1. Map of the perimeter of the Sinai Thyme (*Thymus decussatus*) patches upon the Mount Sinai massif, with the dots indicating isolated individuals outside patches: (1) Farsh Safsafa; (2) Farsh Shoeib; (3) Farsh Loza; (4) Lower Hammar; (5) Upper Hammar; (6) Gulley Zahtuna; (7) Gulley Sharr; (8) Elia Circle; (9) Elia Garden; (10) Farsh Elia. The monastery of St Katherine is seen in the top right of the map.

Transects started in mid-April and finished at the end of June. Since the lifespan of an adult was estimated by James (2006a) to be 3–6 days, we assumed that butterflies seen on any one transect had not been seen on any previous transect, and also that each individual was only seen once during the transect (the butterflies are extremely sedentary: see James 2006c). Larval phenology was recorded in 2010 based on weekly hand searches of 131 plants in Farsh Shoeib.

The numbers of adults recorded in Farsh Shoeib in 2010–2012 were compared to previous survey data collected between 2002 and 2009 (Gilbert et al. 2010).

Analysis of data

All analyses used the statistical package R 2.14.1 (R Development Core Team 2012) and models were simplified

in accordance to Zuur et al. (2009) based on the Akaike Information Criterion (AIC) using stepwise backwards deletion of model terms. The phenology was compared amongst years using three summary indices for each plant: (i) the average phenological score; (ii) the week when the first flower was seen; and (iii) the week of peak flowering. The average phenological score was the mean score attained per plant per year based on eleven weekly surveys from April to mid June. Weeks were counted from the 1st April in both years. Non-flowering plants were excluded from analysis (7 excluded in 2011, 58 in 2012, $n = 532$ each year).

To test for temporal variation in phenology in Farsh Shoeib, a one-way ANOVA was used, using the R routine *glm*, with the three summary indices (as above) as response variables and year as a factor ($n = 851$ in 2002, 642 in 2010, 100 in 2011 and 2012). The average phenological score had a normal distribution and significance was assessed with an F -ratio, whilst the other two indices had a Poisson error structure and were assessed using a χ^2 test. Spatio-temporal differences across the massif were tested with a two-way GLM with patch and year (2011 and 2012) as factors.

A further GLM compared the butterfly flight season amongst years, with the week in which each individual butterfly was seen as the response variable and the year and patch as factors. Some patches in some years had no butterflies, reducing degrees of freedom. This analysis assumed the butterflies seen each week were independent of one another (because butterfly lifespan is only 3–6 days); although not perfect, a normal distribution of residuals was the best fit: significance was assessed with an F -test. To check on the assumption of independence, we also compared the weighted (by numbers) average peak flight period per patch between years using a paired Wilcoxon test, excluding the patches without sightings in 2012.

To compare the flight period in Farsh Shoeib we again assumed that the weekly numbers of butterflies were independent and used a Kruskal–Wallis test, comparing the weekly numbers from the end of April. A Pearson correlation tested the association between relative butterfly abundance and peak flowering across all patches in 2011 and 2012.

Results

Plant flowering phenology

The 2010 flowering season in Farsh Shoeib was clearly (Fig. 2a) more advanced than the other years, whilst the other three years all had similar phenological timings. 2011 had the latest phenology (with the lowest average score and week of peak flowering), while in 2012 it was slightly earlier than in 2002 and 2011. There were highly significant differences in the average phenological score ($F = 43.8$, $df = 3.1534$, $p < 0.001$), the week of first flower ($\chi^2 = 165$, $df = 3$, $p < 0.001$) and week of peak flowering ($\chi^2 = 96.2$, $df = 3$, $p < 0.001$).

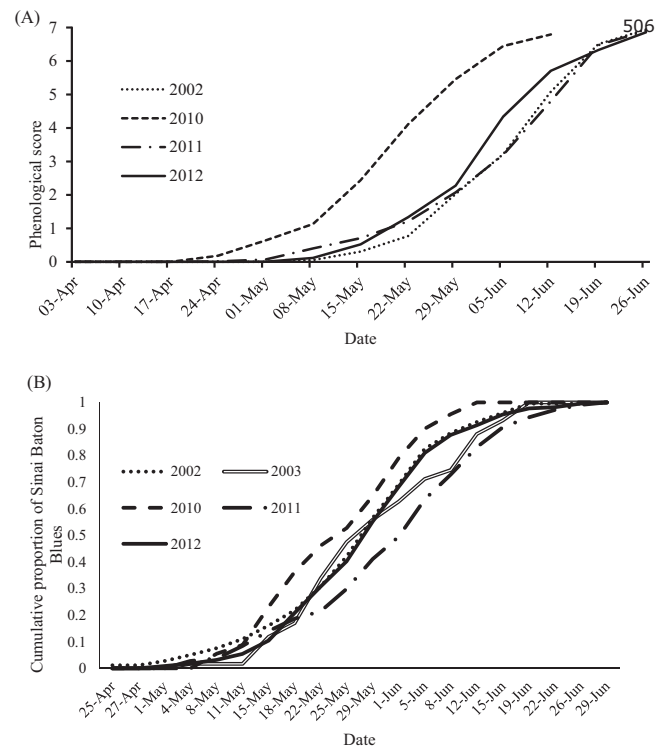


Fig. 2. Comparisons of (A) the flowering season of *Thymus decussatus* in Farsh Shoeib as recorded by the mean phenological score in 2002, 2010, 2011 and 2012, see Appendix A: Table 2, and (B) the cumulative proportion of Sinai Baton Blue butterflies seen in Farsh Shoeib in 2002, 2003 and 2010–2012.

The average phenological scores amongst patches across the massif (Fig. 3) were significantly different between years ($F = 20.4$, $df = 1.984$, $p < 0.001$), amongst patches ($F = 45.1$, $df = 9.984$, $p < 0.001$) and with a significant interaction ($F = 2.69$, $df = 9.984$, $p < 0.01$). The average phenology was earlier in 2012 in the majority of patches; Lower Hammar remained the earliest-flowering patch whilst Farsh Safsafa was the last to flower; there was approximately a 2–3 weeks difference in flowering between these two patches in 2011. Comparing the phenologies in detail, the 2012 flowering commenced later but the flowering season was more condensed, with peak flowering occurring slightly earlier (Fig. 2a).

Butterfly phenology

The adult flight period (Figs. 2B and 4) in Farsh Shoeib varied significantly amongst years ($\chi^2 = 3.56$, $df = 4$, $p = 0.006$). 2010 had the earliest flight period over the years with the first peak in mid-May whilst the remaining patches peaked consistently towards the end of May/beginning of June. Overall, 2011 had the latest flight period. In 2010, larvae appeared on the plants towards the end of the main flight season, when butterfly numbers were decreasing. Larvae were first seen when plants were at their flowering peak (Fig. 5), with the

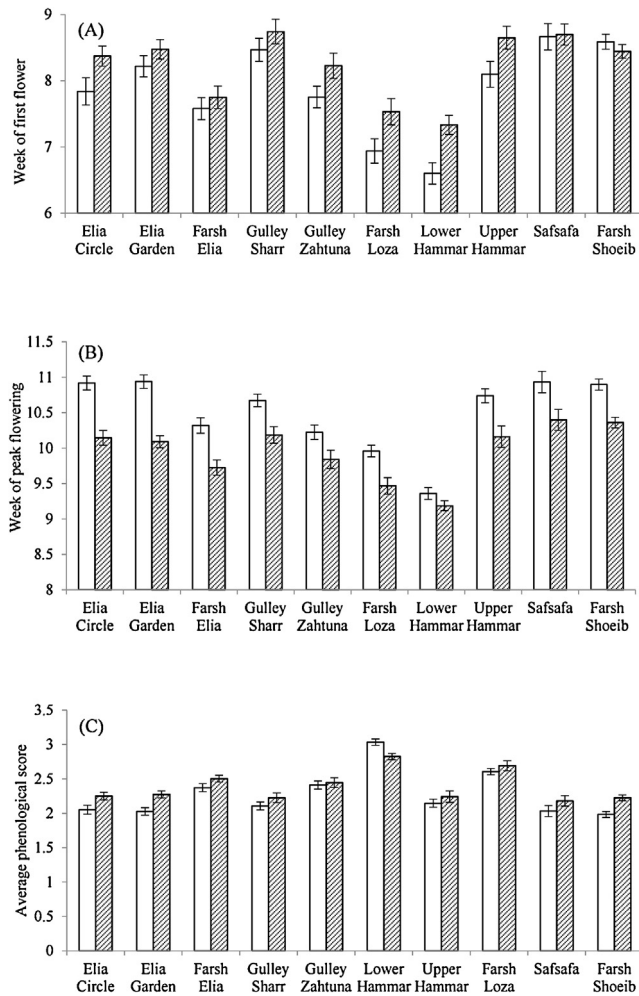


Fig. 3. Comparisons of the phenology of *Thymus decussatus* on the Mt. Sinai massif showing the (A) week of first flower (B) week of peak flowers and (C) average score in 2011 (white bars) and 2012 (striped). Mean ± SE.

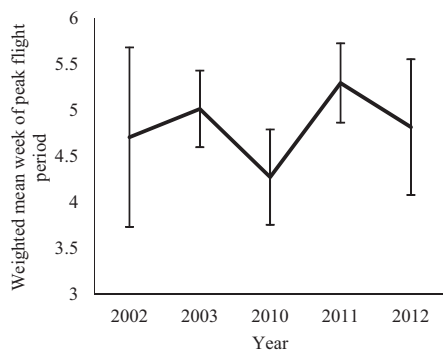


Fig. 4. The weighted average peak flight period in 2002, 2003 and 2010–2012 in Farsh Shoeib. Week count commencing the first of May. Weighted mean ± SE.

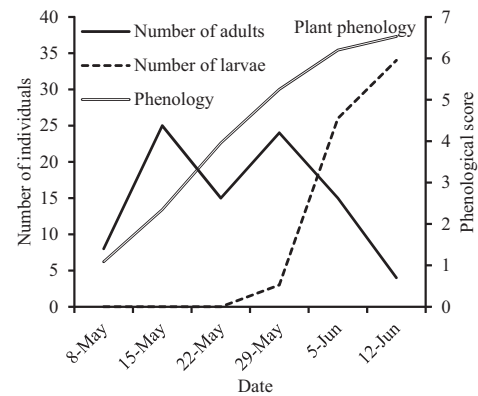


Fig. 5. Number of Sinai Baton Blue larvae and adults compared to the flowering phenology of the host plant seen in Farsh Shoeib in 2010.

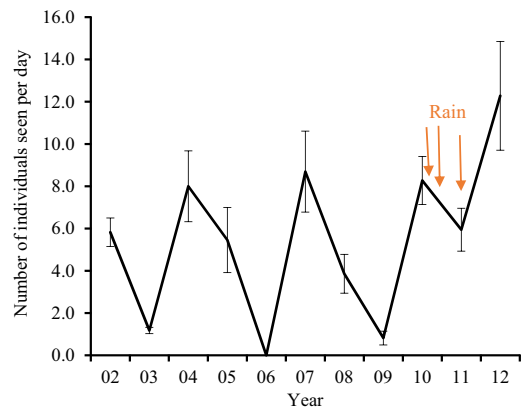


Fig. 6. The number of Sinai Baton Blue butterflies seen per day in Farsh Shoeib (mean ± SE). The number of individuals is known by marking in 2002–2003, but the data for 2004–2012 assume that individuals were not seen more than once owing to the short life span of the adult butterflies. The orange arrows represent rainfall. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.) The data from 2002–2009 is from Gilbert et al. 2010.

majority of buds open. However, flowering was finishing in the weeks when the majority of larvae were counted: inflorescences were dying and plants were beginning to produce seeds. The data from 2010 to 2011 appeared to confirm the cyclical pattern of crashes (Fig. 6) that leave the population close to extinction, followed by recovery. However, 2012 was an unexpected peak year, with the highest number of sightings per day since 2002.

The majority of butterflies were seen in Farsh Shoeib, with 56.3% of all sightings in 2011 and 87.7% in 2012 (Table 1). 2012 was a peak year for butterflies in Farsh Shoeib, with the numbers almost doubling over the previous year, but numbers in the other patches of the massif appeared to have crashed. Farsh Elia and Farsh Loza remained the second and third largest populations, despite their numbers halving; together with Farsh Shoeib the three patches contained 96% of all the butterflies seen on the massif in 2012 (Table 1).

Table 1. Number of transects with sightings of Sinai Baton Blues and total number of butterflies seen in each of the named patches of Sinai Thyme over an 11-week period. Twenty-two transects were carried out in each patch in 2011, and 21 in 2012.

Patch	Transects with butterflies		Total number of butterflies	
	2011	2012	2011	2012
Farsh Shoeib	21	18	112	200
Farsh Loza	11	6	21	8
Gulley Zahtuna	6	3	16	3
Farsh Elia	11	6	23	9
Elia Garden	5	2	8	2
Gulley Sharr	2	0	5	0
Upper Hammar	2	2	2	2
Lower Hammar	4	2	9	2
Elia Garden	5	2	8	2
Elia Circle	1	0	1	0
Safsafa	0	0	0	0

There were no significant differences in the timings of the flight period (the average week in which a butterfly was seen) amongst the ten patches ($F=1.67$, $df=7.436$, $p=0.115$), but there was a difference overall between years ($F=23.5$, $df=1.443$, $p<0.001$; mean week 6.66 [2011] vs. 5.80 [2012]); there was no evidence of any interaction ($F=0.88$, $df=6.430$, $p=0.51$). There were no significant differences in the weighted average peak flight period between years ($W=10$, $df=6$, $p=0.578$). Although positive, there was also no significant correlation between the week of peak flowering and peak butterfly abundance ($r=0.36$, $df=18$, $p=0.12$) (Fig. 7).

Discussion

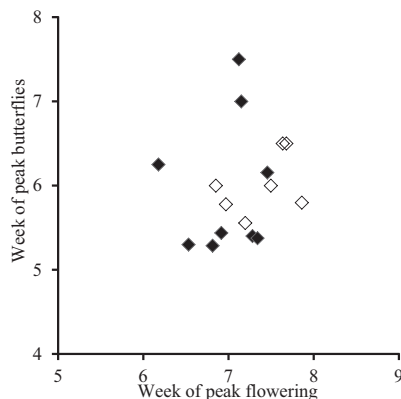
Since the resources in this system (the flowers) are only available for just a few weeks per year, spatial and temporal variation in phenology of either plant or butterfly could have major effects on butterfly abundance unless the flight period is synchronised with flowering. We found that flowering in one year (2010) was some two weeks earlier than in the

four other studied years, butterfly phenology in that year was also one–two weeks earlier. Thus the response mechanisms of both plant and butterfly appear to maintain phenological synchrony overall. The spatial differences of up to two weeks in flowering between different patches of host plants might act as an insurance for the butterfly against the temporal variation in the availability of larval resources (cf. Weiss et al. 1988).

The two-week change in phenology in 2010 in Farsh Shoeib is a notably large temporal shift, considering the flowers are only present for approximately 6 weeks in any one year. The phenological shift could have been induced by air temperature since 2010 had an uncharacteristically warm period in March that may have advanced development. Other plants in the area, such as the Sinai Milkweed (*Asclepias sinaica*: Asclepiadaceae) also had advanced flowering in 2010 when compared to 2011 (Stine Simensen, 2011, pers. comm). The 2012 phenology was similar to 2002 and 2011, and hence is more likely to be closer to the long-term norm, with 2010 uncharacteristically early.

There were also strong spatial differences in flowering phenology across the Mt. Sinai massif, with up to two–three weeks difference amongst patches in 2011. The fact that Lower Hammar consistently flowered first and Safsafa/Farsh Shoeib last suggests that spatial variation in flowering is controlled by localised topographic differences acting through variation in microclimate; for example, aspect influences exposure to the sun, and hence the length of time available for photosynthesis (Gaston et al. 2004). There is also evidence that thyme flowering responds to variation in macroclimate since the shifts in flowering are consistent in every patch across the massif. In 2012 the onset of flowering was later, but the peak and culmination of flowering were earlier, condensing the flowering season; this kind of response is also seen in plants exposed to experimental warming (Sherry et al. 2007).

A shorter flowering season accompanied with a lower density of inflorescences is a problem for the Sinai Baton

**Fig. 7.** Weighted averages of the week of peak flowering and peak butterfly sightings in 2011 (black) and 2012 (open diamonds) on the Mt. Sinai massif. Excluding patches without any butterfly sightings.

Blue. 2012 had significantly fewer flowers available to larvae, and the shorter flowering period on an already narrow time window could cause population decline. The detrimental consequences of greater mortality and higher levels of competition for limited resources could easily increase the extinction risk for this highly endangered butterfly (Powell & Logan 2005; Visser & Holleman 2001).

An optimistic sign is that the butterfly flight period appears also to have shifted in Farsh Shoeib: both flowering and flight period occurred earlier in 2010, suggesting that both species respond to climate in the same way. The butterfly flight period did not show evidence of spatial or temporal variation across the massif, but did show temporal variation among years and at the one patch studied in detail (Farsh Shoeib). The small population numbers in the majority of the patches coupled with low detectability may increase the error in the estimates of the timing of the flight period, masking putative fluctuations.

The response mechanisms are important since asynchrony could still be a problem if the phenology of the host and herbivore respond to the same cue but by different magnitudes between years, although long-term synchronisation is possible. The outlook is less optimistic if the two species use different environmental cues, or have different levels of sensitivity to the same cues (Robinet & Roques 2010; Van Asch et al. 2007). It is possible that the butterfly is adapted to the long-term average phenology across all thyme patches, and hence appears relatively unchanging in the face of relatively large spatial and temporal changes in thyme phenology within single patches. Since we think movement is relatively rare (James 2006a), within a patch, annual abundance would be greatly affected by the bottom-up forces of resource availability to the larvae.

Population dynamics in arid environments are commonly controlled by bottom-up forces, with primary productivity predominantly governed by rainfall and the corresponding resource pulse, often with a time lag in response (Boggs & Inouye 2012; Letnic & Dickman 2010; Schwinning et al. 2004). When resources become abundant, primary consumers can undergo a population boom due to alleviated competition (Letnic & Dickman 2010; Ostfeld & Keesing 2000). Insect populations have a large instantaneous rate of increase and as a consequence are sensitive to changes in carrying capacity (Gotelli 2008) which may explain the population cycles here. There was a large increase in the resources available to the butterfly between 2010 and 2011. In Farsh Shoeib there was a 10-m² increase in thyme leafage, and flower production doubled, probably caused by the heavy rainfall of Spring and Summer 2010 (pre and during flowering) and Spring 2011 (pre flowering) (Thompson 2013), and in the following year (2012) there were the highest number of individual butterflies per day since records began in 2002. This may perhaps be an indication of delays in the response of the butterfly population to variation in resource availability, which might drive cyclic behaviour.

Resource levels probably play a key role in generating the population cycles of the Sinai Baton Blue. The first two instars feed exclusively on buds, and subsequent instars on the flowers (James 2006c). In 2010 the majority of larvae in Farsh Shoeib were found at the end of the flowering season, when resources were diminishing quickly and the proportion of dead flowers was dramatically increasing; this suggests that this cohort may have run short of food, causing the population to decline in 2011 (cf. Fig. 5). However, the apparent regularity of the peaks and troughs in abundance (Gilbert et al. 2010) suggests that the cycle cannot be driven by the effects of stochastic forces such as weather on the carrying capacity.

Alternative causes could be natural enemies, an induced plant defence response or feedback on plant reproduction via herbivore density (Agrawal 1999; Boggs & Freeman 2005; Veldtman et al. 2007). In principle the alternation of induction of defence chemicals followed by their suppression as herbivore density rises and falls could generate population cycles, although it is not clear why thyme plants would do this in synchrony with one another. An alternative herbivore-induced defence is the shifting of flowering to minimise damage from insect herbivores (Ohgushi 2005), as seen in the white spruce (*Picea glauca*: Pinaceae) (Quiring & Mckinnon 1999). This could cause population cycles, as well as explaining the dramatic shifts in thyme phenology (Quiring & Mckinnon 1999). These interactions may not be mutually exclusive explanations, and could drive the Sinai Baton Blue cycle synergistically.

The populations in the patches other than Farsh Shoeib on the massif crashed in 2012, with fewer than a third the numbers of 2011. This suggests that the Sinai Baton Blue exists as separate populations with asynchronous cycles. The Farsh Shoeib population appears to have crashed to very low numbers repeatedly over the past decade. If these are more-or-less separate populations existing as a metapopulation, then asynchrony will help limit simultaneous extinctions via dispersal from neighbouring patches, extending the longevity of the metapopulation (Pandit et al. 2013).

Overall, the phenology of the Sinai Baton Blue appears broadly synchronised to the flowering of its host plant across patches, but appears not to follow temporal (amongst years) or spatial (amongst patches) variations in flowering closely. Spatial variation in flowering could act as an insurance mechanism against butterfly emergence being too out of synchrony in any one year. Butterfly populations on different patches appear to vary asynchronously. The best data from Farsh Shoeib appear to show substantial fluctuations, apparently with a three-year cycle, potentially facing extinction when the population drops to its low points. If extinction occurred it would be an important event for the butterfly metapopulation (James 2006a), although modelling suggests that two other patch populations are more critical to its long-term survival (Hoyle & James 2005). The causes of the population crashes are unknown, but undoubtedly the large shifts in thyme phenology affect the available resources,

especially if the magnitude in shift is not perfectly matched by the butterfly. Although the cycles seem fairly large, and hence the status of the Sinai Baton Blue seems precarious, the species has survived successfully so far for many thousands of years. It is possible that dispersal from neighbouring patches is vital in rescuing the metapopulation from extinction (see James 2006a). This highlights the importance of neighbouring patches and the need for conservation across multiple patches, not just in Farsh Shoeib.

Acknowledgements

We would like to thank the following: Mr Mohamed Qotb and the staff of the St Katherine Protectorate for their help and advice during this work; Haitham Zalata, Amy Shepherd and Oliver Masters for their help in the field and Nasr Mansour for his infinite local knowledge; the financial assistance of the Mohamed bin Zayed species conservation fund which made this work possible; and anonymous referees, who helped clarify the message of this paper.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2014.05.003>.

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