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Species' traits predict phenological responses to climate change in butterflies

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Abstract. How do species' traits help identify which species will respond most strongly to future climate change? We examine the relationship between species' traits and phenology in a well-established model system for climate change, the U.K. Butterfly Monitoring Scheme (UKBMS). Most resident U.K. butterfly species have significantly advanced their dates of first appearance during the past 30 years. We show that species with narrower larval diet breadth and more advanced overwintering stages have experienced relatively greater advances in their date of first appearance. In addition, species with smaller range sizes have experienced greater phenological advancement. Our results demonstrate that species' traits can be important predictors of responses to climate change, and they suggest that further investigation of the mechanisms by which these traits influence phenology may aid in understanding species' responses to current and future climate change.

Key words: butterflies; climate change; diet breadth; long-term monitoring; overwintering stage; phenology; phylogeny; range size; United Kingdom.

INTRODUCTION

Evidence is accumulating rapidly that species are shifting their latitudinal distributions, elevation ranges, and phenologies in response to recent climate changes (reviewed in Parmesan 2006). Identifying characteristics of organisms that determine their sensitivity to environmental change is crucial to ecological forecasting and conservation planning (Pimm et al. 1988, Dennis 1993, Akçakaya et al. 2006). For example, the IUCN Red List of Threatened Species states that species with specialized habitat or microclimate requirements, narrow environmental tolerances, dependence on environmental cues or interspecific interactions, and poor dispersal ability are most susceptible to climate change (IUCN 2009). Yet, whether species' traits influence their sensitivity has scarcely been tested (but see Lenoir et al. 2008). Here we test whether the traits of British butterflies can predict advancements in the date of first appearance in response to recent climate warming. Spring phenology has been

identified by the IPCC (Intergovernmental Panel on Climate Change) as an important metric for detecting responses to climate change and accounts for the majority of the currently reported climate change responses (IPCC 2007). Furthermore, phenological responses to climate change have important implications for individual fitness, population persistence, and community structure (Møller et al. 2008, Chuine 2010, Miller-Rushing et al. 2010), including responses driven by phenological mismatches in plant–pollinator mutualisms (Thomson 2010), plant–insect interactions (Visser and Both 2005), and multitrophic interactions (Both et al. 2009).

Butterflies are prominent among the evidence of ecological responses to recent climate changes. The majority of butterflies studied have shifted their distributions northward (Parmesan et al. 1999, Parmesan 2006) and have moved upward in elevation (Descimon et al. 2005, Parmesan 2005, Wilson et al. 2005). The date of first appearance has advanced for 26 of 35 butterfly species in the United Kingdom (Roy and Sparks 2000), for all 17 species examined in Spain (Stefanescu et al. 2003), and for 16 of 23 species in California, USA (Forister and Shapiro 2003). Although it is clear that climate change drives phenological change in butterflies, there is considerable variation in both the direction and magnitude of these changes among species

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(Parmesan 2006). Past attempts to use species' traits to account for this variation and predict future phenological responses have had mixed success (Stefanescu et al. 2005, Sparks et al. 2006); however, it is unclear whether this is due to low explanatory power of species' traits or to limited species numbers and study durations.

Here we use the long-term U.K. Butterfly Monitoring Scheme (UKBMS), an exemplar data set for detecting species' responses to climate change, to test whether organismal and ecological traits influencing fitness (henceforth termed species' traits) can predict phenological responses. Indeed, the UKBMS data confirmed phenological shifts for the majority of butterflies between 1976 and 1998 (Roy and Sparks 2000). We do not replicate such detailed assessments of phenological shifts, but rather examine the ability of species' traits to predict the shifts occurring for 44 butterfly species during the 1.5°C increase in spring temperature and 1°C increase in summer temperature since 1976 (Meteorological Office Hadley Centre; data *available online*).³

We focused our analyses on several species' traits that have been suggested to influence the ability of butterflies to respond to climate change (Dennis 1993, Forrest and Miller-Rushing 2010): diet breadth, overwintering stage, dispersal ability, and range size. Specifically, we hypothesized that: (1) species with broader diets would show greater advancement in phenology, as they would be less dependent on tracking the phenology of individual host plants; (2) species with more advanced overwintering stages would show greater advancement in phenology, as overwintering adults are more mobile than other developmental stages and can readily respond to warmer spring temperatures without the need for further development; (3) species with greater dispersal ability and larger range size would show less advancement in phenology, as these species would have a greater ability to track their current habitats; and (4) multivoltine species would show greater advancement in phenology, as climate warming has been linked to increased voltinism in butterflies (Altermatt 2010), and multivoltine species might also be more likely to show greater advances in phenology.

MATERIALS AND METHODS

Butterfly species

We used phenological data from a long-term data set maintained by the U.K. Butterfly Monitoring Scheme (UKBMS) for the date of first appearance of 44 butterfly species (Appendix: Table A1) (see Plate 1). The collection of these data is described in detail elsewhere (Pollard and Yates 1993), but briefly, observations of 51 species of butterflies (as of 1998; see Roy and Sparks 2000) at sites distributed across the United Kingdom have been taken weekly from April to September each

year since 1976. The date of first appearance used in our analyses is the mean annual date of first appearance (starting with the first day of the monitoring survey, 1 April; for multivoltine species, the date of first appearance for the first generation) across all monitoring sites. The species that we used in our analyses are a subset of those 51 species: we excluded species for which we did not have complete species' trait data. We also excluded one migratory species for which range and habitat data were difficult to assess and interpret.

Phenological response

We focused our analyses on changes in date of first appearance. Date of first appearance serves as a simple but informative proxy for complex species' responses to climate change mediated by population density, distribution, and habitat use. Although some have criticized the use of the absolute date of first appearance (which can be biased as a result of systematic changes in sampling effort and population abundance over time; van Strien et al. 2008), we used the mean date of first appearance averaged across all study transects for a given species to mitigate potential bias. A common alternative metric, peak date of appearance, is generally less sensitive to sampling effort and population trends (Moussus et al. 2010), but is difficult to interpret when comparisons are being drawn across taxa (e.g., butterfly species) that differ in their number of annual generations. We emphasize that the main goal of our analysis is to examine *relative* differences in the degree of phenological change with respect to species' traits, rather than to obtain unbiased estimates of the magnitude of phenological change. For comparison with previous work on phenological change in U.K. butterflies (see Roy and Sparks 2000), we standardized the date of first appearance data by calculating the mean change per decade (in days) for butterfly species with at least 20 years of available phenological data (most had ≥ 30 years, maximally spanning 1976 to 2008; see Appendix: Table A1).

Species' traits

Diet breadth was estimated by the number of host plant species used by larvae, as reported by Hardy et al. (2007). Estimates of dispersal ability were based on composite scores of mobility, as described by Cowley et al. (2001). Overwintering stage was treated as a factor with groups comprising species that overwinter as eggs, larvae, pupae, or adults. For one species (*Pararge aegeria*) that overwinters in multiple stages (larva and pupa), we re-performed analyses for each stage; because these results were qualitatively similar, we arbitrarily present results for the earliest overwintering stage. Data for overwintering stage were obtained from Dennis (1993). Voltinism was also treated as a factor, with groups comprising species with one generation per year (univoltine) or at least two generations per year (multivoltine). Voltinism data were obtained from Asher

³ (<http://www.metoffice.gov.uk/climate/uk/datasets/Tmean/date/UK.txt>)

et al. (2001). We also considered range size covariates, including the percentage of national 10-km grid cells occupied within a given species' range (Cowley et al. 2001), the latitudinal extent of a given species on the British mainland by category (1, <25%; 2, <50%; 3, <75%; 4, <100% of the total latitudinal span of the United Kingdom; see Dennis 1993), and the northern range edge of a given species (the seconds of latitude of the farthest northern grid cell with at least two presences; see Asher et al. 2001).

Statistical analyses

All statistical analyses were performed using R (version 2.9.1; R Development Core Team 2009). Diet breadth, mobility score, percentage of grid cells occupied, and seconds of latitude of the farthest northern grid cell were natural-log-transformed to satisfy model assumptions of normality. We additionally included the baseline annual date of first appearance (the date of first appearance in 1975, the year prior to the start of UKBMS phenological observations), which we calculated based on the slope of the regression of the date of first appearance as a function of year. This term was included to account for the potential effect of relative annual time of appearance on the degree of phenological advancement. Linear models with all possible combinations of the explanatory variables (excluding voltinism, which had very little explanatory power in preliminary analyses) and their two-way interactions were generated. In all cases, the response was the mean change in date of first appearance per decade.

We used a model selection approach (Burnham and Anderson 2002) to identify a subset of top models with strong levels of empirical support (ΔAIC_c 0–2). We used AIC_c (AIC corrected for small sample sizes) in all analyses rather than AIC , as our sample size divided by the number of model parameters was <40 in all cases. We accounted for model uncertainty by performing model averaging (sensu Burnham and Anderson 2002).

Phylogenetic autocorrelation

We used a phylogeny of U.K. butterfly species from Cowley et al. (2001) to estimate the strength of the phylogenetic signal in our data based on maximum likelihood estimates of Pagel's λ (Pagel 1999; λ ranges from 0 to 1, with larger values indicating stronger phylogenetic autocorrelation). We then reanalyzed the top models identified by ΔAIC_c , taking phylogenetic structure into account (cf. Orme et al. 2009).

RESULTS

All 44 butterfly species tended to advance their date of first appearance (Fig. 1; Appendix: Fig. A1), and 32 of 44 species experienced statistically significant advances (Appendix: Table A1) (also see Plate 1). Several traits were significant predictors of the degree of phenological advancement, including diet breadth, overwintering stage, baseline annual date of first appearance, and the

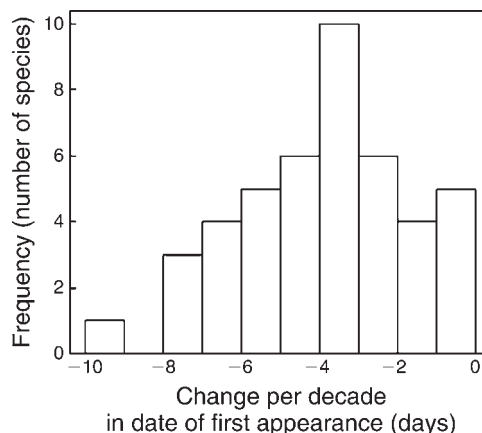


FIG. 1. A frequency distribution shows that each of the 44 butterfly species in the U.K. study has advanced its date of first appearance since 1976.

interaction of latitudinal extent with the percentage of national 10-km grid cells occupied (Fig. 2, Table 1). Other traits, including dispersal ability, voltinism, and the northern range edge were poor predictors of phenological advancement (main effects and interaction effects between and involving these terms were not present in any of the best-fitting models, and therefore were removed from further consideration). Five models consisting of combinations of the significant predictors (see Appendix: Table A2) were found to have strong levels of empirical support (ΔAIC_c 0–2), and explained a moderate amount of the variation in phenological advancement (multiple R^2 values ranged from 0.43 to 0.52, and adjusted R^2 values ranged from 0.30 to 0.38).

Species with more host plant species at the larval stage experienced a lesser degree of advancement in their date of first appearance compared to species with fewer host plant species (Fig. 2b). In addition, species that overwinter as adults had significantly greater advances in date of first appearance compared to species that overwinter as larvae ($t = -3.71$, $df = 33$, $P = 0.0037$) and pupae ($t = -4.25$, $df = 33$, $P < 0.0001$; Tukey's post hoc test; Fig. 2a). However, no further significant differences were detected in all remaining pairwise comparisons between overwintering stages. Species with earlier baseline annual dates of first appearance tended to experience greater advancements in date of first appearance (Fig. 2c).

Although the main effects for the percentage of grid cells occupied and latitudinal extent had weak support, their interaction was an important predictor of phenological advancement (Fig. 2d), indicating that more widespread, dense species experience less phenological advancement (see *Discussion*). Interactions between the percentage of grid cells occupied and diet breadth, and between latitudinal extent and diet breadth, were largely unimportant (Appendix: Fig. A2), because they arose infrequently during the model selection process (Appen-

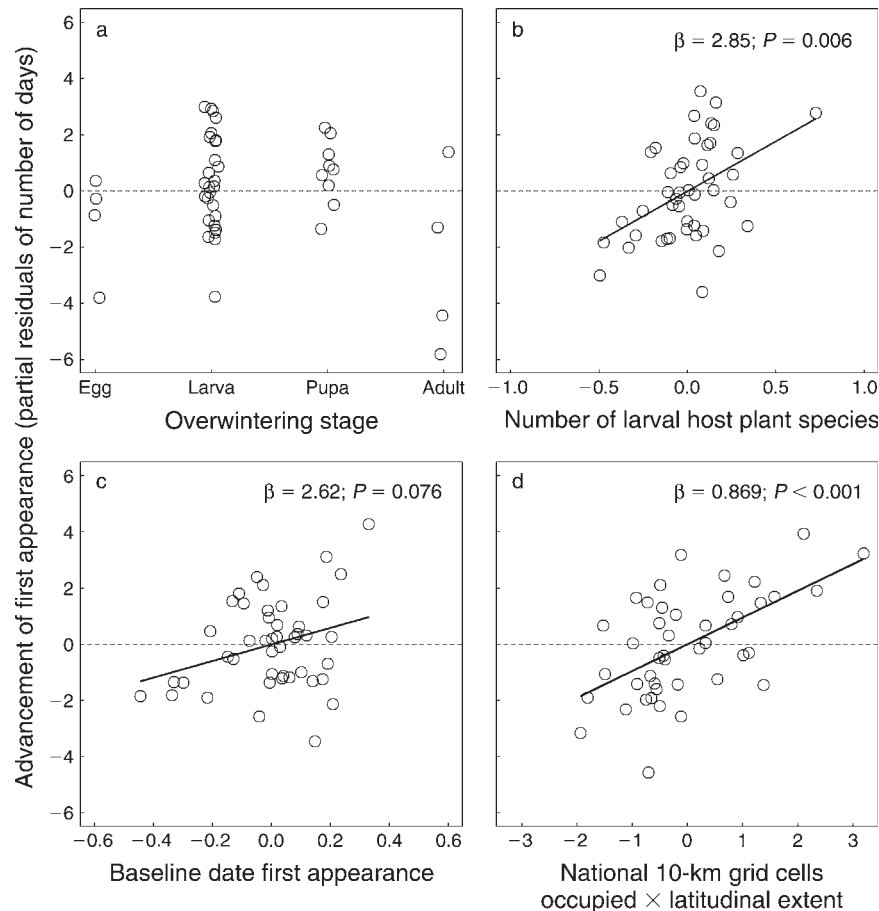


FIG. 2. The ability of species' traits to predict phenological change. (a) Partial residuals (residuals of regressing the response variable on the independent variables, but omitting the independent variable of interest) for change per decade in date of first appearance are presented for each category of overwintering stage; note that the points have been jittered for visualization. (b–d) Added variable plots (see Velleman and Welsch 1981; partial residuals plotted against the 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), based on a model containing all terms identified as part of the top model subset during the model selection process. Only results for significant predictors of phenological change are shown here (see also Appendix: Fig. A2). Regression statistics are based on model-averaged coefficients (see Table 1). The dashed line at zero corresponds to the change in date of first appearance per decade for all species (-3.92 ± 2.20 days, mean \pm SD). Points below the dashed line indicate species with greater phenological advancement (more change) compared to points above the line (less change).

dix: Table A2) and were not significant in the ANCOVA performed on the full model (Table 1).

Most of the explanatory power of our models was attributable to species' traits, as we detected little remnant evidence of phylogenetic nonindependence. For each of the top five models selected on the basis of ΔAIC_c , models that accounted for phylogenetic autocorrelation (using maximum likelihood estimates where $\lambda < 0.0001$ for each of these models) were not significantly different from models that did not account for phylogenetic autocorrelation (where $\lambda = 0$). Therefore, we omitted phylogenetic corrections from our analyses to decrease the probability of type II error (false negative), which can arise from incorporating nonsignificant phylogenetic structure into statistical models (e.g., Kunin 2008). In addition, there was negligible phylogenetic signal in models where the

response and each explanatory variable were considered separately, and an intercept-only model for the response ($\lambda < 0.0001$; $\chi^2 < 0.0001$; $P \gg 0.05$, in all cases). Some traits, including overwintering stage, number of larval host plant species, percentage of national 10-km grid cells occupied, and baseline annual date of first appearance, exhibited moderate phylogenetic signal when considered individually outside of the linear modeling framework (based on Blomberg's K ; see Appendix: Table A3), indicating that some traits may still be phylogenetically conserved.

DISCUSSION

Our results confirm basic phenological patterns reported in this study system a decade ago by Roy and Sparks (2000). We found that most butterfly species have significantly advanced their date of first appearance

TABLE 1. Model-averaged (MA) coefficients with corresponding standard errors, and complementary results from ANCOVA on a model containing all parameters identified in the top model subset for U.K. butterflies.

Parameter	β_{MA} (SE _{MA})	F^\dagger	P
Intercept	-11.1 (8.90)	5.34	0.0272
ln(date of first appearance 1975)	2.62 (1.62)	3.36	0.0758
Overwintering stage		7.14	0.0008
Egg [‡]			
Larva	0.737 (1.10)		
Pupa	2.08 (1.59)		
Adult	-4.10 (1.82)		
ln(no. larval host plant species)	2.85 (1.24)	8.70	0.0058
ln(percentage national 10-km grid cells)	-0.234 (1.04)	0.00001	0.997
U.K. latitudinal extent	-1.39 (1.19)	1.84	0.184
ln(no. larval host plant species) × ln(percentage national 10-km grid cells)	-1.03 (0.530)	1.68	0.203
ln(no. larval host plant species) × ln(U.K. latitudinal extent)	-1.36 (0.464)	2.56	0.119
ln(percentage national 10-km grid cells) × U.K. latitudinal extent	0.869 (0.249)	16.1	0.0003

Notes: For each parameter, model-averaged coefficients were based on weighted means of coefficients from the top model subset, weighted by the Akaike weight w_i for each model, i , in which the term occurs (see Appendix: Table A2 for Akaike model weights; for model averaging, see Burnham and Anderson [2002]). The model analyzed with ANCOVA was a model containing all the parameters identified by the model selection process: change per decade in date of first appearance = ln(date of first appearance in 1975) + overwintering stage + ln(number of larval host plant species) + ln(percentage of national 10-km grid cells occupied) + latitudinal extent + ln(number of larval host plant species) × ln(percentage of national 10-km grid cells occupied) + ln(number of larval host plant species) × latitudinal extent + ln(percentage of national 10-km grid cells occupied) × latitudinal extent. Significant P values (<0.05) are in bold.

[†] The F test and corresponding P value for overwintering stage reflect the global F test for assessing the significance of overwintering stage; see *Results* for post hoc analyses of all pairwise comparisons of the four overwintering stages. Type III SS: df = 1, 33 for all terms except the overwintering stage, where df = 3, 33.

[‡] The reported coefficients are the differences between the egg overwintering stage (arbitrarily set as the baseline level for treatment contrasts) and each remaining overwintering stage.

over the past 30 years. Indeed, our ability to detect significant phenological changes was greatly improved with these long-term data. Many species with nonsignificant changes in the date of first appearance based on 20 years of data (Roy and Sparks 2000) had significantly advanced their first appearance based on the comparable 30-year data set used in our analyses (Appendix: Table A1). This underscores the value of such long-term data sets in understanding organismal responses to climate change.

Although species' traits have been suggested to influence phenological responses to recent climate change, this relationship has rarely been addressed empirically. Efforts to interpret phenological responses in an ecological and evolutionary context are fairly nascent, but progressing rapidly (Forrest and Miller-Rushing 2010). Our approach allowed us to identify characteristics of U.K. butterfly species that best predicted their degree of phenological advancement. Further investigation of the mechanisms by which these characteristics influence phenology may aid in understanding vulnerability to climate change (Heikkinen et al. 2010).

We found that species' traits can be important predictors of the degree to which U.K. butterfly species have advanced their date of first appearance since 1976. Species with a narrower diet breadth expressed greater phenological advancement (Fig. 2b). This finding was unexpected, as phenological advancement may be limited by the availability of host plants (Memmott et al. 2007, van Asch and Visser 2007, Pelini et al. 2009)

and generalist host plant use has been observed to facilitate the climate-driven range expansion in U.K. butterfly species (Braschler and Hill 2007). However, it may be that phenological advancement of specialized butterflies was enabled by the phenological advancements of an individual host plant. Species with greater numbers of potential host plants may be buffered from such shifts in plant phenology (reviewed in Bale et al. 2002).

We found that species that overwintered as adults had a greater degree of phenological advancement than species that overwintered as larvae or pupae (Fig. 2a). Adults are more mobile than other developmental stages, and this may allow them to respond rapidly to warm spring temperatures. Caution is necessary when interpreting this finding, as most U.K. butterflies overwinter as larvae or pupae (four species overwinter as adults in our analyses).

Species with earlier baseline dates of first appearance tended to exhibit greater advancements (Fig. 2c). This may reflect the fact that species that emerge earlier have experienced a greater mean increase in spring temperature (1.5°C) relative to summer (1.0°C) since 1975 or tend to overwinter in more advanced stages (Dennis 1993). The timing of warming has been observed to influence the phenological responses of early- and late-season grasshoppers (Nufio et al. 2010).

The negative relationship between phenological advancement and the interaction of latitudinal extent (percentage of the U.K. mainland occupied) with the percentage of national 10-km grid cells occupied (Fig.

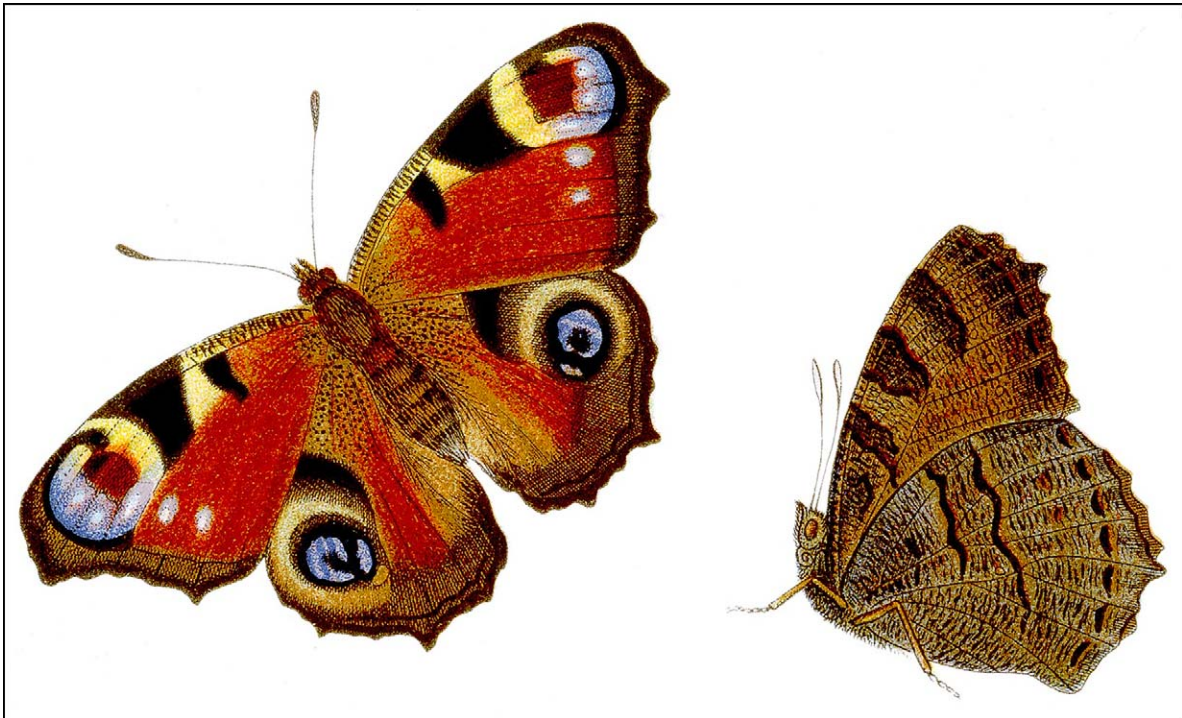


PLATE 1. The European peacock butterfly, *Inachis io*, a species which has significantly advanced its date of first appearance since 1976. The drawing is from entomologist Jacob Hübner's (1761–1826) *Das kleine Schmetterlingsbuch*.

2d), indicates that species that are more narrowly distributed (occupy a relatively smaller percentage of grid cells within their latitudinal extent) express greater phenological advancement. Widely distributed species may have a limited ability to expand their range boundaries or habitat niches (Oliver et al. 2009), which could correspond to a phenological change. Although it is clear that phenology influences the ability of a species to complete its life cycle and thus persist in an area, the link between phenological and range shifts is still murky (Chuine 2010).

The influence of range size did not appear to be mediated by an interaction with diet breadth (Appendix: Fig. A2), despite a growing body of evidence suggesting that butterfly use of resources (e.g., habitat type, diet breadth, and host plant growth strategy) can vary with butterfly population density, distribution, and overall range size (Cowley et al. 2000, 2001, Warren et al. 2001, Dennis et al. 2004). Our preliminary analyses of the U.K. butterfly fauna indicated little relationship between phenological advancement and larval host plant type (dicots, grasses, non-grass monocots, gymnosperms; see Beck and Fiedler 2009) and between phenological advancement and butterfly density (assessed at local, regional, national, and global scales; see Cowley et al. 2001).

Other traits including dispersal ability and voltinism had little explanatory power in predicting the advancement of first appearance. The predictive ability of

dispersal may have been limited by difficulties in quantification (Cowley et al. 2001). Although there is growing evidence demonstrating that species' voltinism may be altered as a consequence of climate change (Tobin et al. 2008, Altermatt 2010), how an organism's current voltinism status influences phenological responses to climate change is less clear (Dennis 1993, Roy and Sparks 2000, Stefanescu et al. 2003, Tobin et al. 2008, Altermatt 2010). Others likewise have found little evidence to suggest that voltinism is a strong predictor of phenological change (Stefanescu et al. 2003, Sparks et al. 2006), potentially because the complex relationships between climate change, insect development, and the cues that initiate and terminate diapause produce idiosyncratic responses (Tobin et al. 2008).

Interestingly, phylogenetic relatedness among species explained very little variation in species' phenological responses. This result is somewhat surprising, as it suggests that although some traits (e.g., overwintering stage, diet breadth, and range size) can predict species' phenological responses, these traits are not highly conserved among closely related species (see Appendix: Table A3). In contrast, phylogeny proved to be a good predictor of the degree to which climate changes over the last 150 years in Concord, Massachusetts, USA have shifted flowering time, abundance, and persistence of plant species (Willis et al. 2008). This discrepancy points to the importance of studying species' traits in the

context of climate change, rather than relying solely on phylogenies.

Our analysis suggests the viability of using species' traits such as overwintering stage, diet breadth, and range size to predict U.K. butterfly species' phenological responses to climate change. Presently, few studies have examined how these traits influence species' responses to climate change (but see Stefanescu et al. 2003, Sparks et al. [2006] for butterflies). For example, grasses and those species restricted to mountain habitats experienced more pronounced range shifts in response to 20th century climate change (Lenoir et al. 2008) and perennial plants exhibited more pronounced shifts in flowering time (Crimmins et al. 2009). In a study across U.K. taxa, Thackeray et al. (2010) found that lower trophic levels exhibit the most pronounced phenological shifts. The results of these studies and our results presented here suggest the importance of species' traits in predicting responses to climate change. Further effort in this area is needed to understand how these traits influence species' responses to climate change and the fitness consequences of such relationships.

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APPENDIX

Supporting results for phenological advancement, phylogenetic signal, and statistical model selection (*Ecological Archives* E092-083-A1).