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Phenological shifts in hoverflies (Diptera: Syrphidae): linking measurement and mechanism

Running head: Phenological shifts in hoverflies

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Abstract

An understanding of ecological and evolutionary responses to global environmental change requires both a robust measurement of the change that is occurring and a mechanistic framework for understanding the drivers of that change. Such a requirement provides a challenge because biological monitoring is often ad hoc, and mechanistic experiments are often performed under highly simplified conditions. This study integrates multiple datasets to evaluate our current knowledge of the measurement and mechanism of phenological shifts in a key pollinator taxon: the hoverflies (Diptera: Syrphidae). First, two large, complementary and independent monitoring datasets are used to test for trends in phenology: an ad hoc national recording scheme containing >620,000 records, and standardised monitoring with consistent methods over 30 years. Results show that ad hoc and standardised recording data give quantitatively the same value for phenological advance in hoverflies (ca. 12 days·°C^{-1} on average at the beginning of the flight period), supporting the value of biological recording for the measurement of global ecological change. While the end of the flight period appears static in ad hoc recording, the standardised dataset suggests a similar advance as in the beginning of the flight period. Second, an extensive traits dataset and a novel database of laboratory-derived developmental data on Syrphidae (153 published studies) are used to test for mechanistic patterns in phenological shifts. The only species trait that influenced phenology was voltinism, where species with more generations per year exhibit stronger phenological advances. We demonstrate considerable variation in the laboratory-derived sensitivity to temperature but this does not match field-derived measures of phenology. The results demonstrate that, as for many taxa, we have a strong understanding of the patterns of global ecological change but that we currently lack a detailed mechanistic

45 understanding of those processes despite extensive research into the fundamental biology of
46 some taxonomic groups.

Introduction

Global climate change drives three main categories of biological response: species are shifting their geographical ranges towards the poles ("range shifts", Chen, et al. 2011), transitioning between life-history stages earlier ("phenological shifts", Menzel, et al. 2006), and becoming smaller at maturity (Daufresne, et al. 2009). Although exceptions exist to each, these patterns appear to be broadly consistent across taxa, suggesting general biological phenomena (Parmesan 2006). Phenological shifts, in particular, have been detected in a range of taxa, including flowering plants, insects, amphibians, birds, and mammals (for a review see Thackeray, et al. 2010). The lack of long-term monitoring for many taxa has necessitated the use of various types of biological records including standardised monitoring schemes, ad hoc recording networks, and digitised museum specimens (Powney and Isaac 2015). Although detailed methodologies have been developed that allow substantial insight from these datasets (Hassall and Thompson 2010, Isaac, et al. 2014, Moussus, et al. 2010), there are few cases in which ad hoc data derived from citizen science can be cross-validated using standardised datasets.

Many studies, such as those reviewed above, have described responses to climate change in the field, but there has been less effort directed towards the mechanisms underpinning those patterns. A mechanistic understanding of global change requires the study of particular phenomena under controlled conditions with links (often via mesocosms or field trials) to observations in the natural world. Such programmes of research span the continua of ecological validity and ecological relevance to provide a comprehensive answer to complex questions, but are rare due to the requirement for substantial research effort. Notable exceptions include the International Tundra Experiment, which has used experimental warming compared against field monitoring to

70 demonstrate that climate is influencing plant communities (Elmendorf, et al. 2015), experimental
71 rearing of birds to demonstrate phenological advance (Visser, et al. 2009), and aquatic mesocosm
72 experiments that simulate future warming scenarios (e.g. Eklöf, et al. 2012). However, there is a
73 substantial gap in our knowledge of how (or, indeed, if) fundamental aspects of species biology
74 at the level of the organism are causally related to large-scale spatial and temporal patterns in
75 abundance and diversity.
76
77 The hoverflies (Diptera: Syrphidae) have received relatively little attention in the literature
78 relating to global change despite being a significant contributor to pollination (Larson, et al. 2001,
79 Ssymank, et al. 2008), particularly in higher latitudes, and playing a commercially important role
80 in biocontrol of agricultural and horticultural pests (Tenhumberg and Poehling 1995). Successful
81 pollination and biocontrol are dependent upon maintaining temporal associations with particular
82 resources (flowers, pests), making the Syrphidae particularly reliant upon seasonal timing to
83 maximise their fitness and their associated ecosystem services. However, Syrphidae also exhibit
84 a range of different traits that might influence exposure to environmental conditions with
85 different degrees of buffering of ambient temperature. Adults feed on pollen and nectar, but
86 larvae exhibit a wide range life-history strategies including saprophagy, commensalism with
87 social insects, and above-ground carnivory (Rotheray and Gilbert 2011). Species also differ in
88 their seasonal development in the UK, with voltinism ranging from a single generation to up to
89 four generations, and other species exploiting southern environmental conditions before arriving
90 in the UK as migrants. While some species overwinter as larvae, others overwinter as adults. As
91 such, a range of traits may be expected to influence the extent to which phenological shifts vary
92 between species. A previous study of 20 hoverfly species in the UK sampled at a single site

93 between 1991 and 2007 showed a range of phenological shifts in first sighting, last sighting,
94 peak abundance and total abundance (Graham-Taylor, et al. 2009). A more detailed analysis of a
95 20-year dataset of syrphid abundance and flowering times showed that syrphids tracked plant
96 phenology despite changing climate (Iler, et al. 2013). Other studies have tended to consider
97 syrphids along with other components of the pollinator community as a functional pollinator unit
98 without investigating more nuanced patterns within the group (Memmott, et al. 2007). Work is
99 still needed to describe species-level shifts in phenology over long time periods of environmental
100 warming, and to explore the mechanistic basis for the phenological shifts that have been
101 observed.
102
103 Previous studies have called for greater integration of ecological and physiological aspects of
104 phenology, and the clarification of organism- (i.e. the physiological basis for changes in
105 development time) vs population-level (i.e. the statistical distribution of phenological events
106 across multiple individuals) phenomena (Forrest and Miller-Rushing 2010). This study presents a
107 complementary view of syrphid phenology using both approaches. At an organism-level we have
108 produced a novel database of studies that have described the relationship between temperature
109 and development in syrphids, and we make use of an extensive traits database for the group. At
110 the population-level we make use of data derived from citizen science on syrphid occurrence
111 collected using an ad hoc methodology, combined with a second long-term (30-year) dataset of
112 monthly, standardised sampling in a single location. All datasets are complemented by an
113 extensive phylogeny based on morphological and molecular data. These data are used together to
114 provide robust tests of two central hypotheses: (i) UK Syrphidae are advancing their phenology
115 in response to recent climate change; and (ii) species-level phenological shifts are influenced by

116 traits that alter sensitivity to environmental temperature (laboratory-derived developmental rates,
117 migration, voltinism, larval food source, saproxylic feeding mode, commensalism, and the
118 overwintering stage).
119
120 **Methods**
121 *Phylogenetic data*
122 We take two approaches to constructing a phylogeny of UK Syrphidae: the first tree is based on
123 expert opinion combined with morphological data (hereafter "Expert tree"), and the second is a
124 mixed morphological and molecular tree derived using Bayesian methods ("Bayesian tree"). For
125 the first genus-level tree, the deeper phylogenetic relationships were derived from comparative
126 morphology (Rotheray and Gilbert 1999) and expert opinion (FSG). Species were added to genus
127 tips with random structure and branch lengths were estimated using the methods of Grafen
128 (Grafen 1989). The final Expert Tree can be found in Figure S1. For the second tree, larval
129 morphological data from Rotheray and Gilbert (1999) were combined with barcoding data to
130 construct a new phylogeny for 123 species (see Table S1 for sequence reference codes). COI
131 sequences were accessed from the Barcode of Life Data Systems (BOLD)
132 (http://www.barcodinglife.org/) using the *bold* package in R (Chamberlain 2014), converted to
133 FASTA using *seqinr* (Charif and Lobry 2007) and aligned using MUSCLE (Edgar 2004). The
134 combined morphological and molecular data were used to construct a phylogenetic tree based on
135 Markov Chain Monte Carlo (MCMC) methods (Nylander, et al. 2004) in MrBayes (v3.2;
136 Ronquist, et al. 2012). A distance matrix based on DNA similarity was created based on
137 Kimura's 2-parameter distance (Kimura 1980), from which a neighbour-joining tree was
138 constructed using *phangorn* (Schliep 2011). The final Bayesian Tree can be found in Figure S2.

To evaluate congruence between the Expert and Bayesian trees, the trees were reduced to their shared taxa (n=95) and a Mantel test was used to compare the matrices of pairwise phylogenetic distances between the trees. This showed a very strong correlation ($r=0.756$, $p<0.001$), confirming the similarity of the trees generated using the two approaches. Qualitatively, as with so many phylogenies based on limited molecular data, the Bayesian tree has some basal peculiarities (e.g. *Anasimyia* as basal, *Volucella* as basal to all non-microdontine syrphids), but further up it resembles the Expert Tree in many respects, hence the strong correlation in the Mantel test. While we ran all phylogenetic analyses using both trees, the results were quantitatively similar and so we present only the data from the Expert Tree, which is likely to have more accurate resolution of basal relationships and which contains a greater number of species (n=257, compared to n=123 for the Bayesian Tree). A comprehensive set of statistical outputs can be found with (i) no phylogenetic control, (ii) control using the Bayesian tree, and (iii) control using the Expert tree in the Supplementary Information.

Measurement of shift: Ad hoc recording

Hoverfly sightings were provided by the Hoverfly Recording Scheme (HRS, accessed 28/01/2015), which at time of access contained 621,407 relating to 288 species and showed a strong period of growth through to 1990 (Figure 1A) over a period of recent warming (Figure 1B). The HRS, like other datasets derived from citizen science, requires a phase of data validation and verification (Ball and Morris 2012). Validation of HRS data involves checking that grid references, dates, and species names are formatted correctly. Verification uses the National Biodiversity Network Record Cleaner software to check for consistency in grid references and dates (e.g. a grid reference may be formatted correctly, but located at sea).

Species identification is then verified by checking that the record is consistent with the distribution and phenology of the species, with reference to photographs accompanying the record where available. Further evidence is requested from the recorder in the case of uncertain records, including checking of specimens. Such data quality checks help to reduce errors in the dataset. Records were pooled for each species in each year, and the distribution of flight dates was used to calculate phenological variables – an approach that has been shown to produce reliable results using a similar dataset of UK butterfly records (Bishop, et al. 2013). Due to a possible confounding effect of latitude on phenology (e.g. Hurlbert and Liang 2012), we present data for only the 371,889 records of 272 hoverfly species found south of a line denoting a northing value of 300000 on the British National Grid (300 km north of the origin of the grid, 52.45-52.60°N due to the relative curvature of the projected British National Grid). Percentiles have been shown to be more robust to variation in recorder effort than absolute dates (Moussus, et al. 2010), and so the 5^{th}, 50^{th} and 95^{th} percentiles of the distribution of flight dates (hereafter $FD_{0.05}$, $FD_{0.50}$ and $FD_{0.95}$, respectively) were calculated for each species in each year between 1960 and 2014 in which that species was recorded 30 or more times. Species were included only if there were 30 or more records in each of 20 or more years (Sparks and Menzel 2002; n=215).

Measurement of shift: Standardised recording

Syrphidae abundance data are available from weekly records carried out at a single recording site by a single researcher (JO) in Leicester, UK (52.645°N, -1.079°E), between 1972 and 2001 using a standard Malaise trap. This remarkable time series involved the collection of 60,689 specimens of 95 species of syrphid across 821 weekly samples over this 30-year period (for details on this study and many more conducted at the same site, see Owen 2010). Data for the commoner and

185 easily identified species are used here: voucher specimens are in JO's collection. The dataset is
186 also independent of the HRS dataset, having not been submitted to the recording scheme and
187 falling ca. 5 km outside of the region of the UK on which our HRS analysis focuses. We
188 calculate $FD_{0.05}$, $FD_{0.50}$, and $FD_{0.95}$ dates as described above for the HRS, using the standardised
189 sampling data. The same constraints were used: species were included only if there were at least
190 20 years of data with at least 30 specimens caught.
191
192 *Temperature data*
193 A daily temperature record was selected for each of the biological recording datasets. For the
194 HRS dataset, the Central England Temperature (CET) series (Parker, et al. 1992) gives a daily
195 aggregate temperature measurement for central England. For the standardised dataset, daily
196 temperatures were taken from a weather station situated 10.0 km from the sampling site
197 (Newtown Linford, UK station source ID=569, 52.680°N, -1.216°E).
198
199 *Mechanisms of shift: Species traits*
200 We extracted five traits from the SyrphTheNet (StN) traits database (Speight, et al. 2013): (i)
201 food source of the larvae (microorganisms, n=72; predators, n=133), (ii) number of generations
202 per year (1-4), and whether the species was (iii) commensal (yes, n=24; no, n=193), (iv)
203 saproxylic (yes, n=36; no, n=181), or (v) migratory (yes, n=22; no, n=195). Small numbers of
204 species exhibiting rare trait states were excluded in analyses of the food source of the larvae
205 (herbivores, n=1; mixed microorganisms/herbivore, n=6; mixed microorganisms/predators, n=3;
206 omnivorous, n=2). Only species overwintering in the larval stage were present in the dataset after
207 the exclusion of rare species, and so this trait was disregarded. StN uses fuzzy coding where

multiple trait states are observed to allocate different species according to their association with particular trait states using a scale from 0 to 3: 0 = no association , 1 = minor association, 2 = moderate association, 3 = maximum association. Voltinism is classified on a four point scale (<1, 1, 2, >2 generations per year) and these were converted to intermediate numbers of generations per year by reclassifying into four categories (1, 2, 3, 4) and calculating a mean voltinism score weighted by the association.

Mechanisms of shift: Developmental rates

Data on developmental rates through different life-history stages were extracted from 153 studies, which provided 811 records of temperature and development rate for at least one life-history stage, and 225 measures of total pre-adult development (oviposition-eclosion) under specified temperatures (Table S2). For each study, the temperature of rearing was extracted along with the duration of life-history stages: egg duration, larval duration (including of individual instars, if provided), pupal duration, and total duration. Where maximum and minimum values were presented without averages, the mean was assumed to be the midpoint of minimum and maximum. Ideally total pre-adult developmental duration would be used in the analysis, but this was present for a smaller subset of species than individual life-history stages and so larval and pupal duration were used. Egg, larval, pupal, and total development times are highly correlated, as would be expected from insect development rate isomorphy (Jarošík, et al. 2004; see Figure S3 for details). For each species, where sufficient data existed, two measures of developmental rate were calculated. The first was the regression slope between the developmental rate (1/development time) and the rearing temperature, to give a measure of the thermal sensitivity of development in each species. The second was a mean estimate of

development rate at temperatures between 20 and 22°C which allowed comparable measures of developmental rate for a greater number of species. These temperatures were chosen to maximise the number of species included.

Data analysis

Measurement of phenological shift - Linear regression models were conducted with each of the three flight dates as the response variable and with either temperature or year as predictors. The strength of the relationship between temperature or year and phenology was represented by the Pearson correlation coefficient and the rate of change in phenology was represented by the regression coefficient for temperature (days·°C^{-1}) or year (days·yr^{-1}). Additional results are shown in the supplementary materials for species with fewer than 20 years of data for completeness. To assess whether the hoverfly community was advancing its phenology on average, we fitted an intercept-only generalised least squares (GLS) model to the data using the gls function in the nlme package (Pinheiro, et al. 2013) in R (R Development Core Team 2013). We then incorporated the phylogenetic data for the subset of species that were included in our Expert Tree (see Supplementary Information; n=257) using phylogenetic GLS (PGLS) in the ape package (Paradis, et al. 2004) in R. To test for agreement between the phenological shifts recorded in ad hoc and systematic datasets, we performed Pearson correlations on the correlation and regression coefficients for $FD_{0.05}$, $FD_{0.50}$, and $FD_{0.95}$ against temperature. Additionally, we tested the hypothesis that the phenological shifts detected using ad hoc recording were quantitatively similar to those from standardised monitoring using reduced major axis (RMA) regression to fit a best-fit regression slope to the data. RMA allows for the fitting of regression models where there is error in both variables, as is the case in the estimation of phenological

shifts and developmental rates (Legendre and Legendre 1998). If the slope did not differ significantly from a gradient of 1 then we considered there to be agreement between the two forms of measurement.

Mechanism of phenological shift - The relationship between the three flight dates and both temperature and year was compared across each of the five traits (larval food source, voltinism, commensalism, saproxylism, migration) using generalised least squares (gls) in nlme. Phylogenetic autocorrelation was incorporated into models using a correlation matrix under a Grafen covariance structure implemented in ape. All traits were treated as categorical variables apart from voltinism, which was treated as a continuous variable. To test whether thermal dependence of development could be used to predict phenological shifts in biological records, we used RMA regression to test for a relationship between thermal sensitivity of larval development, larval and pupal development rate at 20-22°C, and the correlation and regression coefficients of $FD_{0.05}$ against annual temperature using both the ad hoc and systematic recording datasets. RMA was applied using the lmodel2() function in the lmodel2 package (Legendre 2011).

Results

Measurement of shift: Ad hoc recording

Of the 215 species studied, 200 (93.0%) exhibited a negative correlation between $FD_{0.05}$ and year (155 [72.1%] statistically significant), and 198 (92.1%) exhibited negative correlations between $FD_{0.05}$ and temperature (137 [63.7%] statistically significant; Figure 2B). However, as shown in Figure 2C and D, the proportions of significant negative correlations between temperature and the flight dates decline substantially in the middle (189 negative, 73 significant and negative,

277 Figure 2C) and end (97 negative, 12 significant and negative, Figure 2D) of the flight period.
278 Data for the relationship between year and the flight dates show a similar pattern: the proportions
279 of significant negative correlations between year and the flight dates decline substantially in the
280 middle (151 negative, 50 significant and negative) and end (37 negative, 3 significant and
281 negative) of the flight period (Table S3). These patterns appear to indicate an extension of the
282 beginning of the flight period under climate warming without an accompanying extension of the
283 end of the flight period. Figure 2A also suggests that the most-recorded species (i.e. those with
284 the greatest numbers of years of data included in the analysis) exhibit the strongest trends.
285
286 The extents of the phenological shifts also varied among the three sections of the flight period.
287 The regression results show that the mean change in $FD_{0.05}$ in response to temperature was -
288 12.475 days·°C^{-1} (95%CI -13.818 to -11.132), while shifts of $FD_{0.50}$ were -7.082 days·°C^{-1} (-
289 6.074 to -8.090) and shifts of $FD_{0.95}$ were 0.649 days·°C^{-1} (-0.475 to 1.773; data are summarised
290 in Figure 2 with full data for species-level responses to temperature and year in Table S3).
291 PGLS showed that the sample of Pearson correlations and regression coefficients were
292 significantly different from zero after control for phylogenetic autocorrelation in $FD_{0.05}$
293 (correlation: $t=-16.355$, $p<0.001$; regression: $t=-11.208$, $p<0.001$) and $FD_{0.50}$ (correlation: $t=-$
294 10.965, $p<0.001$; regression: $t=-9.284$, $p<0.001$) but not $FD_{0.95}$ (correlation: $t=0.556$, $p=0.579$;
295 regression: $t=0.981$, $p=0.329$; $n=117$ in all cases). Significance tests showed that there was no
296 significant phylogenetic signal in mean species $FD_{0.05}$ ($\lambda=0.219$, $p=0.312$) but a phylogenetic
297 signal was present in $FD_{0.50}$ ($\lambda=0.578$, $p=0.001$) and $FD_{0.95}$ ($\lambda=0.608$, $p=0.001$). There was no
298 evidence of a phylogenetic signal in the correlation or regression coefficients of temperature
299 against any flight date ($\lambda<0.001$, and $p\approx1$ in all cases). Comprehensive analysis of phylogenetic

300 signal and significance of community shifts using Bayesian and Expert trees can be found in
301 Table S4.
302
303 *Measurement of shift: Standardised recording*
304 Of the 16 species for which there were sufficient records to perform the analysis, 15 (93.8%)
305 showed negative correlations with TEMP, with 5 significant negative correlations, and 13
306 species (81.3%) exhibited negative correlations between $FD_{0.05}$ and TIME of which 3 were
307 significant negative relationships (Figure 2F). The extents of the phenological shifts for the
308 standardised monitoring did not vary among the three sections of the flight period as was the
309 case in the HRS analysis. The mean change in $FD_{0.05}$ in response to temperature was -12.139
310 days·°C^{-1} (95%CI: -17.102 to -7.176, Figure 2F), while shifts of $FD_{0.50}$ were -11.832 days·°C^{-1} (-
311 16.55 to -7.114, Figure 2G) and shifts of $FD_{0.95}$ were -8.854 days·°C^{-1} (-12.371 to -5.337, Figure
312 2H; see Table S6 for the full results). PGLS showed that the sample of Pearson correlations and
313 regression coefficients were significantly different from zero after control for phylogenetic
314 autocorrelation in $FD_{0.05}$ (correlation: $t=-7.100$, $p<0.001$; regression: $t=-5.151$, $p<0.001$), $FD_{0.50}$
315 (correlation: $t=-5.068$, $p<0.001$; regression: $t=-4.978$, $p<0.001$), and $FD_{0.95}$ (correlation: $t=-5.663$,
316 $p<0.001$; regression: $t=-5.185$, $p<0.001$). These results suggest that the entire flight period of the
317 species involved in the Owen analysis is shifting at approximately the same rate at the front,
318 middle and end of the period. Comprehensive analysis of phylogenetic signal and significance of
319 community shifts using Bayesian and Expert trees can be found in Table S4.
320
321 *Comparison of ad hoc and standardised recording datasets*

There were significant correlations between the regression (R=0.470, p=0.006, n=32, Figure 5A) and correlation coefficients for the relationship between $FD_{0.05}$ and temperature (R=0.442, p=0.011, n=32, Figure 5B) between the Owen and HRS analyses. RMA showed that the intercept did not differ significantly from zero (-9.036, 95% CI -13.786-3.468) and the slope of the relationship did not different significantly from 1 (0.734, 95% CI 0.357-1.726). Due to concerns over leverage effects from outliers in Figure 5A, we calculated hat-values (a measure of the influence of a point on a regression slope) for all points and excluded any points with hat-values greater than 2x the average hat-value. Recalculating the RMA regression with those high leverage points excluded gave a slope of 1.051 (95% 0.294 to -7.506) and an intercept of -3.915 (95% -13.530 to -112.635). The negative upper confidence intervals arise from the upper bound of the confidence interval passing the vertical, and so the resulting bound is negative. Hence, the confidence bounds are substantially wider without the high leverage points and so the results should be treated with caution. However, there is evidence that the standardised and ad hoc measures of phenology exhibit agreement both qualitatively and quantitatively in terms of the advance of phenology in hoverflies.

Mechanisms of shift: Species traits

The only trait for which there was evidence of a link with phenological shift (the strength of the phenological response in $FD_{0.05}$, as indicated by the correlation coefficient between $FD_{0.05}$ and TEMP or YEAR) was voltinism, where a greater number of generations per year were associated with stronger phenological advances (Figure 3A, Table 1). A comprehensive traits analysis of phenological shifts using Bayesian and Expert trees can be found in Table S5. Although an analysis of trait-dependence of shifts in the Owen dataset was carried out, the small sample sizes

345 (16 species) led to weak statistical power. Results for these tests are shown in Table S5 and show
346 no convincing patterns after accounting for multiple tests.
347
348 *Mechanisms of shift: Developmental rates*
349 The full dataset showed a strong relationship between development time and temperature when
350 species were pooled for egg ($R=0.523$, $p<0.001$, $n=352$), larval ($R=0.283$, $p<0.001$, $n=565$),
351 pupal ($R=0.412$, $p<0.001$, $n=520$) and total development ($R=0.341$, $p<0.001$, $n=240$). However,
352 for those species that were well-represented in the literature (measurements taken at >2
353 temperatures) there were inconsistent temperature-development relationships. *Episyrphus*
354 *balteatus* showed a positive relationship but with substantial variability, *Eumerus vestitus*
355 showed a strong relationship with low variability, and *Scaeva pyrastri* showed little change in
356 development rate with temperature (Figure 4). Model II regression showed no relationship
357 between species' larval development rates and field measures of phenological shift (Figure 3B),
358 but there was a significant positive relationship between pupal development rate at 20-22°C and
359 the correlation of $FD_{0.05}$ and temperature ($r=0.661$, $p=0.014$, $n=13$, Figure 3C), suggesting that
360 slower development at those temperatures was associated with a stronger phenological response.
361 Although there was evidence of a negative trend in the relationship between development-
362 temperature regression coefficients and the rate of phenological change (indicating greater
363 phenological advance in species for which there is a greater acceleration in development as
364 temperature increases), the sample size does not allow any firm conclusions (Figure 3D).
365
366 **Discussion**

Through the integration of multiple strands of biological evidence – laboratory rearing experiments, phylogenetics, traits analysis, field ecology and citizen science – this study has provided a comprehensive attempt to measure and explain the phenological shifts of a key pollinator taxon. Strong phenological shifts were found that were consistent across both standardised monitoring (-12.139 days·°C^{-1}, 95%CI: -17.102 to -7.176) and citizen science approaches (-12.475 days·°C^{-1}, 95%CI -13.818 to -11.132). Not only do these two methods provide congruent estimates of the aggregate phenological advances within the Syrphidae, but there is also evidence of a correlation at a species-level between the rate of phenological shift. However, physiological relationships between temperature and development derived from laboratory studies show equivocal links to species-specific phenological shifts in the field. Although there is a range of traits that could conceivably influence phenology in this diverse taxon, only species with greater numbers of generations in each year exhibit stronger phenological shifts accounting for evolutionary relationships between taxa. Finally, a phylogenetic signal seems to be present in the average timing of the middle and end of the flight period, but not the beginning or the rates of change in phenology.

The responses of British hoverflies to environmental warming are striking both in their strength and their consistency. Figure 2 suggests increasing consistency among species as the number of years of recording increases, which is characteristic of a more accurate estimation of an average effect size. Previous analyses of UK hoverflies have provided limited data on interspecific variation such that it is not possible to compare those data with the result from the present study (Graham-Taylor, et al. 2009). However, it is clear that the trends observed are qualitatively similar: there is a considerable advance of the beginning of the flight period with a less clear

390 trend for the end of the flight period, suggesting an elongation of the period of activity. The only
391 other study of syrphid phenology also provided results that were not focused on particular
392 syrphid species' responses, rather expressing change in terms of date of snowmelt or degree day
393 accumulation (Iler, et al. 2013). However, again there is a strong climatic signal in Iler et al.'s
394 data that corresponds with the strength of the results observed in the present study. Taking the
395 change in phenology per year from Table S3, we see that the mean shift in $FD_{0.05}$ is 0.601
396 (±0.057 SE) days·year^{-1}, which is similar to the 0.531 days·year^{-1} reported by Graham-Taylor et
397 al. (2009), and both of which are considerably higher than the 0.25 days·year^{-1} reported in the
398 meta-analysis of Menzel et al. (2006). However, it is worth noting that the durations of the
399 studies and metrics used are different in all three cases. We present our raw results in the
400 supplementary information such that future researchers are able to provide a clearer comparison
401 with our findings. The observed advances in the start of the flight period were around 12
402 days·°C^{-1}. This is considerably greater than the shifts recorded in UK flowering plants of
403 between 1.7 and 6.0 days·°C^{-1} (Fitter and Fitter 2002), 4 days·°C^{-1} (Fitter, et al. 1995), or 2-10
404 days·°C^{-1} (Sparks, et al. 2000), in line with previous studies showing greater rates of advance in
405 insects than in plants (Gordo and Sanz 2005, Visser and Both 2005).
406
407 Phylogenetic correlation in phenology has been shown to be inconsistent across other taxa.
408 Large-scale analyses of plant phenology suggest that there is a strong phylogenetic pattern in the
409 cues to which plants are responding (Davies, et al. 2013). Some more focused studies have also
410 detected a phylogenetic signal in phenological shifts both through time and with increasing
411 temperature (Willis, et al. 2008), while others have found a pattern with temperature but no shift
412 over time (Davis, et al. 2010). In line with our findings, plant communities across the northern

413 hemisphere have been shown to exhibit strong phylogenetic signals in the timing of flowering,
414 but not in the response of those flowering dates to temperature (Wolkovich, et al. 2013). Other
415 studies have shown that only the first flowering period and peak flowering period were
416 phylogenetically-correlated, while last flowering and length of flowering period were not
417 (CaraDonna and Inouye 2014). Insect phenology shows a degree of phylogenetic correlation
418 where groups of related species share traits that impede responses to climate change (e.g. the egg
419 diapause in Odonata, Hassall, et al. 2007). However, it may be that where traits are more labile
420 the phylogenetic signal can be lost and the traits themselves constitute the main predictor of
421 species responses to climate (e.g. butterflies, Diamond, et al. 2011). Our observation that the
422 flight period itself is phylogenetically correlated but the response to change is not suggests that
423 the flight period under relatively stable conditions is cemented in place by an accumulation of
424 other traits that are not temperature sensitive. Under the highly dynamic conditions of
425 contemporary climate change, only those species that have not accumulated additional
426 phenological cues can respond rapidly. Hence, there may be an antagonistic effect between
427 evolutionary inertia represented by an accumulation of non-thermal phenological cues during
428 periods of relative climatic stasis (e.g. glacial maxima and minima), and the ecological plasticity
429 that enables species to shift rapidly when climate begins to change (e.g. relatively rapid climate
430 shifts during glacial transitions).
431
432 The data collected from a large, ad hoc recording network as a part of the Hoverfly Recording
433 Scheme are shown to correlate with data from a standardised survey spanning 30 years, although
434 interesting differences are present. The fact that the end of the flight period does not show a
435 significant advance in the HRS data, but does show a significant advance in the systematic

436 recording supports suggestions that recorders focus on early sightings in recording schemes
437 (Bishop, et al. 2013). That the end of the flight in the systematic dataset appears to be advancing
438 to the same degree as the beginning of the flight period suggests that phenological decoupling in
439 syrphid-plant pollinator networks may not be mitigated by greater overall activity periods (as
440 suggested by Iler, et al. 2013). While a growing number of computational and statistical
441 techniques have evolved to deal with the complexities of varying recorder effort in
442 heterogeneous biological record datasets (Isaac, et al. 2014), more reassuring is the fact that in
443 this analysis there is evidence of congruence between the ad hoc data and a standardised dataset.
444 What is unclear is to what extent the single standardised dataset is a "true" reflection of the
445 biological signal, and hence the validation of biological records would certainly benefit from
446 multiple, independent comparisons. Because effort in citizen science programs is often expended
447 to check data validity at point of collection (e.g. Newman, et al. 2003), it seems reasonable to
448 suggest that each long-term citizen science initiative dedicate a small portion of its resources to
449 these "anchors" against which the larger datasets can be compared. It would be of great interest
450 to see whether other long-term, standardised monitoring sites (e.g. moth, suction, or Malaise
451 traps) correlate with complementary ad hoc data for the same taxa. If this were the case then
452 perhaps the problems associated with ad hoc biological recording have been overstated.
453
454 The diversity of feeding traits, overwintering stages, and patterns of habitat use within the
455 Syrphidae produce opportunities for interspecific variation in exposure to ambient temperatures
456 that might mediate phenological shifts. However, despite a comprehensive analysis of available
457 data, both in traits databases and derived from experimental studies of development, there were
458 far fewer patterns than might have been predicted. First, the laboratory-derived measures of

459 development produced only very equivocal correlations with field measures of phenology. It is
460 clear that either (i) the mechanisms underlying phenological variation in the field cannot be
461 grasped using reductive laboratory studies, or (ii) the data-mining of studies has not produced a
462 dataset of sufficient detail or quality to reveal those mechanisms. More reassuring is the evidence
463 that a greater number of generations in a year is associated with stronger phenological advances.
464 Although climate change has been shown to increase voltinism (Altermatt 2010), it is unclear
465 what the link might be between a given number of generations per year and phenological
466 advance. The answer may lie in the more rapid embryological development in multivoltine
467 species which has been shown in aquatic insects (Gillooly and Dodson 2000). This pattern is also
468 seen in the present study in the egg development times at 20-22°C which are negatively
469 correlated with voltinism ($R=-0.553$, $p=0.050$, $n=13$). This more rapid development time may
470 allow greater exploitation of warmer springs.
471
472 This study provides a nuanced view of the measurement and mechanisms underlying large-scale
473 ecological change through the integration of ecology, physiology, phylogenetics, and citizen
474 science. Taken together, the results suggest that the common hoverflies in general are advancing
475 the beginning of their flight periods at a greater rate than many other taxa. Ad hoc recording
476 suggests that hoverflies are expanding their flight periods, while standardised recording suggests
477 that the end of the flight period is also responding (although not to the same extent). As such,
478 there is no reason based on phenological shifts to believe that the function of this taxon as
479 biocontrol agents and pollinators is at risk under current climate change. Although rare species
480 are unlikely to have been included in this analysis, the ecosystem services provided by Syrphidae
481 (and, indeed, many other taxa) are generated mainly by the small number of very common

482 species and are only supplemented by the rarer species (Kleijn, et al. 2015). The results
483 demonstrate the utility of ad hoc recording data, particularly when supported by data from
484 standardised monitoring, for the detection of large scale ecological trends. Despite many
485 candidate traits that may be predicted to influence the phenological response, only voltinism
486 appears to correlate with variation in phenological shifts, with species exhibiting greater numbers
487 of generations per year showing stronger phenological advances. We suggest that higher
488 numbers of generations per year may be associated with higher egg development rates, and these
489 may allow a subset of species to exploit ephemeral microclimates in early spring. However, there
490 are equivocal relationships between laboratory-derived measures of development rate under
491 varying temperature, and how species are responding to changes in environmental temperature
492 under climate change. This weak link between existing laboratory and field data on syrphid
493 development suggests that experiments geared specifically towards studying phenology may be
494 required to reveal the mechanism underlying phenological shifts in this group.
495
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497 FG and CH would like to dedicate this manuscript to the memory of Dr Jennifer Owen, whose
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507

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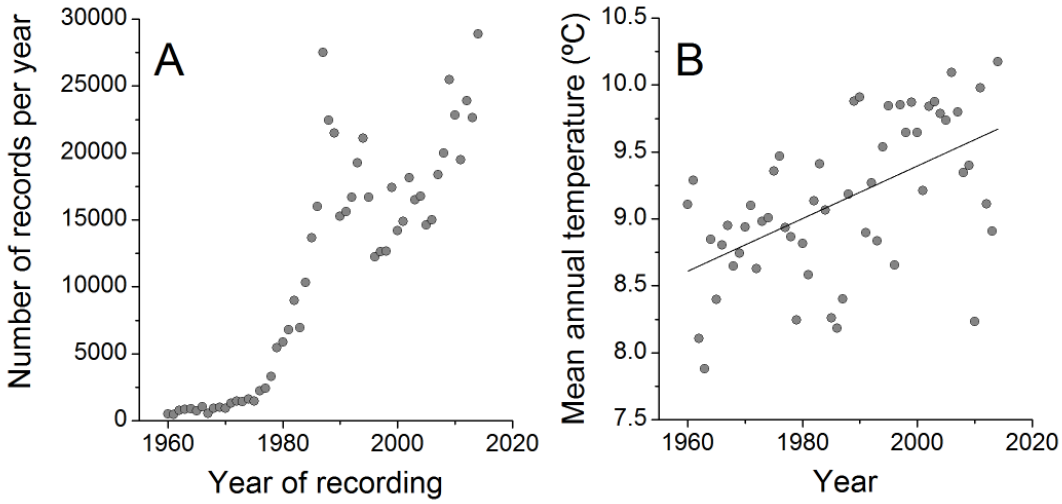

628

629 *Figure 1: Changes in (A) the number of records in the Hoverfly Recording Scheme dataset and*

630 *(B) mean annual temperature (from the Central England Temperature time series) over the*

631 *course of the study period.*

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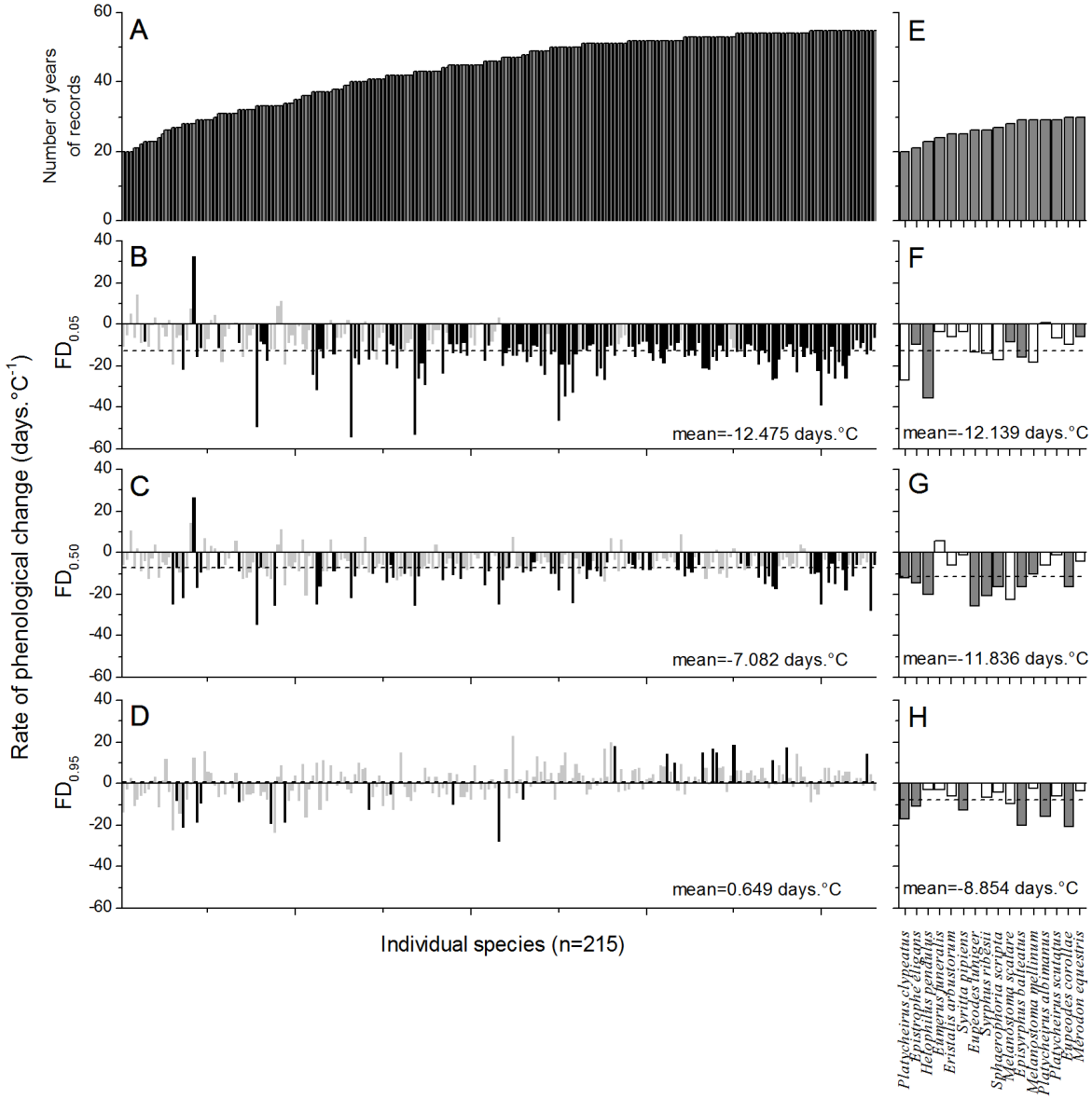

Figure 2: Phenological change in UK hoverflies (Diptera: Syrphidae) using two different datasets: biological records (A-D) and a 30-year standardised monitoring dataset (E-H). (A) and (E) show the number of years of data used in the analysis for each species. For each species the remaining panels show the rate of change of the 5% flight date ($FD_{0.05}$, shown in B and F), 50% flight date ($FD_{0.50}$, shown in C and G), and 95% flight date ($FD_{0.95}$, shown in D and H) in

639 *response to changing temperature. Rates of change are all measured in days per °C change in*

640 *temperature. For B-D and F-H, black bars represent $p<0.05$, grey bars indicate $p\geq0.05$.*

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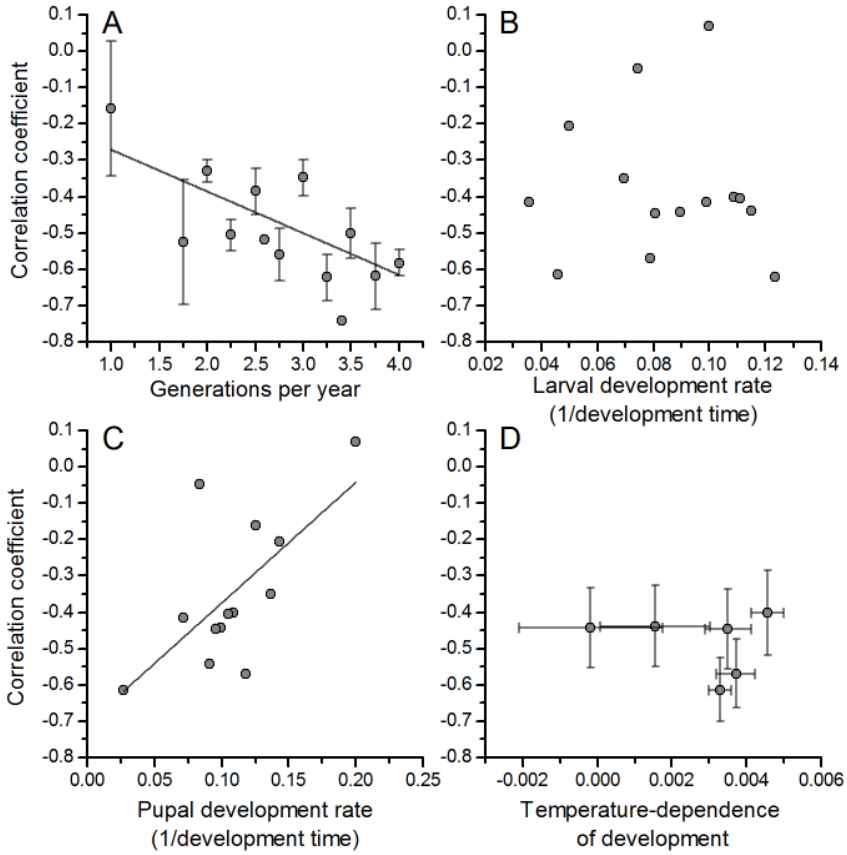


642

643 *Figure 3: The relationship between phenological response from ad hoc recording (Pearson*

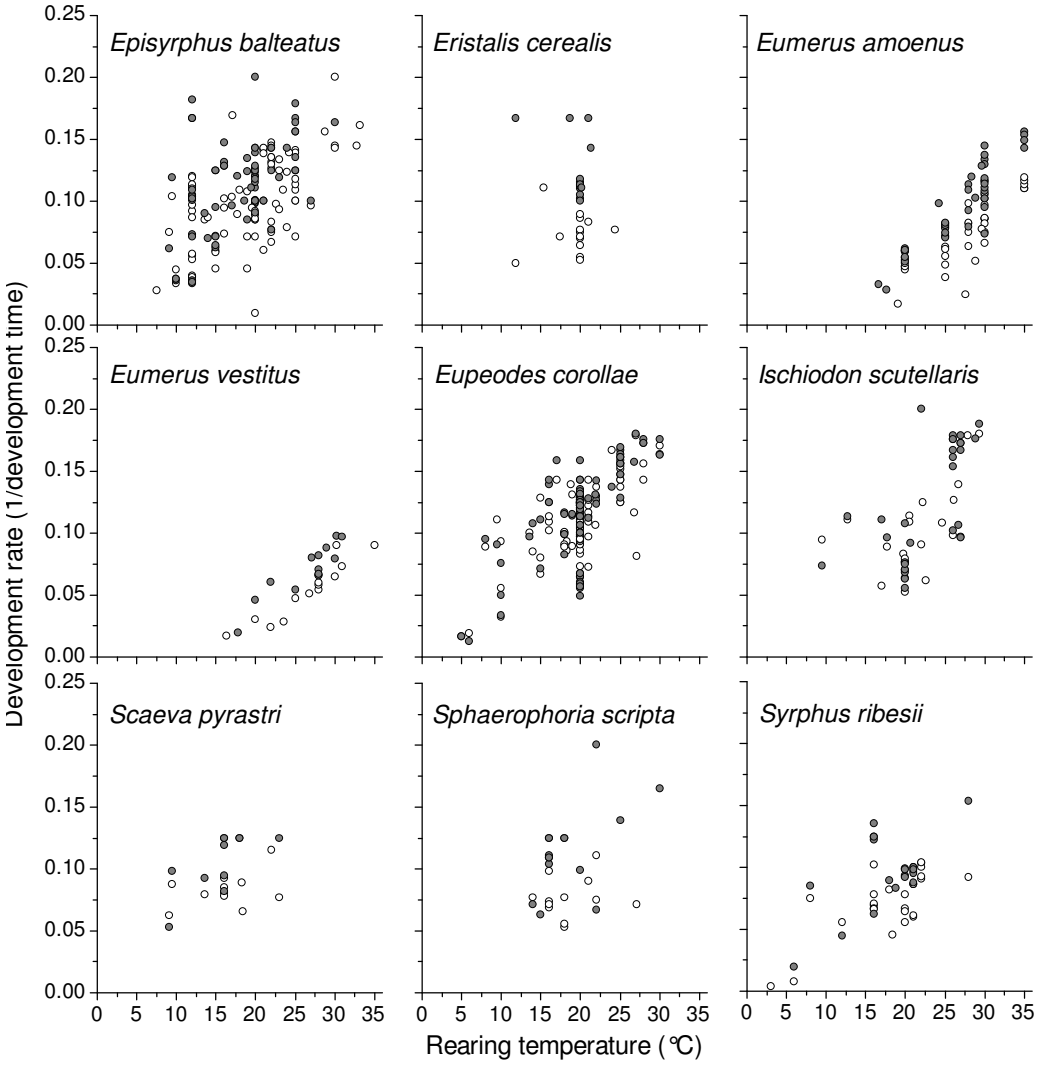
644 *correlation between $FD_{0.05}$ and temperature) and species traits: (A) the number of generations*

645 *per year (using fuzzy coding, see text for details), (B) laboratory larval development rate at 20-*

646 *22°C, (C) laboratory pupal development at 20-22°C, and (D) the temperature dependence of*

647 *development measured as the slope of the relationship between temperature and development*

648 *rate. In B-D, each point is a species. Error bars in A and D represent 1SE.*



649

650 *Figure 4: Laboratory estimates of interspecific variability in larval (open symbols) and pupal*

651 *(filled symbols) development time in relation to temperature in nine well-studied species of*

652 *hoverflies.*

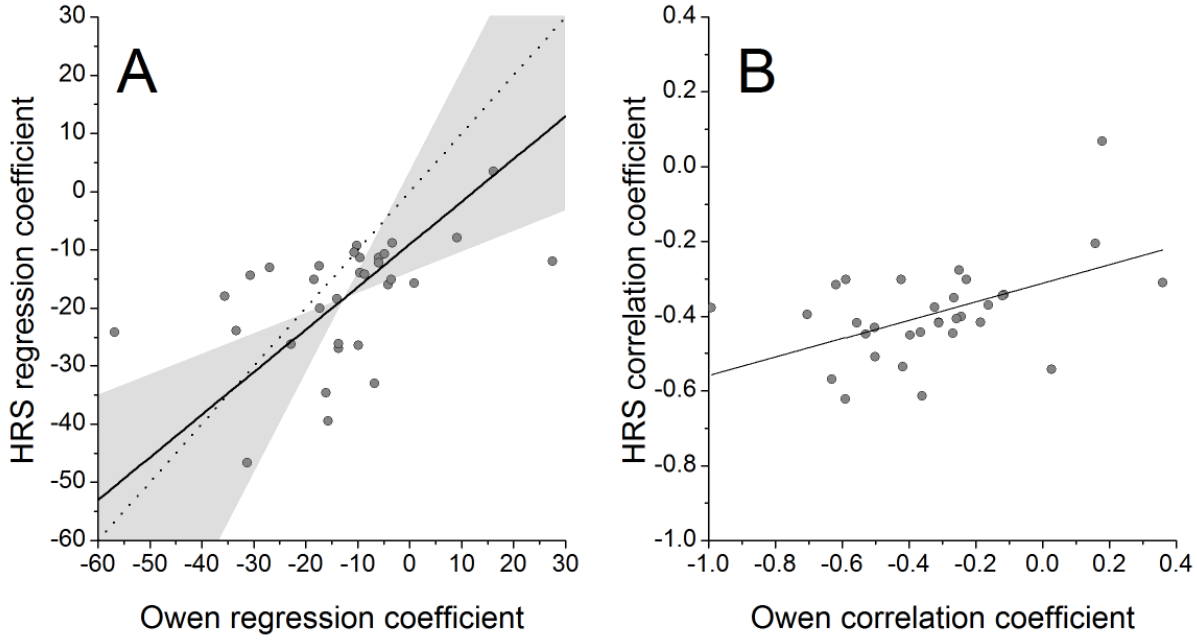


Figure 5: Relationships between (A) the extent (days·°C^{-1}) and (B) the strength (Pearson correlation coefficient) of the phenological response in $FD_{0.05}$ to temperature in ad hoc (HRS) and standardised (Owen) analyses. Solid line in (A) indicates the RMA regression line and shaded area is the 95% confidence interval, with the dotted line showing the 1:1 relationship.

Table 1: Analysis of the strength of the phenological advance (Pearson correlation between $FD_{0.05}$ and either year or temperature) against species traits, both without (GLS) and with (PGLS) control for phylogenetic autocorrelation. Test statistics are F-statistics for all traits apart from voltinism, which are t-statistics.

	Generalised least squares (GLS)					Phylogenetic generalised least squares (PGLS)				
	Temperature response		Temporal response			Temperature response		Temporal response		
	Test stat	p	Test stat	p	n	Test stat	p	Test stat	p	n
Voltinism	0.616	0.434	**9.370**	**0.003**	181	**15.697**	**<0.001**	**21.699**	**<0.001**	83
Larval food	0.364	0.547	0.175	0.677	169	0.141	0.708	0.553	0.459	83
Saproxylic	1.044	0.308	0.569	0.452	181	0.039	0.843	0.003	0.956	83
Commensalism	0.425	0.516	0.738	0.392	181	0.110	0.741	0.495	0.484	83
Migration	0.554	0.458	2.281	0.133	181	0.179	0.674	0.247	0.620	83

665 **Supplementary Information Legends**

666 Figure S1: "Expert tree" with genus-level phylogeny derived from larval characters (Rotheray &
667 Gilbert, 1999) and inferences based on expert opinion, and species arranged within genera using
668 random branching. See Table S1 for details of the COI sequences used and main text for the
669 analytical procedures by which those sequences were processed.

670

671 Figure S2: Neighbour joining tree for 123 species of hoverfly (Diptera, Syrphidae) constructed
672 using Bayesian methods from COI sequences and morphological data (Rotheray & Gilbert,
673 1999). See Table S1 for details of the COI sequences used and main text for the analytical
674 procedures by which those sequences were processed.

675

676 Figure S3: Relationship between the duration of egg, larval, pupal and total pre-adult
677 development in hoverflies.

678

679 Table S1: Codes for sequences used in the construction of the NJ tree for hoverflies (Diptera:
680 Syrphidae). See Figure S1 for the finished neighbour joining tree and the main text for the
681 analytical procedures by which those sequences were processed.

682

683 Table S2: Full dataset of relationships between temperature and developmental rate in hoverflies
684 reported in the literature. Details of column headings are given in the metadata, with a full
685 bibliography of all 153 studies given in a separate sheet.

686

687 Table S3: Full dataset of relationships between temperature, date, and flight periods in hoverflies
688 derived from the Hoverfly Recording Scheme.
689
690 Table S4: Results of statistical analysis to test for a difference between samples of phenological
691 responses (PC=Pearson correlation, Reg=regression coefficient) of different parts of the flight
692 period (5=5th percentile, 50=50th percentile, 95=95th percentile) and zero. Results are all from
693 generalised least squares analysis with a floating intercept, fitted without phylogenetic
694 autocorrelation ("Uncontrolled") and using two different hoverfly phylogenies.
695
696 Table S5: Results of statistical analysis to test for an effect of species traits on phenological
697 responses (Pearson correlations between annual temperature or year). Results are all from
698 generalised least squares analysis with a floating intercept, fitted without phylogenetic
699 autocorrelation ("Uncontrolled") and using two different hoverfly phylogenies. "--" indicates no
700 data due to the presence of only one trait value in that dataset. Significant results are highlighted
701 in **bold**.
702
703 Table S6: Full dataset of relationships between temperature, date, and flight periods in hoverflies
704 derived from standardised recording (see main text for details).