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The influence of life history traits on the phenological response of British butterflies to climate variability since the late-19th century

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Abstract

Many species of plants and animals have advanced their phenology in response to climate warming in recent decades. Most of the evidence available for these shifts is based on data from the last few decades, a period coinciding with rapid climate warming. Baseline data is required to put these recent phenological changes in a long-term context. We analysed the phenological response of 51 resident British butterfly species using data from 83,500 specimens in the collections of the Natural History Museum, London, covering the period 1880-1970. Our analysis shows that only three species significantly advanced their phenology between 1880 and 1970, probably reflecting the relatively small increase in spring temperature over this period. However, the phenology of all but one of the species we analysed showed phenological sensitivity to inter-annual climate variability and a significant advancement in phenology in years in which spring or summer temperatures were warm and dry. The phenologies of butterfly species were more sensitive to weather if the butterfly species was early flying, southerly distributed, and a generalist in terms of larval diet. This observation is consistent with the hypothesis that species with greater niche breadth may be more phenologically sensitive than species with important niche constraints. Comparison of our results with post-1976 data from the UK Butterfly Monitoring Scheme show that species flying early in the year had a greater rate of phenological advancement prior to the mid-1970s. Additionally, prior to the mid-1970s, phenology was influenced by temperatures in March or April, whereas since 1976, February temperature had a stronger influence on the phenology. These results suggest that early flying species may be approaching the limits of phenological advancement in response to recent climate warming.

Introduction

Changes in phenology, that is changes in the timing of key life stage events in response to shifts in seasonal weather patterns, have been documented in a wide range of organisms (Parmesan 2007, Thackeray et al. 2010). Most studies, however, have been based on relatively short time-series, often covering the last few decades, which coincide with a period of rapid climatic warming. Little phenological information is currently available from earlier in the 20th century or from the 19th century to put these recent changes into a long-term perspective and to disentangle the long-term impacts of climate change from responses to short-term climate variability (Sparks and Yates 1997, Sparks et al. 2006). Nevertheless, long-term datasets of over 100 years, in the form of specimens and accompanying metadata, which are suitable for studying biotic response to climate change, do effectively exist within natural history museum collections (Johnson et al. 2011). In this study, we use the recently digitised British butterfly collection in the Natural History Museum, London, UK, to investigate how the phenology of British butterflies has changed in response to long-term climate variability since the late 19th century.

British butterflies are arguably among the best known insect groups in the world. Much of this information is derived from the activities of amateur enthusiasts who have collected specimens and observations for over 200 years. Since 1976, thousands of 'citizen scientists' have contributed records to the United Kingdom Butterfly Monitoring Scheme (UKBMS) on a weekly basis, providing a detailed picture of the distribution and flight periods of butterfly species throughout Britain (Brereton et al. 2015). Analysis of the UKBMS data has provided researchers with insights into the phenological and distributional responses to recent climate change of many of these

species (Roy and Sparks 2000, Diamond et al. 2011). Until now, however, information on long-term trends was largely lacking (Sparks et al. 2006).

Analyses by Altermatt (2010) in central Europe, Polgar et al. (2013) in the USA, Kharouba et al. (2014) in Canada, and Brooks et al. (2014) in the UK have demonstrated the potential of museum datasets to provide information on the phenological response of butterflies to changing seasonal temperatures since the late 19th century. Now, following a recent major digitisation programme (the iCollections Initiative) (Blagoderov et al. 2012) at the Natural History Museum, London (NHM), collections data are readily available for over 183,000 specimens of all the British butterfly species. About 83,500 of these specimens include data that can be used in a phenological analysis (day and place of collection in the field and in sufficient numbers (> 4 specimens) in a given year). Most of these specimens were collected between 1880 and 1970 so they provide a complementary dataset to the UKBMS data and provide a unique opportunity to investigate the long-term phenological change in most of the resident British species. After 1970 there are relatively few butterfly specimens in the NHM collections as public interest switched from collecting butterflies to photographing and observing them. For several of the species (e.g. *Carterocephalus palaemon, Thymelicus acteon, Hamearis lucina, Satyrium pruni*) we have analysed, phenological data were not previously available because the species were either too rare or their cryptic behaviour made them too difficult to observe.

The time of the year that an adult butterfly is on the wing is mainly determined by the over-wintering stage (i.e. egg, larva, pupa or adult), but the emergence date of the adult is most likely to be influenced by day length and seasonal temperatures. Temporal and spatial changes in seasonality affect the phenology of a species depending on the magnitude of seasonal change and the sensitivity of that species. The adult emergence

date may be expected to be earlier in the year in populations of a species in southern Britain compared with northern populations, or earlier in the same population in warm years compared with cool years. During a sustained period of climatic warming the entire British butterfly fauna may begin to show an advance in phenology. As the phenology of the butterfly's food plant is driven by phenological cues, which may be different from those of the butterfly, there is the potential for future temporal mismatches. These may have cascading effects through the food web and wider impacts on ecosystem functioning, species diversity and community persistence (Harrington et al. 1999, Visser and Both 2005).

The response of species to changing seasonality is not uniform but dependent on life-history and behavioural traits which can modify the sensitivity and rate at which a species may respond phenologically. Using UKBMS data between the years 1976-2008, Diamond et al. (2011) investigated how larval host breadth, dispersal ability, overwintering stage, voltinism, range size and northern range edge affected the phenological response of 44 species of British butterflies. Kharouba et al. (2014) investigated how these same ecological traits and, in addition, flight season length and timing of flight season influenced the phenological response of 204 species of Canadian butterflies using 48,000 georeferenced records from the Canadian National Collection of Butterflies over a period of 139 years.

Using a broader range of life history traits, we bring a new perspective to the work outlined above by using the NHM collections to investigate the phenology of 51 resident British butterfly species since the late 19th century and the influence of a broader range of life history traits than in previous studies. We address the question of whether the advancing phenological trend apparent in some species since 1976 (Roy and Sparks 2000) began before this date or whether phenological change earlier in the

20th century was non-directional and reflected annual climate variability. Following the work of Brooks et al. (2014) we hypothesise that long-term trends in phenological advancement were weaker or absent in species prior to 1970 because increases in average temperature between 1880 and 1970 was relatively small in comparison to the warming climate trend since 1970. We also use the NHM collections to test and expand on the results of previous authors by examining the life history traits that most influence the sensitivity of the phenological response, and whether phenological sensitivity has changed through time. Following the work of Miller-Struttmann et al. (2015), we hypothesise that species with generalist life history traits show higher rates of phenological change than specialist species because generalist species have the flexibility to exploit a wider range of habitat options. Furthermore, as suggested by the results of Brooks et al. (2014), we hypothesise that late flying species have increased their rate of phenological advancement since 1976, reflecting the trend in warmer summers since that date, whereas the rate of phenological advancement in early flying species has slowed as they approach their physiological limits.

Materials and methods

Butterfly data

The data used in this study were all derived from the British butterfly collection held at the NHM. Each of the approximately 183,000 British butterfly specimens held in the NHM collections and the associated data labels have been digitally imaged and the data on the labels transcribed to a database, and imported into the NHM collection database KeEMU (Blagoderov et al. 2012, Paterson et al. 2016). The specimens have all been reliably identified to species by specialist lepidopterists. Nomenclature follows Thomas and Lewington (2010).

Specimen collection data were available from 1841 to 1999 but in most species analysis was restricted to the years between 1880 and 1970 due to insufficient numbers of specimens for reliable analysis in consecutive years outside this range. Records were included in the analysis only if the data labels specified i) the location of collection to at least county level, ii) the day of collection, iii) the specimens were not reared in captivity. This left approximately 83,500 records available for analysis. Longitude and latitude were determined for each location by calculating the centroid and accuracy radius from polygons drawn around the collection locality using the GeoRef software tool (www.georef.com), based on Google Earth. Dates that varied by more than three standard deviations from the mean collection date were treated as outliers and excluded from further analysis, as were specimens from locations remote from the known 20th century distribution as these were likely to be in error rather than representing historic range shifts. Records from Ireland and the Channel Islands were not analysed. Extinct and migrant species were not included in the multiple regression analysis and there were insufficient data available for *Apatura iris* and *Thecla betulae*.

Collection dates were converted to day number after December 31st. For each species, the median, 10th and 90th percentile collection dates were calculated for each year in which there were five or more records (Brooks et al. 2014). Species having two flight periods per year, representing different generations, showed a bimodal distribution. These could be divided into first generation and second generation where there was a clear gap between flight periods of at least one day or clear minima in abundance, to just a few specimens, between the collection dates of the two flight periods. In some species (*Coenonympha pamphilus, Polyommatus icarus, Pieris napi* and *P. rapae*) the start of the second generation flight period overlapped the end of the first generation flight period. In *Aglais urticae* and *Pararge aegeria* there were three overlapping peaks

in the flight season. In these species calculation of the 10th percentile collection data of the second generation was not meaningful.

Museum data were compared with mean first appearance data from the UK Butterfly Monitoring Scheme (UKBMS) for the years 1976-1998, which were analysed by Roy and Sparks (2000).

Phylogeny construction

A phylogeny of all British butterflies was assembled using cytochrome c oxidase subunit I sequences taken from GenBank (Benson et al. 2009). British species not included in our phenological analysis were included in the phylogenetic analysis to improve accuracy of the topology and branch lengths. Removal of species once a phylogeny is built does not affect the accuracy of the placement of those remaining species. Several nodes were constrained, and *P. machaon* defined as an outgroup, using information from recently published phylogenies that are based on more loci than the present study (Wahlberg et al. 2009, Mutanen et al. 2010; see supporting information Figure A1 for both the finished phylogeny and constraint information). The sequences were aligned in Geneious (v.5.3; http://www.geneious.com/), and a two-codon (1&2, 3) GTR+γ+I (with four rate categories) substitution model was used for five separate analyses using BEAST (Drummond et al. 2006, Drummond and Rambaut 2007, Drummond et al. 2012). To choose the DNA substitution model, one BEAST run was performed with all possible combinations of GTR models with γ and invariant site models, no, two, and three separate codon positions, and the SDR model (Shapiro et al. 2006). The posterior likelihood of these runs was then compared according to Bayes factors as calculated in Tracer (Rambaut and Drummond 2012) using Suchard et al.'s (2001) method. All BEAST analyses used a different random starting tree, a relaxed

lognormal clock, ran for five million generations, and were sampled every 2000

generations. The runs were checked for convergence and mixing, and to make sure that

all parameters had an estimated sample size greater than 300 using Tracer (Rambaut and

Drummond 2012). The five runs from the optimal DNA substitution model were

combined with a 10% burn-in, and then their maximum clade credibility tree used for

all further analyses.

Climate data

The Central England Temperature (CET) series provides monthly air temperatures for a

triangular area of central England bounded by Lancashire, London and Bristol. Mean

monthly temperatures were initially compiled by Manley (1974) for each year from

1659 to 1973. This was later extended to 1991 by Parker et al. (1992) and is now

regularly updated by the Meteorological Office Hadley Centre

(http://www.metoffice.gov.uk/hadobs/hadcet/). Mean monthly minimum temperature

data for this region are also available, beginning in 1878 (Parker and Horton 2005) and

mean monthly precipitation data for central England from 1873 (Alexander and Jones

2000). Although the CET series has been shown to be broadly representative of the UK

(Duncan 1991, Croxton et al. 2006), many of the butterflies used in our study were

collected in southern England, at lower latitudes than the area covered by the CET

series. Therefore, the influence of location was also investigated by allocating each

record for all species to the appropriate one of the nine UK districts designated by the

Meteorological Office Hadley Centre

(http://www.metoffice.gov.uk/climate/uk/summaries/datasets). The relevant mean

monthly and mean minimum and maximum air temperatures were then used in the

analysis on a regional basis. Median, 10th and 90th percentiles for each species were

regressed against the mean monthly climate of all the appropriate meteorological districts for that year using a weighted regional temperature, with weights equal to the regional distribution of records of that species. Thus the mean temperatures used in our analysis tended to reflect those districts which included the most records for a particular year. There were insufficient specimens of each species to calculate median, 10th and 90th percentiles for each meteorological district. Regional climate data were available from 1910 only so regressions using regional climate data were restricted to the years between 1910 and 1970.

Analysis

The relationship between spring temperature (March – May) and 10th percentile, median and 90th percentile collection date, and length of collection period (range of 10th to 90th percentiles) was examined for single generation species and the first generation of species that have at least two generations in one year, using correlation coefficients to test for the most responsive measure of collection date. The relationship with summer temperature (June – August) was also examined for these single generation species and the second generation of the species with more than one generation in a year. Trends over time using 10th percentile, median and length of collection period were examined using regression with year as the explanatory variable.

Stepwise regression was then used to relate collection date to temperature and precipitation. Initially, potential explanatory variables included mean monthly temperatures for the year preceding collection dates and year (for unexplained changes over time). For example, *Pyrgus malvae* specimens were collected between day 113 (23 April) and day 162 (11 June), so mean monthly temperatures for July to December of the previous year and January to June of the current year were included in the analysis.

In subsequent analyses, mean monthly minimum temperatures and mean monthly precipitation for the current year were also included. Significant variables were selected by stepwise regression using forwards selection, backwards elimination and best subsets selection procedures in R software version 3.0.0 (R Core Team 2013). Models were fitted using the *MASS* (Venables and Ripley 2002) and *leaps* (Lumley and Miller 2009) packages. Variance inflation factors (VIF) were determined using the *car* package (Fox and Weisberg 2011) and the statistical significance of additional variables tested using Akaike Information Criterion (AIC) and then Bayes Information Criterion (BIC) to reduce the chance of over fitting the model. Only significant variables were included in the final models.

Species trait analysis

Only resident species were included in the traits analysis, although four species (*I. io, G. rahmni, A. urticae* and *P. c-album*), which overwinter in Britain as adults and have a second flight period during the summer, were also omitted. This was because the overwintering generations were poorly represented in the NHM collections compared with the summer generations, even though UKBMS data suggest that adults from overwintering generations are at least as numerous as adults in the summer generation. We included 14 ecological and life history traits in the comparative analysis, which were derived from various sources (Table 1), and were analysed to determine how traits influence phenological response to inter-annual weather variation. Traits data used in the analysis for each species are shown in Supplementary material Appendix 1, Table A1a and A1b. The slope in 10th percentile collection date against spring CET from each species model formed the response variable for the analysis. Because traits of related taxa may be similar due to common ancestry, and therefore not statistically independent

(phylogenetic autocorrelation) (Felsenstein 1985, Harvey and Pagel 1991), trait-trend relationships were examined using phylogenetically informed regression via the *pgls* function from the R package *caper* (Orme et al. 2012). We used a phylogeny of British butterfly species (see above for details) and estimated the level of phylogenetic correction via maximum likelihood (Pagel 1999, Freckleton et al. 2002).

To determine the main trait correlates of our species trends we used a multi-model inference approach. We applied the *dredge* function of the R package *MuMIn* (Barton 2013) to fit a linear regression model for all possible combinations of explanatory trait variables and then ranked them based on AIC. We extracted the model averaged coefficient for each trait that was present in at least one candidate model from the subset of top models and identified the importance of each trait based on its frequency in the subset of top models. The importance scores and the model averaged coefficients were used to determine the main traits for explaining species trends. The top set of candidate models was defined as models with ΔAIC $\leq$ 7 (Burnham et al. 2011). For each set of strongly correlated variables (r > 0.7) we retained one variable in the maximal model. The retained variable was selected as the one that showed the lowest level of correlation with all other traits. While it is possible to run the dredge function with all traits, models with multicollinearity may be included in the top subset of models and in turn would influence the model averaged coefficients, which is clearly not desirable. All analyses were carried out using R 3.2.0 (R Core Team 2015).

Model-averaging using AIC is commonly used to detect important variables when faced with a large set of potential predictor variables (Burnham & Anderson, 2003). However, its application to PGLS models is complicated by the co-estimation of the multiplier of

the phylogenetic variance-covariance matrix that accounts for phylogenetic non-independence (Pagel's Lambda, Delta, or Kappa; see Freckleton et al. 2002). Changing the predictor variables in a model affects the estimated phylogenetic multiplier, yet this source of uncertainty does not propagate through the AIC-selection procedure. Therefore, we cannot distinguish the change in AIC that is due to the change in predictor variables from that due to the change in evolutionary model. In our most complex models estimated Pagel's Lambda was negligible, and not significantly different from zero, which is consistent with no detectable influence of phylogeny. Since estimates from PGLS models with Lambda values of zero are equivalent to standard regression (Freckleton et al. 2002, Symonds and Blomberg 2014), we present results based on *dredge* standard regression models.

Results

The number of useable specimens available per species ranged from 169-11779 (mean = 1589). On average 57.2% of specimens available for each species were used in the analysis (range 30-75%). The number of useable specimens available in each year between 1880 and 1970 ranged from 18-2322 (mean = 861.1), peak numbers were collected between 1920 and 1950, with a drop during the Second World War (1939-1945) (Fig. 1). The number of years between 1880 and 1970 for which sufficient data were available varied between species; the maximum was 79 years (for *Polyommatus icarus*, first generation) and the minimum was 15 years (for *Erebia epiphron*, first generation) (mean across all species = 44 years).

Species showing phenological trends through time

In the 51 resident species we analysed, the 10th percentile collection date between 1880 and 1970 shifted directionally between -4.5 and +4.0 days per decade (mean 0.1) (Fig. 2), the median collection date shifted directionally between -3.1 and +1.8 days per decade (mean 0.2), and the duration of collection period shifted directionally between -3.1 and +6.5 days per decade (mean 0.3). Spring temperatures (CET) increased on average by 0.09°C per decade over this time period. In 30 species the 10th percentile collection date advanced, but this was significant in only three species (*A. cardamines, A. agestis* and *M. galathaea*). In two species, *T. acteon* and *L. camilla*, the 10th percentile collection date was significantly later (Table 2). The median collection date of 29 species advanced from 1880-1970, of which four species showed a significant trend (*P. rapae* 1st generation), *A. cardamines, A. agestis* and *A. adippe*), whereas *T. lineola, S. pruni, L. camilla, A. aglaja* and *M. jurtina* showed a significant trend towards later dates over this time period (Table 2). Duration of collection period increased between 1880 and 1970 in 33 species and this was significant in nine species, the most extreme being 2nd generation *P. rapae* (4.5 days per decade) and 2nd generation *P. c-album* (6.5 days per decade). One species (*C. tullia*) showed a significant reduction in the length of the collection period (1.0 days per decade) (Table 2).

Relationship with 10th percentile collection date

In all species there is a positive correlation between 10th percentile collection date and median collection date (r = 0.28 − 0.96; mean = 0.69 ± 0.13). This relationship is significant in all species except *Aricia artaxerces*. In all but two species there is a significant negative correlation between 10th percentile collection date and duration of collection period (r = -0.92 − -0.0.1; mean = -0.51 ± 0.18). The exceptions are *Inachis io* and 2nd generation *P. rapae* which have a non-significant positive relationship.

Phenological sensitivity to temperature

We found that 34 univoltine species, the 1st generation of 13 species and the 2nd generation of 12 species showed an advancement of between 1 and 9 days in 10th percentile collection date per 1°C rise in spring CET. Five univoltine species, the 1st generation of one species (*P. rapae*) and 2nd generation of two species (*C. argiolus* and *E. epiphron*) showed no change. Two univoltine species (*N. quercus* and *T. betulae*), 1st generation of one species (*P. brassicae*) and 2nd generation of one species (*L. sinapis*) showed a delay (Fig. 3) Of the 51 resident species included in the multiple regression analysis (Table 3), only two species (*E. aethiops* and 2nd generation *E. epiphron*) did not show a significant relationship between 10th percentile collection date and mean monthly Central England temperature and/or precipitation. Forty-six species showed a significant advancement in 10th percentile collection date of between 17.3 and 1.2 days per 1°C rise (mean 5.2). In 1st generation *P. rapae* 10th percentile collection date was delayed by 7.5 days in response to minimum May temperatures. When regional weather data were used in the analysis the 10th percentile collection date of 1st generation *P. rapae* advanced by 5.4 days per 1°C rise but *H. lucina*, 2nd generation *P. rapae*, and 1st generation L. *phlaeas* no longer showed a significant relationship with regional weather. We compared rates of phenological advancement in univoltine and 1st generation multivoltine resident species in response to CET mean monthly temperatures derived from the NHM dataset (1880-1970) with rates of change derived from an analysis of the UKBMS dataset (1976-1998) (Roy and Sparks 2000). This shows that rates of phenological advance in spring emerging species tend to be higher in the 1880-1970 period than in 1976-1998. Conversely, rates of phenological advancement in summer emerging species tend to be lower in the 1880-1970 period than in 1976-1998 (Fig. 4).

Early emerging, single generation species and 1st generation populations of other species were most likely to show an advanced 10th percentile collection date when March or April temperatures were warm, whereas the date was delayed by cool minimum temperatures or high rainfall in those months (Fig. 5). On the other hand, late flying univoltine species and 2nd generation populations of other species tended to show advancement when temperatures in June or July were warm whereas the date was delayed when temperatures were low or rainfall high in those months (Fig. 5).

Influence of life history traits on phenological sensitivity

We found little evidence of phylogenetic signal in our models, and therefore a comparison of model results with and without correction for phylogenetic autocorrelation showed no significant differences. Results from simple (non-phylogenetically informed) regression are presented. Several of the traits examined co-varied and so were not included in the final analysis. The traits correlation matrix is shown in the supplementary material (Supplementary material Appendix 1, Table A2). Our analyses indicated that 10th percentile collection date of all years taken together (covaries with first week of appearance, mean collection date, over-wintering stage), number of core host plants, and northern range boundary (covaries with latitudinal extent) are important predictors of phenological advancement. The other traits we examined had little influence (<50% importance) on phenological advancement (Table 4). The results indicate that, in response to inter-annual weather variation, species that are on the wing earlier in the year tend to show greater advancement in phenology than later flying species (Fig. 6a). Species having a more southerly latitudinal extent show greater phenological advancement than species with more northerly range boundaries (Fig. 6b). Finally species with a wide range of core host plants during the larval stage

show greater phenological advancement than species with a narrow range of cost host plants (Fig. 6c).

Discussion

Phenological response and rates of change

In this discussion we focus on the results produced by our analysis using regional climate data as this is most likely to reflect the phenological response of local populations, and so represent more reliable results. However, in those species in which insufficient data were available to produce significant results, due to the reduction in the range of years with available climate data, we will consider the results generated by analyses based on CET data.

Our new results support the conclusion of an earlier study on four British butterfly species (Brooks et al. 2014) that the NHM collection can provide useful information on the long-term phenological response of British butterfly species. The specimens were collected without experimental design, and as a result may contain some forms of bias (e.g. there are more records from southern than northern Britain). As we are examining temporal trends in phenology, a real concern here would be a bias in temporal trends but we have no evidence for this. However, to ensure our analyses were based on only the most reliable unbiased data, we used strict data exclusion criteria, and only estimated phenological metrics for species:year combinations with at least five records. Furthermore, we used three metrics of phenological shift all of which were significantly correlated with weather conditions, supporting the reliability of this approach for such museum data.

Our results show that 10th percentile collection date, median collection date and length collection period were significantly correlated with weather conditions in almost all

species analysed (Table 3; Fig. 3) and therefore reflects butterfly phenology. This suggests that 10th percentile collection date approximates mean first appearance date, median collection date approximates peak flight date and collection period is related to length of flight period.

Only three species in our time series analysis showed a significant advancement in 10th percentile collection date over the period 1880-1970 and a further four species significantly advanced their median collection date (Table 2). This contrasts with a time series analysis by Roy and Sparks (2000) of 35 species of British butterflies using UKBMS data. These authors found that 13 species had significantly advanced their mean first appearance date during the period 1976 to 1998. Furthermore, the rate of advancement in *M. galathea* (4.6 days per decade) and *A. cardamines* (7.6 days per decade) was about 2 or 3 times greater, respectively, than we found for these species in our analysis. The phenological response in the third species, *A. agestis*, was not significant in the analysis of UKBMS data (Roy and Sparks 2000). The difference between these results probably reflects the greater average increase in CET spring temperatures in the years between 1976 and 1998 (1.5°C) than in the period 1880-1970 (0.8°C). A similar result was found by Bartomeus et al. (2011) in an analysis of 10 species of North American bees where rate of phenological advancement was more than twice as much between 1970 and 2010 than during the period 1870-1970.

Only two species (*E.aethiops* and *E. epiphron*, both restricted to Scotland and the English Lake District) did not show a significant relationship between 10th percentile collection date and variability in monthly temperature and precipitation (Table 3). The 10th percentile collection date of spring emerging species was advanced when spring months were warm and dry, and species that emerged during the summer were more likely to be influenced by summer weather conditions than spring weather conditions.

Advancement of emergence dates in years of warm, dry springs has been shown in other studies of butterfly phenology using monitoring data and museum collections (Sparks and Yates 1997, Roy and Sparks 2000, Diamond et al. 2011, Polgar et al. 2013). However, contrary to these results, an analysis of central European Lepidoptera by Altermatt (2010) suggests that there has been a delay in phenology of late-flying lepidopteran species since 1980. Diamond et al. (2014) found that several butterfly species occupying urban environments in Ohio, USA, also exhibited delayed phenology in response to rising temperatures.

Roy and Sparks (2000), in their analysis of 1976-1998 UKBMS data, found mean February temperature was significant in explaining phenological response in the regression models of 15 of the 18 species with one flight period they investigated. The remaining three species in their dataset are late flying and showed a response to May and June temperatures. In our study, February temperature was selected as significant in only two of the species investigated by Roy and Sparks (2000) (i.e., *A. paphia* and *M. jurtina*). In contrast, the phenology of the 10 spring flying species in our study was influenced by March, April and May temperatures. The six summer flying species in our analysis were influenced by temperatures in June or July, which corroborates the results of Roy and Sparks (2000). This supports the earlier conclusion of Brooks et al. (2014), based on an analysis of four species, that prior to the steep increase in spring temperatures in the late 1980s, mean February temperatures were too cold to influence the emergence date of British butterflies and that temperatures in March, April and May were more important.

As in previous studies of rates of phenological advancement across a wide range of organisms (Sparks and Crick 1999, Roy and Sparks 2000, Bartomeus et al. 2011, Miller-Rushing and Primack 2008, Polgar et al. 2013), most of the species we

investigated showed a phenological advancement of between 2 and 10 days per 1°C rise. However, we also found that rates of change of early emerging species tended to be higher in the period 1880-1970 than in the UKBMS data between 1976-1998 (Roy and Sparks 2000). On the other hand, species emerging later in the summer had lower rate of change in 1880-1970 compared with the UKBMS data from 1976-1998 (Roy and Sparks 2000). This would appear to support the hypothesis put forward by Brooks et al. (2014) that the species emerging earliest in the year are now approaching a limiting date, perhaps connected with day length or temperature cues which break the winter diapause, before which it is not physiologically possible to emerge. The lower rates of advancement found in the NHM analysis than in the UKBMS analysis of summer emerging species probably reflects the effects of higher summer temperatures of recent decades when compared to summer temperatures earlier in the 20th century. These results appear to contradict those found by Altermatt's (2010) analysis of central European Lepidoptera who found that emergence dates of late flying species have become relatively later since 1980 and early season fliers are getting earlier since 1980. Unlike Sparks et al. (2006), who found that October temperatures in the year preceding emergence were significant in influencing emergence dates in late flying Lepidoptera species, we did not find such a strong relationship in our analysis of late flying butterfly species in general. Nevertheless, we did find that September and October temperatures of the previous year were significant in determining the phenology of *N. quercus*, a late summer species, and *E. aethiops* and 1st generation *L. sinapis*, which both fly in the summer. However, we caution that we performed many statistical tests and so finding these results as statistically significant could, potentially, be due to multiple-testing.

Traits analysis

We examined whether the variation in sensitivity of phenological responses (discussed above) was explained by species traits. We found that the timing of the flight season was the most important trait in determining sensitivity of phenological response. Species flying earlier in the year tend to advance the first flying date at a greater rate than species flying later in the year. This result supports data presented by Diamond et al. (2011) who used the 1976-2008 UKBMS data to examine how traits might influence the phenological response in British butterflies. Diamond et al. (2011) postulated that this response may reflect the greater mean increase in spring temperatures compared to summer temperatures since 1975. However, in the years spanned by the NHM dataset (approximately 1880-1970) spring CET have increased by approximately 0.8 °C and summer CET have increased by about 0.5°C so this is unlikely to be the driver of this response. In their study of Canadian butterfly species over a period of 139 years, Kharouba et al. (2014) also found that early flying species were more sensitive phenologically than later flying species. They attributed this as a response to higher variability in spring temperatures than summer temperatures. However, there is little difference in the variability of spring CET (range = 3.9°C; SD = 0.82°C) and summer CET (range = 3.4°C; SD = 0.78°C) so this is unlikely to account for our results. In general, insects that emerge earlier in the year tend to advance their phenology greater than later emerging species (Hassall et al. 2007 (dragonflies), Altermatt 2010 (Lepidoptera), Bartomeus et al. 2011 (bees)). Hassall et al. (2007) suggest that phenology of later emerging species is influenced by both spring and summer temperatures which may moderate their phenological sensitivity.

The number of core host plants used by a species was also found to have a strong influence on the phenological sensitivity of the butterfly species we investigated. Species with a greater number of core host plants tended to have greater phenological

advancement than species in which larvae feed on fewer plant species. This may reflect differences in niche flexibility since species with a broad range of host plants are more likely to find plants in a suitable condition whenever they emerge than those with a restricted diet-breadth. Similarly, Miller-Struttmann et al. (2015) found that generalist foraging bees were favoured over specialist species during declines in floral resources following warmer summers. Although our result corroborates earlier studies which also show that availability of host plants may limit phenological advancement (Memmott et al. 2007 (insect pollinators), van Asche and Visser 2007 (Lepidoptera), Pelini et al. 2009 (butterflies)), it contrasts with the analysis of Diamond et al. (2011) on British butterflies. These authors found that butterfly species with a narrow diet breadth were phenologically more sensitive than species with a broad diet breadth and postulated that this response may have been driven by phenological advancement in the butterfly's host plant. However, there is a strong outlier in the results of Diamond et al. (2011) which may have skewed their results in this direction. Altermatt (2010) found that the number of host plants used by central European Lepidoptera did not their affect phenological sensitivity but that species feeding on woody plants were more sensitive than species feeding on herbaceous plants. In our analysis we considered the influence of habitat traits on the phenological sensitivity of British butterfly species but found that species using woodlands were no more sensitive than grassland species.

Another strong predictor of phenological sensitivity in our NHM dataset was the relative position of a species' pre-1970 northern distributional range boundary. Species with a more southerly northern range boundary tended to have advanced their phenology more than species with a more northerly range boundary. Although Diamond et al. (2011) did not find a significant relationship between phenological response and latitudinal extent, they did find that species with a restricted distribution expressed

greater phenological advancement than more widely distributed species. Widely distributed species may have less opportunity to expand their habitat niche or range boundary and this may in turn limit phenological response (Oliver et al. 2009, Diamond et al. 2011). Altermatt (2010) found no difference in phenological sensitivity between narrowly and widely distributed species of central European Lepidoptera.

In addition to species with an early flight season, Kharouba et al. (2014) found that mobility was also a strong predictor of phenological advancement, such that species with low dispersal ability were more sensitive phenologically than those with greater dispersal capabilities. This may reflect the ability of better dispersers to track suitable climatic conditions. However, mobility was not ranked highly in our analysis or that of Diamond et al. (2011). Kharouba et al. (2014) suggest that because Diamond et al. (2011) based their analysis on temporal phenological shifts, whereas the analysis of Kharouba et al. (2014) was based on direct temperature sensitivity, this may account for the discrepancy. However, as our analysis was also based on direct temperature sensitivity and we did not find mobility to be a significant trait, so this is unlikely to be the reason for the differences in these results.

Five species showed a significant advancement in 10th percentile or median collection date over the period 1880-1970 and six species showed a significant delay over this period (Table 1). Species showing a significant advancement in 10th percentile or median collection date are on the wing by the second week in June whereas species showing a significant delay begin their flight season after this date. This result may therefore reflect the greater phenological sensitivity of early flying species. Nine species showed a significant increase in flight season duration from 1880-1970, which corroborates the results of Roy and Sparks (2000) that species advancing their phenology also increase the length of their flight season. *C. tullia*, a late-flying,

northern upland species, is the only species which exhibited a significantly reduced length of flight season.

Conclusions

Our study underlines the potential of natural history museum collections to provide information on the response of biota to long-term climate change. When these collections are digitised the data become readily available and amenable for rapid analyses. Our study confirms that prior to 1970 few species of British butterfly were showing any long-term trends in phenological advancement, whereas since the mid-1970s the results of Roy and Sparks (2000) show that an increasing number of species have advanced their phenologies in response to climatic warming. This supports our hypothesis that long-term trends in phenological advancement were weaker or absent in species prior to 1970 because increases in average temperature between 1880 and 1970 were relatively small in comparison to the warming climate trend since 1970. Comparison of our results with those of Roy and Sparks (2000) show that temperatures in February, rather than March or April, are now most likely to influence the emergence of species flying in the spring. Moreover, the rate of phenological advancement in early flying species has slowed since the mid-1970s, compared with earlier in the century.. This supports our hypothesis that some species flying early in the spring may now be approaching the limit of phenological advancement as they have less flexibility to emerge earlier in the year due to other factors constraining their emergence date .

Our results indicate that early-flying species with relatively southerly distributions and which exploit a broad range of larval food plants are likely to advance their phenology at a greater rate than species that fly later in the year, have a wide distribution and that specialise on a few larval food plants. This supports out hypothesis that species with

generalist feeding strategies show higher rates of phenological change than more specialised feeders.

Acknowledgements

References

Alexander, L.V. and Jones, P.D. 2000. Updated precipitation series for the U.K. and discussion of recent extremes. - Atmos. Sci. Lett. 1: 142-150.

Altermatt, F. 2010. Tell me what you eat and I'll tell you when you fly: diet can predict phenological changes in response to climate change. – Ecol. Lett. 13: 1475–1484.

Bartomeus, I. et al. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. – P. Natl. Acad. Sci. USA 108: 20645-20649.

Barton, K. 2013. MuMIn: Multi-Model Inference. R package version 1.9.5. - http://cran.r-project.org.

Benson, D.A. et al. 2009. Genbank. - Nucleic Acids Res. 37: D26–D31.

Blagoderov, V. et al. 2012. No specimen left behind: industrial scale digitization of natural history collections. - ZooKeys 209: 133–146.

Brereton, T.M. et al. 2015. United Kingdom Butterfly Monitoring Scheme report for 2014. - Centre for Ecology and Hydrology and Butterfly Conservation.

Brooks, S.J. et al. 2014. Natural history museum collections provide information on phenological change in British butterflies since the mid-19th century. – Int. J. Biometeorol. 58: 1749–1758.

Burnham, K.P. and Anderson, D.R. 2003. Model Selection and Multimodel Inference: A Practical Information – Theoretic Approach. Springer.

Burnham, K.P. et al. 2011. AICc model selection in the ecological and behavioral sciences: some background, observations and comparisons. – Behav. Ecol. Sociobiol. 65: 23–35.

Cowley, M.J.R. et al. 2001. Density–distribution relationships in British butterflies. I. The effect of mobility and spatial scale. – J. Anim. Ecol. 70: 410–425.

Croxton, P.J. et al. 2006. How well do the Central England Temperature and England and Wales Precipitation series represent the climate of the UK? – Int. J. Climatol. 26: 2287-2292.

Dennis, R.L.H. 1993. Butterflies and Climate Change. - Manchester University Press.

Dennis, R.H.L. and Shreeve, T.G. 1989. Butterfly wing morphology variation in the British Isles: the influence of climate, behavioural posture and the hostplant-habitat. - Biol. J. Lin. Soc. 38: 323-348.

Diamond, S.E. et al. 2014. Unexpected phenological responses of butterflies to the interaction of urbanization and geographic temperature. - Ecology 95: 2613-2621.

Diamond, S.E. et al. 2011. Species' traits predict phenological responses to climate change in butterflies. - Ecology 92: 1005-1012.

Drummond, A. and Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. - BMC Evol. Biol. 7: 214.

Drummond, A.J. et al. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. – Mol. Biol. Evol. 29: 1969–1973.

Drummond, A.J. et al. 2006. Relaxed phylogenetics and dating with confidence. - PLoS Biol. 4: e88.

Duncan, K. 1991. A comparison of the temperature records of Edinburgh and central England. - Weather 46: 169-173.

Felsenstein, J. 1985. Phylogenies and the comparative method. – Am. Nat. 125: 1–15.

Fox, J. and Weisberg, S. 2011. An (R) Companion to Applied Regression. 2nd edition. - Sage.

Freckleton, R. et al. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. – Am. Nat. 160: 712–726.

Hardy, P.B. et al. 2007. Specialism for larval and adult consumer resources among British butterflies: implications for conservation. – Biol. Conserv. 138: 440-452.

Harrington, R. et al. 1999. Climate change and trophic interactions. - Trends Ecol. Evol. 14: 146-150.

Harvey, P.H. and Pagel, M. 1991. The Comparative Method in Evolutionary Biology. - Oxford University Press.

Hassall, C. et al. 2007. Historical changes in the phenology of British Odonata are related to climate. - Global Change Biol. 13: 933–941.

Johnson, K. et al. 2011. Climate change and biosphere response: unlocking the collections vault. - Bioscience 61: 147-153.

Kharouba, H.M. et al. 2014. Predicting the sensitivity of butterfly phenology to temperature over the past century. - Global Change Biol. 20: 504–514.

Lumley, T. using Fortran code by Alan Miller (2009) Leaps: regression subset selection. R package version 2.9. - http://CRAN.R-project.org/package=leaps

Manley, G. 1974. Central England Temperatures: monthly means 1659 to 1973. – Q. J. Roy. Meteor. Soc 100: 389-405.

Memmott, J. et al. 2007. Global warming and the disruption of plant–pollinator interactions. – Ecol. Lett. 10: 710–717.

Miller-Rushing, A.J. and Primack, R.B. 2008. Global warming and flowering times in Thoreau's concord: a community perspective. - Ecology 89: 332-341.

Miller-Struttmann, N.E. et al. 2015. Functional mismatch in a bumble bee pollination mutualism under climate change. - Science 349: 1541-1544.

Mutanen, M. et al. 2010. Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. – P. Roy. Soc. B-Biol. Sci. 277: 2839–2848.

Oliver, T. et al. 2009. Changes in habitat specificity of species at their climatic range boundaries. – Ecol. Lett. 12: 1091–1102.

Orme, D. et al. 2012. Caper: Comparative analyses of phylogenetics and evolution in R, R package version 0.5. Available on-line at http://CRAN. R-project.org/package = caper.

Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. – Syst. Biol. 48: 612–622.

Parker, D.E. and Horton, E.B. 2005. Uncertainties in the Central England Temperature series since 1878 and some changes to the maximum and minimum series. – Int. J. Climatol. 25: 1173-1188.

Parker, D.E. et al. 1992. A new daily Central England Temperature Series, 1772-1991. – Int. J. Climatol. 12: 317-342.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. - Global Change Biol. 13: 1860–1872.

Paterson, G.L.J. et al. 2016 Dataset: iCollections. http://dx.doi.org/10.5519/0038559.

Pelini, S.L. et al. 2009. Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. – P. Natl. Acad. Sci. USA 106: 11160–11165.

Polgar, C.A. et al. 2013. Climate effects on the flight period of Lycaenid butterflies in Massachusetts. – Biol. Conserv. 160: 25-31.

R Core Team 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

R Core Team 2015. R: A language and environment for statistical computing. - R Foundation for Statistical Computing. https://www.R-project.org/

Rambaut, A. and Drummond, A. 2012. Tracer v1.5. - http://beast.bio.ed.ac.uk/Tracer.

Roy, D.B. and Sparks, T.H. 2000. Phenology of British butterflies and climate change. - Global Change Biol. 6: 407-416.

Shapiro, B. et al. 2006. Choosing appropriate substitution models for the phylogenetic analysis of protein-coding sequences. – Mol. Biol. Evol. 23: 7–9.

Sparks, T.H. and Crick, H.Q.P. 1999. The times they are a-changing? - Bird Conserv. Int. 9: 1-7.

Sparks, T.H. and Yates, T.J. 1997. The effect of spring temperature on the appearance dates of British butterflies 1883 – 1993. - Ecography 20: 368-374.

Sparks, T.H. et al. 2006. Complex phenological responses to climate warming trends? Lessons from history. – Eur. J. Entomol. 103: 379-386.

Suchard, M.A. et al. 2001. Bayesian selection of continuous-time Markov chain evolutionary models. – Mol. Biol. Evol. 18: 1001–1013.

Symonds, M. R. E. and Blomberg, S. P. 2014. A primer on phylogenetic generalised least squares. – In: Garamszegi, L. Z. (ed.), Modern phylogenetic comparative methods and their application in evolutionary biology. Springer-Verlag, pp. 105–130.

Thackeray, S. J. et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. - Global Change Biol. 16: 3304–3313.

Thomas, J. and Lewington, R. 2010. The butterflies of Britain and Ireland. Edition 2. - British Wildlife Publishing.

van Asch, M. and Visser, M.E. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. – Annu. Rev. Entomol. 52: 37–55.

Venables, W.N. and Ripley, B.D. 2002. Modern applied statistics with S. 4th Edition. - Springer.

Visser, M.E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. - P. Roy. Soc. B-Biol. Sci. 272: 2561-2569.

Wahlberg, N. et al. 2009. Nymphalid butterflies diversify following near demise at the cretaceous/tertiary boundary. - P. Roy. Soc. B-Biol. Sci. 276: 295–4302.

Whalley, P.E.S. 1981. Mitchell Beazley pocket guide to butterflies. - Mitchell Beazley

Figure Legends

Figure 1. Number of useable specimens of British butterflies collected per year in the

NHM collections.
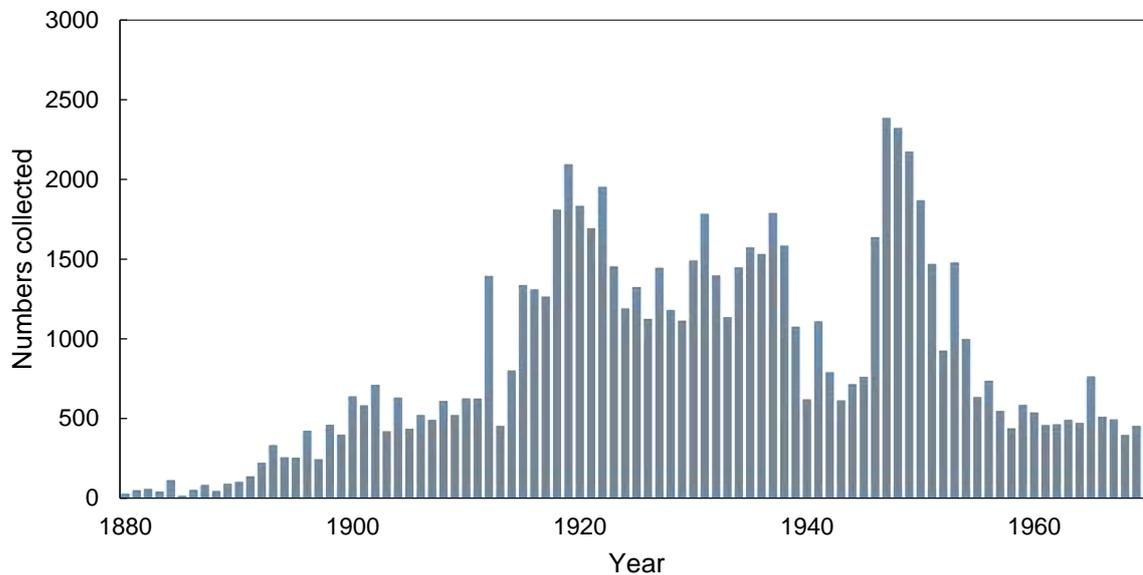
Figure 2. Distribution of slope values of 51 resident British butterfly species (1st and 2nd generation plotted separately) for phenological change through time. Temporal shifts in 10th percentile collection date.
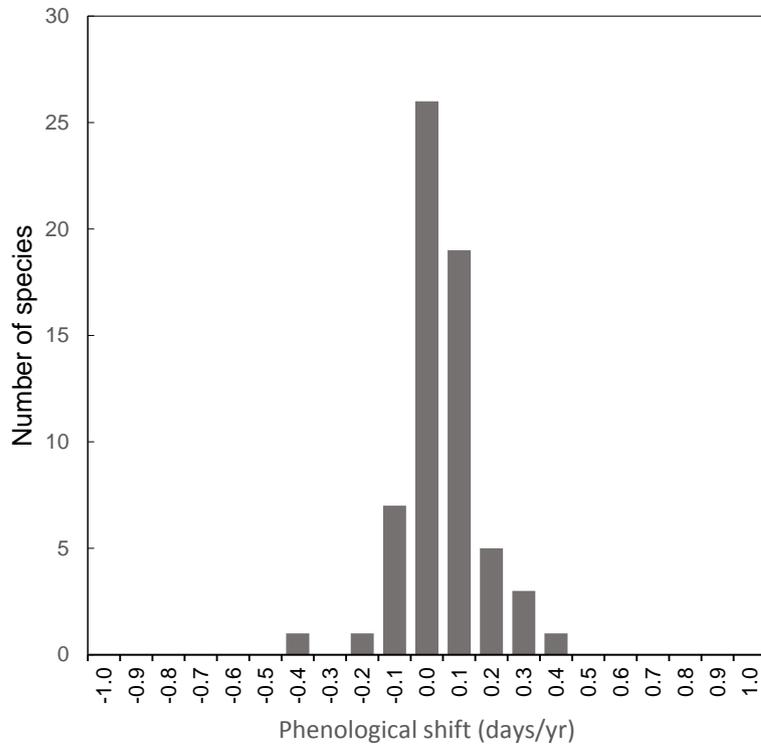
Figure 3. Distribution of slope values of 51 resident British butterflies species (1st and 2nd generation plotted separately) for phenological sensitivity to temperature. Shifts in 10th percentile collection date against mean spring (March, April, May) CET 1880-1970.
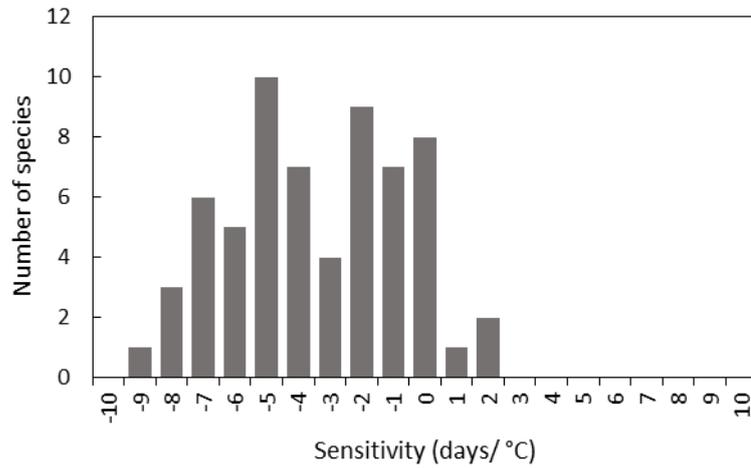
Figure 4. Change in rates of phenological advancement of univoltine and first

generation British butterflies between 1880-1970 (this study) and 1976-1998 (Roy and

Sparks 2000 according to timing of flight season. Positive values on the y-axis indicate

NHM data have a greater response than UKBMS and negative values are vice versa.

Rates of phenological advance of spring emerging species tend to be higher in NHM

data (1880-1970) than found by Roy and Sparks (2000) in UKBMS data (1976-1998).

Rates of phenological advance in summer emerging species tend to be lower between

1880 and 1970 than between 1976 and 1998.
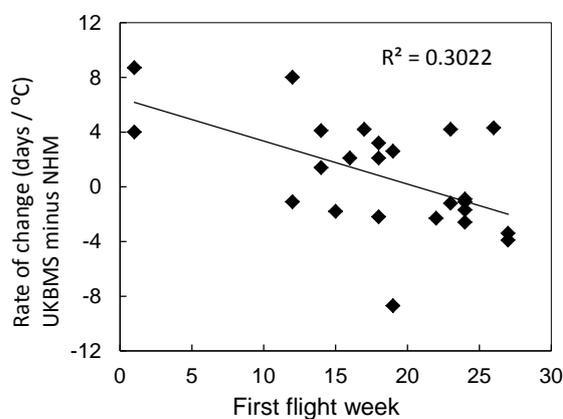
Figure 5. Relationship between phenological sensitivity and mean spring (MAM) (black circles) and mean summer (JJA) (grey triangles) CET temperature in British butterfly species with one flight period each year.
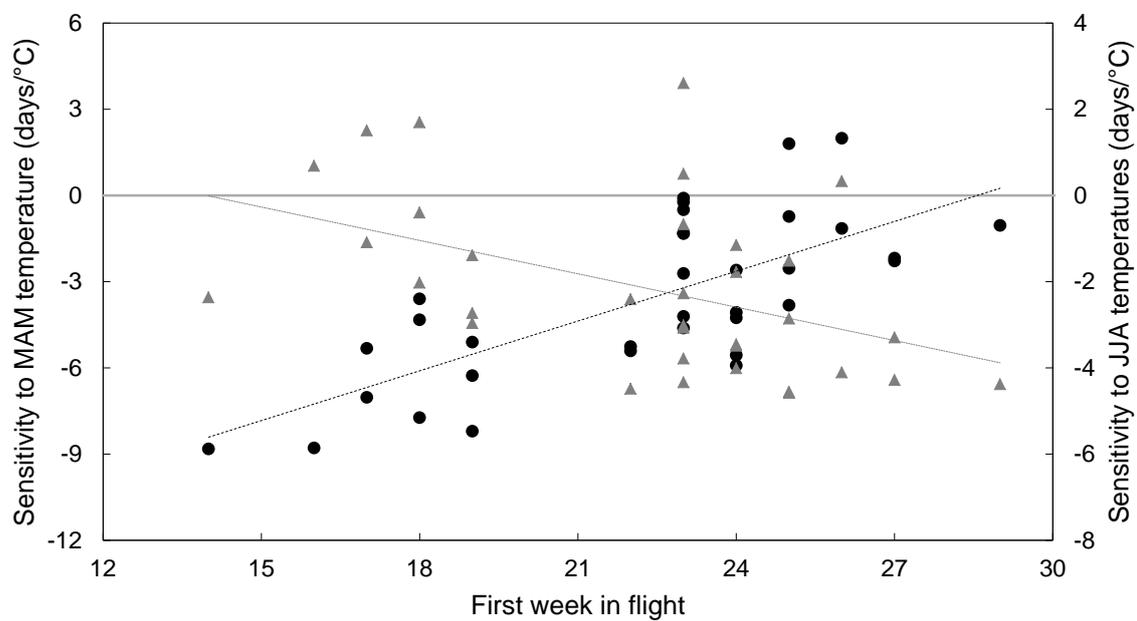
Figure 6. Relationship between three most important traits and phenological advancement. Partial residuals (residuals of regressing the response variable on the independent variables, but omitting the independent variable of interest) are plotted against residuals of each independent variable of interest regressed on all remaining independent variables; regressions of partial residuals on the independent variable residuals are indicated with solid lines. (a) 10th percentile collection date (proxy for timing of flight season) $\beta = 2.46$, $P > 0.001$. Species collected/flying early in the year have advanced more than late collected/flying species. Points below the line indicate species with greater phenological advancement (more change) compared to points above the line (less change). (b) Relationship between number of larval host plants (natural log of number of core host plants) and phenological advancement. $\beta = -0.88$, $P = 0.03$. Species with a greater number of core host plants have advanced more than species with a lower number of host plants. (c) Relationship between latitudinal extent (most northern occupied 10km grid square before 1970) and phenological advancement. $\beta = 1.59$, $P = 0.004$. Species with a more southerly latitudinal extent advanced more than species with a more northerly extent.
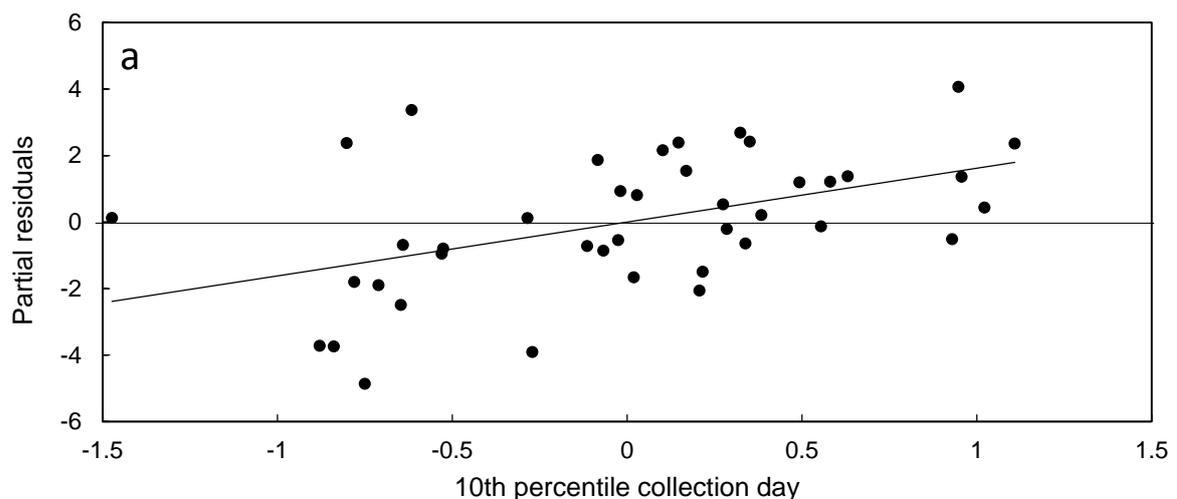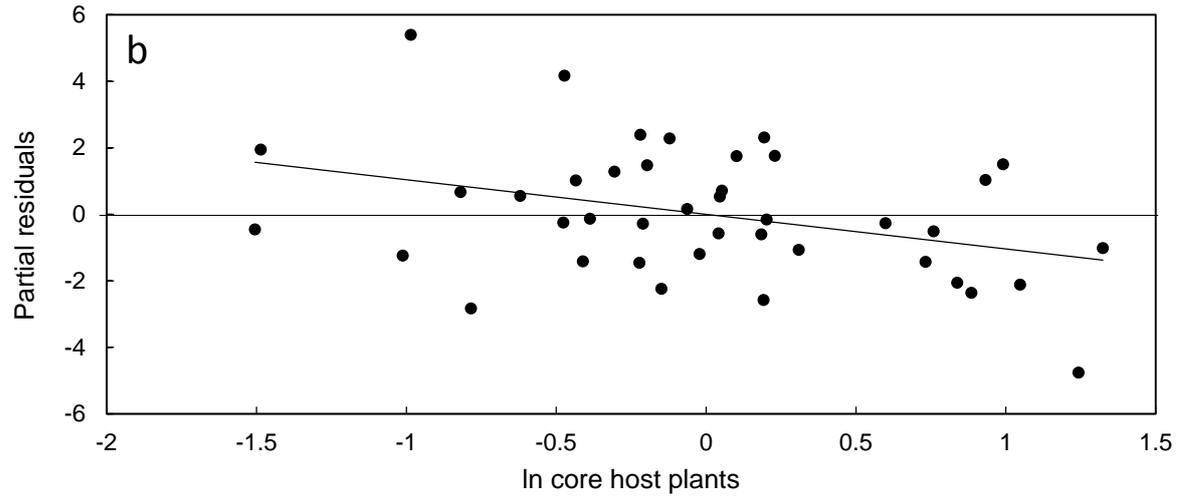
Appendix Figure A1. Butterfly phylogeny. Created as described in main text. Coloured

circles at nodes indicate clades that were constrained to be monophyletic based on

recent multi-locus higher-level Lepidoptera phylogenies; circles in black come from

Wahlberg et al. (2009), while the grey circle is based on Mutanen et al. (2010). *Papilo*

machaon was defined as the out-group for all BEAST analyses.

Table Legends

Table 1. Description of life cycle and ecological traits of British butterfly species used in this analysis.

Trait	Reference	Comment
Diet breadth	Hardy et al. (2007)	Natural log of number of core host plants (CHP); principle host plants (PHP); all host plants (AHP)
Niche breadth	Cowley et al. (2001)	Larval host-plant specificity; larval feeding specificity (parts of plant); level of larval association with ants
Dispersal ability	Cowley et al. (2001)	Mobility score
Mean fore wing length	Whalley (1981)	Millimetres
Overwintering stage	Thomas & Lewington (2010)	Egg; larva; pupa; adult
Voltinism	Thomas & Lewington (2010)	Single; Two; Multiple
Range size (grid squares)	Cowley et al. (2001)	Natural log % 10km grid squares occupied
Range size (latitudinal extent)	Dennis (1993)	<25%; 25-50%; 50-75%; 75-100% of total latitudinal span of UK
Northern range boundary	NBN Gateway [https://data.nbn.org.uk/]	Most northern occupied 10km grid square (pre-1970)
Distribution pattern	Thomas & Lewington (2010)	Northern; southern; eastern; western; widespread
Flight season length	Thomas & Lewington (2010)	Number of weeks as adult
Timing of flight season	Thomas & Lewington (2010)	First week in flight

(week)		
Timing of flight season (mean)	NHM collection	10th percentile, mean and median collection date of all years together
Habitat type	Dennis and Shreeve (1989)	Short grassland ; rank grassland; Woodland

Table 2. British butterfly species showing significant phenological trends through time (1880-1970) for 10th percentile collection date, median collection date and length of collection period. Significance values are from regressions of collection period characteristics on year. Values for change per decade are number of days.

Species	Years	No. of years	Change (days per decade)		
			10th percentile date	Median date	Length of colln period
Thymelicus acteon	1892-1969	26	+2.2*		
T. lineola	1890-1966	43		+1.8**	
T. sylvestris	1889-1970	54			+1.3*
Pieris rapae gen. 1	1891-1961	30		-3.1*	
P. rapae gen. 2	1895-1955	25			+4.5*
Anthocharis cardamines	1884-1970	62	-2.3**	-1.6*	
Satyrium pruni	1906-1950	15		+4.1*	
Lycaena phlaeas gen. 2	1881-1970	73			+2.4*
Aricia agestis gen. 1	1894-1967	46	-1.9**	-1.4*	
Polyommatus icarus gen. 2	1886-1970	77			+1.4**
Limenitis camilla	1893-1965	37	+2.6**	+2.6**	
Aglais urticae	1891-1969	54			+3.3*

Polygonia c-album gen. 2	1912-1948	19			+6.5*
Argynnis adippe	1892-1957	44		-1.2*	
A. aglaja	1893-1970	59		+1.1*	
Pyronia tithonus	1890-1970	68			+0.6*
Melanargia galathea	1882-1970	71	-1.2**		+1.9***
Maniola jurtina	1891-1970	78		+1.4**	+2.0**
Coenonympha tullia	1893-1970	69			-1.0*

* $0.01<P<0.05$, ** $0.001<P<0.01$, *** $P<0.001$; gen. 1 = first generation; gen.2 = second generation.

Table 3. Summary of regression models relating 10th percentile collection dates of resident British butterflies to CET and regional monthly mean and mean minimum temperatures (m) and mean monthly rainfall (r) for the years before 1970. Numbers in the terms columns refer to the month of the year, those prefixed with a letter p refer to a month in the previous year.

	CET (mean monthly temperature)							CET (mean, min monthly; mean monthly ppt)						Regional (mean, min, ppt)				
Species with one flight period each year																			
species	years	n	terms	R2 %	p	change (per 1°C)		n	terms	R2 %	p	change (per 1°C)		years	n	terms	R2 %	p	change (per 1°C)
Carterocephalus palaemon	1892-1959	36	3, 4, p7	40	<0.001	-5.5		36	3, 4, p7	40	<0.001	-5.5		1912-1959	29	4, neg r1	35	0.003	-2.3
Thymelicus acteon	1892-1969	26	Yr, 7	30	0.016	-3.7		26	Yr, 7	30	0.016	-3.7		1912-1969	17	insufficient data			
T. lineola	1890-1966	43	7	23	<0.001	-3.9		43	7	23	0.001	-3.9		1911-1966	32	7	29	0.001	-4.1
Hesperia comma	1892-1969	38	7	39	<0.001	-3.9		38	7	39	<0.001	-3.9		1911-1969	28	7	50	<0.001	-4.6
T. sylvestris	1889-1970	54	6	13	0.009	-2.7		54	6, r3	19	0.004	-2.4		1912-1970	36	m6	13	0.029	-3.2
Ochlodes sylvanus	1895-1970	53	3, 5, 6	32	<0.001	-7.5		53	m3, 5, r6	35	<0.001	-6.2		1911-1970	37	3, r6	38	<0.001	-2.8
Pyrgus malvae	1893-1970	57	4	10	0.018	-2.9		57	r4	12	0.01	n/a		1911-1970	45	4	13	0.014	-3.5
Erynnis tages	1890-1970	51	3, 4	35	<0.001	-5.9		51	3, 4, r3	40	<0.001	-5.4		1911-1970	39	4	23	0.002	-4.0
Anthocharis cardamines	1884-1970	62	Yr, 4	31	<0.001	-4.5		62	Yr, 3, 4, r1	46	<0.001	-6.0		1911-1970	44	4	27	<0.001	-5.8
Callophrys rubi	1896-1967	47	4	17	0.004	-4.8		47	4	17	0.004	-4.8		1911-1967	38	4	21	0.004	-3.9
Neozephrus quercus	1900-1965	21	p9	23	0.029	-6.4		21	p9	23	0.029	-6.4		1912-1965	15	insufficient data			
S. w-album	1896-1956	16	6	21	0.078	-4.6		insufficient data							insufficient data			
Satyrium pruni	1906-1950	15	Yr, p7	56	0.007	-8.0		15	Yr, p7	56	0.007	-8.0		1916-1950	13	insufficient data			
Plebeius argus	1889-1970	76	3, 6, 7	25	<0.001	-5.0		76	3, 6, m7	27	<0.001	-5.8		1911-1970	56	m7	13	0.006	-3.8
Aricia artaxerxes	1893-1968	37	7	4	0.264	+1.4		37	r6	30	<0.001	n/a		1911-1968	31	6, r6	41	0.001	-3.4
Polyommatus coridon	1896-1970	74	6, 7	46	<0.001	-4.3		74	6, 7	46	<0.001	-4.3		1911-1970	60	6, 7	28	<0.001	-3.8
Maculinea arion	1898-1956	43	6	17	0.005	-3.6		43	6	17	0.005	-3.6		1911-1956	31	Yr, 6	54	<0.001	-5.8
Hamearis lucina	1889-1970	51	4	11	0.019	-3.0		51	4	11	0.019	-3.0		1912-1970	40	4	9	0.055	-2.8
Limenitis camilla	1893-1965	37	Yr, 4, 5	44	<0.001	-6.0		37	Yr, 4, 5	44	<0.001	-6.0		1912-1970	31	Yr, 5	39	0.001	-3.9
Boloria selene	1890-1970	71	4, 5	31	<0.001	-7.2		71	4, 5, r4	37	<0.001	-6.8		1911-1970	57	5, r4	35	<0.001	-4.5
B. euphrosyne	1891-1970	68	3, 4	28	<0.001	-3.8		68	3, r4	37	<0.001	-2.2		1911-1970	55	3, r3, r4	47	<0.001	-1.4
Argynnis adippe	1892-1957	44	2, 5	30	<0.001	-5.6		44	5, m2, m7	38	<0.001	-8.8		1912-1957	35	5	13	0.034	-2.4
A. aglaja	1893-1970	59	1, 5	20	0.002	-4.7		59	1, 5	20	0.002	-4.7		1911-1970	46	m1, p11	34	<0.001	-4.5
A. paphia	1888-1965	51	4	14	0.007	-3.3		51	2, r4	29	<0.001	-1.7		1911-1965	38	neg r2, r4	31	0.001	n/a
Euphydryas aurinia	1893-1968	59	3, 4, 5	50	<0.001	-8.7		59	3, 4, 5, r4	56	<0.001	-8.0		1911-1968	47	4, r4, r5	37	<0.001	-2.7
Melitaea athalia	1902-1964	38	Yr, 4	28	0.003	-4.5		38	Yr, 4	28	0.003	-4.5		1918-1964	34	4, r5	39	<0.001	-4.7
Erebia aethiops	1893-1970	34	p9	6	0.143	+2.1		34	p9	6	0.143	+2.1		1912-1970	27	r2	21	0.016	n/a
Pyronia tithonus	1890-1970	68	6, 7	21	<0.001	-3.8		68	6, m7	22	<0.001	-4.5		1912-1970	53	6	21	0.001	-3.6
Melanargia galathea	1882-1970	71	5, 6	32	<0.001	-5.7		71	5, 6	32	<0.001	-5.7		1911-1970	54	6	15	0.004	-3.6
Hipparchia semele	1884-1970	71	3, 6	12	0.012	-4.2		71	3, r4, r6	24	<0.001	-2.0		1911-1970	52	6, r4	19	0.006	-3.4
Maniola jurtina	1891-1970	78	6	10	0.006	-2.4		78	6, m7	15	0.002	-4.3		1911-1970	60	2, 6	22	0.001	-3.5
Aphantopus hyperantus	1890-1970	71	3, 6	22	<0.001	-2.7		71	3, 6	22	<0.001	-2.7		1911-1970	57	6, r3	32	<0.001	-2.9
Coenonympha tullia	1893-1970	69	2, 6	15	0.005	-3.8		69	6, m2, r4	29	<0.001	-4.3		1911-1970	56	Yr, 5, r4	39	<0.001	-3.1

	CET (mean monthly temperature)						CET (mean, min monthly; mean monthly ppt)					Regional (mean, min, ppt)					

Species with two flight periods, but only one generation

species	years	n	terms	R2 %	p	change (per 1°C)	n	terms	R2 %	p	change (per 1°C)	years	n	terms	R2 %	p	change (per 1°C)
Gonepteryx rhamni	1891-1953	26	7	14	0.059	-3.8	26	r6, 7	34	0.09	-3.9	1912-1970	20	m7	20	0.045	-5.8
Inachis io	1900-1964	20	2, 5, 7	60	0.001	-15.8	20	2, 5, 7, r6	83	<0.001	-17.3	1912-1964	16	insufficient data			

Species with two or more flight periods representing different generations

species	years	n	terms	R2 %	p	change (per 1°C)	n	terms	R2 %	p	change (per 1°C)	years	n	terms	R2 %	p	change (per 1°C)
Leptidea sinapis gen. 1	1901-1965	28	p8, p10	41	0.001	-1.2	28	p8, p10	41	0.001	-1.2	1915-1965	24	5, p8	43	0.003	-6.5
Pieris brassicae gen. 2	1896-1959	20	p10	19	0.056	+3.3	20	r1	22	0.035	n/a	1915-1959	17	insufficient data			
P. rapae gen. 1	1891-1961	30	5	30	0.002	+5.6	30	m5	41	<0.001	+7.5	1914-1961	21	3	23	0.003	-5.4
P. rapae gen. 2	1895-1955	25	5	4	0.336	-2.0	25	r2	13	0.075	n/a	1914-1955	19	8	20	0.061	-4.4
P. napi gen. 1	1890-1970	49	4	13	0.010	-4.8	49	4	13	0.010	-4.8	1911-1970	38	3, 4	52	<0.001	-8.4
P. napi gen. 2	1895-1970	39	5	17	0.010	-2.4	39	5, r6	32	<0.001	-2.5	1911-1970	29	r3	10	0.083	-6.9
Lycaena phlaeas gen. 1	1900-1960	30	1	13	0.048	-2.4	30	1, r4	23	0.031	-2.7	1912-1960	26	r3	13	0.070	n/a
L. phlaeas gen. 2	1881-1970	73	p12	3	0.121	-1.6	73	r6	6	0.036	n/a	1911-1970	55	r6	9	0.024	n/a
Cupido minimus gen. 1	1886-1970	61	3	13	0.004	-1.9	61	3	13	0.004	-1.9	1911-1970	43	3	13	0.020	-1.5
Aricia agestis gen. 1	1894-1967	46	Yr, 3, 5	36	<0.001	-4.9	46	Yr, r2, r5	40	<0.001	n/a	1912-1967	37	4, m6	25	0.007	-6.9
A. agestis gen. 2	1894-1965	49	6, 7	24	0.002	-4.9	49	6, 7	24	0.002	-4.9	1911-1965	38	7	23	0.002	-3.4
Polyommatus icarus gen. 1	1890-1970	79	3	24	<0.001	-2.7	79	3	24	<0.001	-2.7	1911-1970	59	3	40	<0.001	-4.6
P. icarus gen. 2	1886-1970	77	7, 8	23	<0.001	-3.3	77	7, m8, r5	31	<0.001	-4.4	1911-1970	59	7, r4	19	0.002	-3.2
P. bellargus gen. 1	1893-1968	66	3, 4, 5	35	<0.001	-7.8	66	r3, 4, 5	39	<0.001	-7.0	1911-1968	54	4, r2	29	0.000	-3.1
P. bellargus gen. 2	1896-1969	63	2, 5, 7	25	<0.001	-5.7	63	2, 5, 7	25	<0.001	-5.7	1911-1969	54	2, r4	32	<0.001	-1.5
Celastrina argiolus gen. 1	1886-1963	38	4	40	<0.001	-5.2	38	4	40	<0.001	-5.2	1912-1963	25	4	21	0.021	-3.6
C. argiolus gen. 2	1887-1970	24	5	14	0.076	-2.6	24	5, r2	28	0.032	-2.4	1911-1970	17	insufficient data			
Aglais urticae gen. 1	1896-1969	28	1	17	0.032	+3.5	28	5, r3, r4	47	0.002	-8.4	1912-1969	24	r4	13	0.083	n/a
A. urticae gen. 2	1891-1967	27	4	26	0.007	-5.1	27	4, r3, r5	51	<0.001	-5.9	1919-1967	24	4	24	0.016	-5.9
Polygonia c-album gen. 1	1912-1965	20	4	21	0.045	-4.8	20	m3, m7	56	<0.001	-14.1	1912-1965	19	insufficient data			
P. c-album gen. 2	1912-1948	19	8	24	0.033	-4.1	19	r7	39	0.004	n/a	1912-1948	19	insufficient data			
Pararge aegeria gen. 1	1896-1967	42	1, 4, p6	35	0.001	-13.3	42	1, 4, p6, r4	42	<0.001	-13.3	1912-1967	37	4	21	0.004	-9.1
P. aegeria gen. 2	1910-1969	29	5	29	0.003	-5.6	29	5, r2	39	0.002	-5.2	1916-1969	28	5	31	0.002	-6.6
Lasiommata megera gen. 1	1896-1970	25	3, 4	57	<0.001	-6.5	25	3, 4, r5	68	<0.001	-6.4	1916-1970	21	r3	49	<0.001	n/a
L. megera gen. 2	1896-1969	33	3, 5, 7	48	<0.001	-8.9	33	2, 5, r6, r7	65	<0.001	-4.4	1917-1969	28	7	26	0.005	-3.8
Erebia epiphron gen. 2	1902-1965	19	6	8	0.229	+1.1	19	r4	20	0.058	n/a	1917-1965	18	insufficient data			
Coenonympha pamphilus gen. 1	1889-1970	72	3, 4, 5	39	<0.001	-6.2	72	3, 4, 5	39	<0.001	-6.2	1911-1970	56	3, 4	33	<0.001	-2.4
C. pamphilus gen. 2	1899-1969	42	p12	12	0.027	-1.7	42	m4, r2	25	0.003	-2.6	1911-1969	41	7	13	0.018	-3.9

Table 4. Influence of traits on phenological sensitivity of 41 British butterfly species with trait data available. Species over-wintering as adults were excluded from the analysis. No phylogenetic autocorrelation was detected.

Explanation	Co-varying traits	Importance
10th percentile collection date	overwintering stage; mean collection date; flight season length; first week in flight; timing of flight season	1
Number core host plants		0.57
Northern range boundary pre-1970		0.57
Habitat		0.47
% 10km grid cells occupied within species range	Latitudinal extent	0.40
Mobility score		0.36
Number all host plants	principle host plants	0.35
Mean of min and max forewing span		0.28
Host breadth		0.20
Niche breadth score		0.18
Max number generations	Typical flight season length; first week in flight	0.15