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1 Species' traits predict phenological responses to climate change in butterflies

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7 Running head: Species' traits and phenological change

8

9 **Abstract**

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

21 **Key words:** diet breadth, overwintering stage, phenology, phylogeny, range size, traits

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23

24 **Introduction**

25 Evidence is accumulating rapidly that species are shifting their latitudinal distributions,
26 elevation ranges, and phenologies in response to recent climate changes (reviewed in Parmesan
27 2006). Identifying characteristics of organisms that determine their sensitivity to environmental
28 change is crucial to ecological forecasting and conservation planning (Pimm et al. 1988; Dennis
29 1993; Akçakaya et al. 2006). For example, the IUCN Red List of Threatened Species states that
30 species with specialized habitat or microclimate requirements, narrow environmental tolerances,
31 dependence on environmental cues or interspecific interactions, and poor dispersal ability are
32 most susceptible to climate change (IUCN 2009). Yet, whether species' traits influence their
33 sensitivity has scarcely been tested (but see Lenoir et al. 2008). Here we test whether the traits of
34 British butterflies can predict advancements in the date of first appearance in response to recent
35 climate warming. Spring phenology has been identified by the IPCC (Intergovernmental Panel
36 on Climate Change) as an important metric for detecting responses to climate change and
37 accounts for the majority of the currently reported climate change responses (IPCC 2007).
38 Furthermore, phenological responses to climate change have important implications for
39 individual fitness, population persistence, and community structure (Møller et al. 2008; Chuine
40 2010; Miller-Rushing et al. 2010; including responses driven by phenological mismatches in:
41 plant-pollinator mutualisms (Thomson 2010); plant-insect interactions (Visser and Both 2005);
42 multitrophic interactions (Both et al. 2009)).

43 Butterflies are prominent among the evidence of ecological responses to recent climate
44 changes. The majority of butterflies studied have shifted their distributions northward (Parmesan
45 et al. 1999; Parmesan 2006) and moved upward in elevation (Descimon et al. 2005; Parmesan
46 2005; Wilson et al. 2005). The date of first appearance has advanced for 26 of 35 butterfly

47 species in the United Kingdom (Roy and Sparks 2000), for all 17 species examined in Spain
48 (Stefanescu et al. 2003), and for 16 of 23 species in California (Forister and Shapiro 2003).
49 While it is clear that climate change drives phenological change in butterflies, there is
50 considerable variation in both the direction and magnitude of these changes among species
51 (Parmesan 2006). Past attempts to use species' traits to account for this variation and predict
52 future phenological responses have had mixed success (Sparks et al. 2006; Stefanescu et al.
53 2005); however, it is unclear whether this is due to low explanatory power of species' traits or
54 limited species numbers and study durations.

55 Here we use the long-term UK Butterfly Monitoring Scheme (UKBMS), an exemplar
56 dataset for detecting species' responses to climate change, to test whether organismal and
57 ecological traits influencing fitness (henceforth termed species' traits) can predict phenological
58 responses. Indeed, the UKBMS data confirmed phenological shifts for the majority of butterflies
59 between 1976-1998 (Roy and Sparks 2000). We do not replicate such detailed assessments of
60 phenological shifts, but rather examine the ability of species' traits to predict the shifts occurring
61 for 44 butterflies during the 1.5 °C increase in spring temperature and 1 °C increase in summer
62 temperature since 1976 (Meteorological Office Hadley Centre; <www.metoffice.gov.uk>).

63 We focused our analyses on several species' traits that have been suggested to influence
64 the ability of butterflies to respond to climate change (Dennis 1993; Forrest and Miller-Rushing
65 2010): diet breadth, overwintering stage, dispersal ability, and range size. Specifically, we
66 hypothesized: (1) species with broader diets would show greater advancement in phenology, as
67 they would be less dependent on tracking the phenology of individual host plants; (2) species
68 with more advanced overwintering stages would show greater advancement in phenology, as
69 overwintering adults are more mobile than other developmental stages and can readily respond to

70 warmer spring temperatures, without the need for further development; (3) species with greater
71 dispersal ability and larger range size would show less advancement in phenology, as these
72 species would have a greater ability to track their current habitats; (4) multivoltine species would
73 show greater advancement in phenology, as climate warming has been linked to increased
74 voltinism in butterflies (Altermatt 2010), and multivoltine species might also be more likely to
75 show greater advances in phenology.

76 **Materials and Methods**

77 *Butterfly species.* We used phenological data from a long-term dataset maintained by the
78 UK Butterfly Monitoring Scheme (UKBMS) for the date of first appearance of 44 butterfly
79 species (Appendix: Table 1). The collection of these data is described in detail elsewhere
80 (Pollard and Yates 1993), but briefly, observations of 51 species of butterflies (as of 1998; see
81 Roy and Sparks 2000) at sites distributed across the UK have been taken weekly from April to
82 September each year since 1976. The date of first appearance used in our analyses is the mean
83 annual date of first appearance (starting with the first day of the monitoring survey, April 1; for
84 multivoltine species, the date of first appearance for the first generation) across all monitoring
85 sites. The species we used in our analyses are a subset of those 51 species: we excluded species
86 for which we did not have complete species' trait data. We also excluded one migratory species,
87 for which range and habitat data were difficult to assess and interpret.

88 *Phenological response.* We focused our analyses on changes in date of first appearance.
89 Date of first appearance serves as a simple but informative proxy for complex species' responses
90 to climate change mediated by population density, distribution, and habitat use. Although some
91 have criticized the use of the absolute date of first appearance—this measure can be biased as a
92 result of systematic changes in sampling effort and population abundance over time (van Strien

93 et al. 2008)—we used the mean date of first appearance averaged across all study transects for a
94 given species to mitigate potential bias. A common alternative metric, peak date of appearance,
95 is generally less sensitive to sampling effort and population trends (Moussus et al. 2010), but is
96 difficult to interpret when comparisons are being drawn across taxa (*e.g.*, butterfly species) that
97 differ in their number of annual generations. We emphasize that the main goal of our analysis is
98 to examine *relative* differences in the degree of phenological change with respect to species'
99 traits, rather than to obtain unbiased estimates of the magnitude of phenological change. For
100 comparison with previous work on phenological change in UK butterflies (see Roy and Sparks
101 2000), we standardized the date of first appearance data by calculating the mean change per
102 decade (in days) for butterfly species with at least 20 years of available phenological data (most
103 had ≥ 30 years, maximally spanning 1976 to 2008; see Appendix: Table 1).

104 *Species' traits.* Diet breadth was estimated by the number of larval host plant species
105 used, as reported by Hardy et al. (2007). Estimates of dispersal ability were based on composite
106 scores of mobility, as described by Cowley et al. (2001). Overwintering stage was treated as a
107 factor with groups comprising species that overwinter as eggs, larvae, pupae and adults. For one
108 species (*Pararge aegeria*) which overwinters in multiple stages (larva and pupa), we re-
109 performed analyses for each stage; because these results were qualitatively similar, we arbitrarily
110 present results for the earliest overwintering stage. Data for overwintering stage were obtained
111 from Dennis (1993). Voltinism was also treated as a factor with groups comprising species with
112 one generation per year (univoltine) or at least two generations per year (multivoltine). Voltinism
113 data were obtained from Asher et al. (2001). We also considered range size covariates, including
114 the percent of national 10 km grid cells occupied within a given species' range (Cowley et al.
115 2001), the latitudinal extent of a given species on the British mainland (1: <25%, 2: <50%, 3:

116 <75%, 4: <100%; see Dennis 1993), and the northern range edge of a given species (the seconds
117 of latitude of the farthest northern grid cell with at least 2 presences; see Asher et al. 2001).

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

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

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

139 Results

140 All 44 butterfly species tended to advance their date of first appearance (Figure 1;
141 Appendix: Figure 1), and 32 of 44 species experienced statistically significant advances
142 (Appendix: Table 1). Several traits were significant predictors of the degree of phenological
143 advancement including diet breadth, overwintering stage, baseline annual date of first
144 appearance and the interaction of latitudinal extent with the percent national 10 km grid cells
145 occupied (Figure 2; Table 1). Other traits, including dispersal ability, voltinism, and the northern
146 range edge were poor predictors of phenological advancement (main effects and interaction
147 effects between and involving these terms were not present in any of the best fitting models, and
148 therefore were removed from further consideration). Five models comprised of combinations of
149 the significant predictors (listed above; see Appendix: Table 2) were found to have strong levels
150 of empirical support ($\Delta AICc$ 0-2), and explained a moderate amount of the variation in
151 phenological advancement (multiple R^2 values ranged from 0.43-0.52, and adjusted R^2 values
152 ranged from 0.30-0.38).

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

161 Although the main effects for the percent of grid cells occupied and latitudinal extent had
162 weak support, their interaction was an important predictor of phenological advancement (Figure
163 2d), indicating more widespread, dense species experience less phenological advancement (see
164 Discussion). Interactions between the percent of grid cells occupied and diet breadth, and
165 between latitudinal extent and diet breadth were largely unimportant (Appendix: Figure 2), as
166 they arose infrequently during the model selection process (Appendix: Table 2) and were not
167 significant in the ANCOVA performed on the full model (Table 1).

168 Most of the explanatory power of our models was attributable to species' traits, as we
169 detected little remnant evidence of phylogenetic non-independence. For each of the top five
170 models selected on the basis of ΔAICc , models that accounted for phylogenetic autocorrelation
171 (using maximum likelihood estimates of λ which were < 0.0001 for each of these models) were
172 not significantly different from models that did not account for phylogenetic autocorrelation
173 (where $\lambda = 0$). Therefore, we omitted phylogenetic corrections from our analyses to decrease the
174 probability of type II error (false negative) which can arise from incorporating non-significant
175 phylogenetic structure into statistical models (*e.g.*, Kunin 2008). In addition, there was negligible
176 phylogenetic signal in models where the response and each explanatory variable were considered
177 separately, and an intercept-only model for the response ($\lambda < 0.0001$; $\chi^2 < 0.0001$; $P \gg 0.05$, in
178 all cases). Some traits, including overwintering stage, number of larval host plant species,
179 percent national 10 km grid cells occupied, and baseline annual date of first appearance,
180 exhibited moderate phylogenetic signal when considered individually outside of the linear
181 modeling framework (based on Blomberg's K; see Appendix: Table 3), indicating some traits
182 may still be phylogenetically conserved.

183 **Discussion**

184 Our results confirm basic phenological patterns reported in this study system a decade
185 ago by Roy and Sparks (2000). We found that most butterfly species significantly advanced their
186 date of first appearance over the past 30 years. Indeed, our ability to detect significant
187 phenological changes was greatly improved with these long-term data. Many species with non-
188 significant changes in the date of first appearance based on 20 years of data (Roy and Sparks
189 2000) had significantly advanced their first appearance based on the comparable 30 year data set
190 used in our analyses (Appendix: Table 1). This underscores the value of such long-term data sets
191 in understanding organismal responses to climate change.

192 Although species' traits have been suggested to influence phenological responses to
193 recent climate change, this relationship has rarely been addressed empirically. Efforts to interpret
194 phenological responses in an ecological and evolutionary context are fairly nascent but
195 progressing rapidly (Forrest and Miller-Rushing 2010). Our approach allowed us to identify UK
196 butterfly species' characteristics that best predicted their degree of phenological advancement.
197 Further investigation of the mechanisms by which these characteristics influence phenology may
198 aid in understanding vulnerability to climate change (Heikkinen et al. 2009).

199 We found that species' traits can be important predictors of the degree to which UK
200 butterfly species have advanced their date of first appearance since 1976. Species with a
201 narrower diet breadth expressed greater phenological advancement (Figure 2b). This finding
202 was unexpected as phenological advancement may be limited by the availability of host plants
203 (van Asch and Visser 2007; Memmot et al. 2007; Pelini et al. 2009) and generalist host-plant use
204 has been observed to facilitate the climate-driven range expansion in UK butterfly species
205 (Braschler and Hill 2007). However, it may be that phenological advancement of specialized
206 butterflies was enabled by the phenological advancements of an individual host plant. Species

207 with greater numbers of potential host plants may be buffered from such shifts in plant
208 phenology (reviewed in Bale et al. 2002).

209 We found that species that overwintered as adults had a greater degree of phenological
210 advancement compared to species that overwintered as larvae or pupae (Figure 2a). Adults are
211 more mobile than other developmental stages, and this may allow them to respond rapidly to
212 warm spring temperatures. Caution is necessary when interpreting this finding, as most UK
213 butterflies overwinter as larvae or pupae (4 species overwinter as adults in our analyses).

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

220 The negative relationship between phenological advancement and the interaction of
221 latitudinal extent (percent of the UK mainland occupied) with the percent of national 10 km grid
222 cells occupied (Figure 2d), indicates that species that are more narrowly distributed (occupy a
223 relatively smaller percentage of grid cells within their latitudinal extent) express greater
224 phenological advancement. Widely distributed species may have a limited ability to expand their
225 range boundaries or habitat niches (Oliver et al. 2009), which could correspond to a phenological
226 change. While it is clear that phenology influences the ability of a species to complete its life
227 cycle and thus persist in an area, the link between phenological and range shifts is still murky
228 (Chuine 2010).

229 The influence of range size did not appear to be mediated by an interaction with diet
230 breadth (Appendix: Figure 2) despite a growing body of evidence suggesting that butterfly
231 resource-use (*e.g.*, habitat type, diet breadth, and host plant growth strategy) can vary with
232 butterfly population density, distribution and overall range size (Cowley et al. 2000, 2001;
233 Warren et al. 2001; Dennis et al. 2004). Our preliminary analyses of the UK butterfly fauna
234 indicated little relationship between phenological advancement and larval host plant type (dicots,
235 grasses, non-grass monocots, gymnosperms; see Beck and Fiedler 2009) and between
236 phenological advancement and butterfly density (assessed at local, regional, national and global
237 scales; see Cowley et al. 2001).

238 Other traits including dispersal ability and voltinism had little explanatory power in
239 predicting the advancement of first appearance. The predictive ability of dispersal may have been
240 limited by difficulties in quantification (Cowley et al. 2001). While evidence is growing which
241 demonstrates species' voltinism may be altered as a consequence of climate change (Tobin et al.
242 2008; Altermatt 2010), how an organism's current voltinism status influences phenological
243 responses to climate change is less clear (Dennis 1993; Roy and Sparks 2000; Stefanescu et al.
244 2003; Tobin et al. 2008; Altermatt 2010). Others have likewise found little evidence to suggest
245 voltinism is a strong predictor of phenological change (Stefanescu et al. 2003; Sparks et al.
246 2006), potentially because the complex relationships between climate change, insect
247 development and the cues that initiate and terminate diapause produce idiosyncratic responses
248 (Tobin et al. 2008).

249 Interestingly, phylogenetic relatedness among species explained very little variation in
250 species' phenological responses. This result is somewhat surprising as it suggests that while some
251 traits (*e.g.*, overwintering stage, diet breadth and range size) can predict species' phenological

252 responses, these traits are not highly conserved among closely related species (see Appendix:
253 Table 3). In contrast, phylogeny proved a good predictor of the degree to which climate changes
254 over the last 150 years in Concord, MA have shifted flowering time, abundance, and persistence
255 of plant species (Willis et al. 2008). This discrepancy points to the importance of studying
256 species' traits in the context of climate change rather than relying solely on phylogenies.

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

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434 Table 1. Model averaged coefficients with corresponding standard errors, and complementary
 435 results from ANCOVA on a model containing all parameters identified in the top model subset.

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Parameter	β_{MAi} (S.E. _{MAi}) ^a	$F^{b,c}$	$P^d > F$
Intercept	-11.1 (8.90)	5.34	0.0272
Date first appearance 1975 (ln)	2.62 (1.62)	3.36	0.0758
	Egg ^c		
	Larva 0.737 (1.10)		
Overwintering stage	Pupa 2.08 (1.59)	7.14	0.0008
	Adult -4.10 (1.82)		
Number larval host plant species (ln)	2.85 (1.24)	8.70	0.0058
Percent nat 10km grid cells (ln)	-0.234 (1.04)	0.00001	0.997
UK latitudinal extent	-1.39 (1.19)	1.84	0.184
Number larval host plant species (ln)	-1.03 (0.530)	1.68	0.203
* Percent nat 10km grid cells (ln)			
Number larval host plant species (ln)	-1.36 (0.464)	2.56	0.119
* UK latitudinal extent			
Percent nat 10km grid cells (ln)	0.869 (0.249)	16.1	0.0003
* UK latitudinal extent			

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438 a. For each parameter, model averaged coefficients were based on weighted means of
 439 coefficients from the top model subset (weighted by the Akaike weight (w_i) for each model, i , in

440 which the term occurs); see Appendix: Table 2 for Akaike model weights (cf. Burnham and
 441 Anderson 2002 for model averaging).

442 *b.* The model analyzed with ANCOVA was a model containing all the parameters identified by
 443 the model selection process. Model specification: Change per decade in date of first appearance
 444 = $\ln(\text{date first appearance } 1975) + \text{overwintering stage} + \ln(\text{number larval host plant species}) +$
 445 $\ln(\text{percent national } 10 \text{ km grid cells occupied}) + \text{latitudinal extent} + \ln(\text{number larval host plant}$
 446 $\text{species}) * \ln(\text{percent national } 10 \text{ km grid cells occupied}) + \ln(\text{number larval host plant species}) *$
 447 $\text{latitudinal extent} + \ln(\text{percent national } 10 \text{ km grid cells occupied}) * \text{latitudinal extent}.$

448 *c.* Type III SS; $\text{ndf} = 1$ and $\text{ddf} = 33$ for all terms except overwintering stage, where $\text{ndf} = 3$.

449 *d.* Terms significant at the $P < 0.05$ level are in bold.

450 *e.* Baseline level for treatment contrasts.

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463 **Figure Legends**

464 Figure 1. A frequency distribution shows that each of the 44 butterfly species has advanced its
465 date of first appearance since 1976.

466 Figure 2. The ability of species' traits to predict phenological change. (a) Partial residuals
467 (residuals of regressing the response variable on the independent variables but omitting the
468 independent variable of interest) for change per decade in date of first appearance are presented
469 for each category of overwintering stage; note that the points have been jittered for visualization.
470 (b-d) Added variable plots (see Velleman and Welsch 1981; partial residuals plotted against the
471 residuals of each independent variable of interest regressed on all remaining independent
472 variables; regressions of partial residuals on the independent variable residuals are indicated with
473 solid lines) based on a model containing all terms identified as part of the top model subset
474 during the model selection process. Only results for significant predictors of phenological change
475 are shown here (see also Appendix: Figure 2). Regression statistics are based on model averaged
476 coefficients (see Table 1). The dashed line at zero corresponds to the mean (± 1 SD) change in
477 date of first appearance per decade for all species (-3.92 ± 2.20 days). Points below the dashed
478 line indicate species with greater phenological advancement (more change) compared to points
479 above the line (less change).

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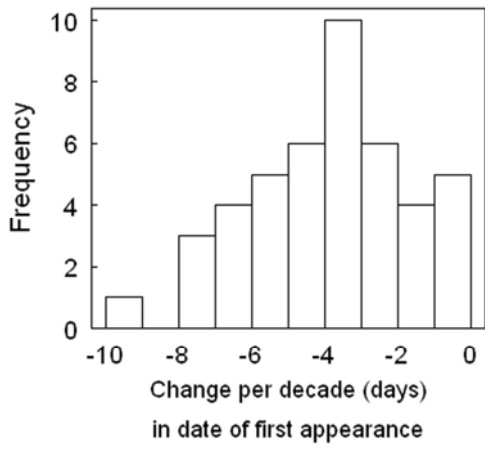
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487 Figure 1



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