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

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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 yr. Results show that ad hoc and standardised recording data give quantitatively the same value for phenological advance in hoverflies (ca 12 $d°C^{-1}$ 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 understanding of those processes despite extensive research into the fundamental biology of some taxonomic groups.

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 (reviewed by 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, Moussus et al. 2010, Isaac et al. 2014), 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 demonstrate that climate is influencing plant communities (Elmendorf et al. 2015), experimental rearing of birds to demonstrate phenological advance (Visser et al. 2009), and aquatic mesocosm experiments that simulate future warming scenarios (Eklöf et al. 2012). However, there is a substantial gap in our knowledge of how (or, indeed, if) fundamental aspects of species biology at the level of the organism are

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causally related to large-scale spatial and temporal patterns in abundance and diversity.

The hoverflies (Diptera: Syrphidae) have received relatively little attention in the literature relating to global change despite being a significant contributor to pollination (Larson et al. 2001, Ssymank et al. 2008), particularly in higher latitudes, and playing a commercially important role in biocontrol of agricultural and horticultural pests (Tenhumberg and Poehling 1995). Successful pollination and biocontrol are dependent upon maintaining temporal associations with particular resources (flowers, pests), making the Syrphidae particularly reliant upon seasonal timing to maximise their fitness and their associated ecosystem services. However, Syrphidae also exhibit a range of different traits that might influence exposure to environmental conditions with different degrees of buffering of ambient temperature. Adults feed on pollen and nectar, but larvae exhibit a wide range life-history strategies including saprophagy, commensalism with social insects, and above-ground carnivory (Rotheray and Gilbert 2011). Species also differ in their seasonal development in the UK, with voltinism ranging from a single generation to up to four generations, and other species exploiting southern environmental conditions before arriving in the UK as migrants. While some species overwinter as larvae, others overwinter as adults. As such, a range of traits may be expected to influence the extent to which phenological shifts vary between species. A previous study of 20 hoverfly species in the UK sampled at a single site between 1991 and 2007 showed a range of phenological shifts in first sighting, last sighting, peak abundance and total abundance (Graham-Taylor et al. 2009). A more detailed analysis of a 20-yr dataset of syrphid abundance and flowering times showed that syrphids tracked plant phenology despite changing climate (Iler et al. 2013). Other studies have tended to consider syrphids along with other components of the pollinator community as a functional pollinator unit without investigating more nuanced patterns within the group (Memmott et al. 2007). Work is still needed to describe species-level shifts in phenology over long time periods of environmental warming, and to explore the mechanistic basis for the phenological shifts that have been observed.

Previous studies have called for greater integration of ecological and physiological aspects of phenology, and the clarification of organism- (i.e. the physiological basis for changes in development time) vs population-level (i.e. the statistical distribution of phenological events across multiple individuals) phenomena (Forrest and Miller-Rushing 2010). This study presents a complementary view of syrphid phenology using both approaches. At an organism-level we have produced a novel database of studies that have described the relationship between temperature and development in syrphids, and we make use of an extensive traits database for the group. At the population-level we make use of data derived from citizen science on syrphid occurrence collected using an ad hoc methodology, combined with a second long-term (30-yr) dataset of monthly, standardised sampling in a single location. All datasets are complemented by an extensive phylogeny based on morphological and molecular data. These data are used together to provide robust tests of two central hypotheses: 1) UK Syrphidae are advancing their phenology in response to recent climate change; and 2) species-level phenological shifts are influenced by traits that alter sensitivity to environmental temperature (laboratory-derived developmental rates, migration, voltinism, larval food source, saproxylic feeding mode, commensalism, and the overwintering stage).

Methods

Phylogenetic data

We take two approaches to constructing a phylogeny of UK Syrphidae: the first tree is based on expert opinion combined with morphological data (hereafter 'Expert tree'), and the second is a mixed morphological and molecular tree derived using Bayesian methods ('Bayesian tree'). For the first genus-level tree, the deeper phylogenetic relationships were derived from comparative morphology (Rotheray and Gilbert 1999) and expert opinion (FSG). Species were added to genus tips with random structure and branch lengths were estimated using the methods of Grafen (Grafen 1989). The final Expert tree can be found in Supplementary material Appendix 1, Fig. A1. For the second tree, larval morphological data from Rotheray and Gilbert (1999) were combined with barcoding data to construct a new phylogeny for 123 species (see Supplementary material Appendix 1, Table A1 for sequence reference codes). COI sequences were accessed from the Barcode of Life Data Systems (BOLD) (<www.barcodinglife.org/>) using the 'bold' package in R (Chamberlain 2014), converted to FASTA using 'seqinr' (Charif and Lobry 2007) and aligned using MUSCLE (Edgar 2004). The combined morphological and molecular data were used to construct a phylogenetic tree based on Markov Chain Monte Carlo (MCMC) methods (Nylander et al. 2004) in MrBayes (ver. 3.2; Ronquist et al. 2012). A distance matrix based on DNA similarity was created based on Kimura's 2-parameter distance (Kimura 1980), from which a neighbour-joining tree was constructed using 'phangorn' (Schliep 2011). The final Bayesian tree can be found in Supplementary material Appendix 1, Fig. A2. 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 1) no phylogenetic control, 2) control using

the Bayesian tree, and 3) control using the Expert tree in the Supplementary material Appendix 1.

Measurement of shift: ad hoc recording

Hoverfly sightings were provided by the Hoverfly Recording Scheme (HRS, accessed 28 January 2015), which at time of access contained 621 407 relating to 288 species and showed a strong period of growth through to 1990 (Fig. 1A) over a period of recent warming (Fig. 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 (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 300 000 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 5th, 50th and 95th 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-yr period (for details on this study and many more conducted at the same site, Owen 2010). Data for the commoner and easily identified species are used here: voucher specimens are in JO's collection. The dataset is also independent of the HRS dataset, having not been submitted to the recording scheme and falling ca 5 km outside of the region of the UK on which our HRS analysis focuses. We calculate $FD_{0.05}$, $FD_{0.50}$, and $FD_{0.95}$ dates as described above for the HRS, using the standardised sampling data. The same constraints were used: species were included only if there were at least 20 yr of data with at least 30 specimens caught.

Temperature data

A daily temperature record was selected for each of the biological recording datasets. For the HRS dataset, the central England temperature (CET) series (Parker et al. 1992) gives a daily aggregate temperature measurement for central England. For the standardised dataset, daily temperatures were taken from a weather station situated 10.0 km from the sampling site (Newtown Linford, UK station source ID = 569, 52.680°N, –1.216°E).

Mechanisms of shift: species traits

We extracted five traits from the SyrphTheNet (StN) traits database (Speight et al. 2013): 1) food source of the larvae (microorganisms, n = 72; predators, n = 133), 2) number of generations per year (1–4), and whether the species was 3) commensal (yes, n = 24; no, n = 193), 4) saproxylic (yes, n = 36; no, n = 181), or 5) migratory (yes, n = 22; no, n = 195). Small numbers of species exhibiting rare trait states were excluded in analyses of the food source of the larvae (herbivores, n = 1; mixed microorganisms/herbivore,

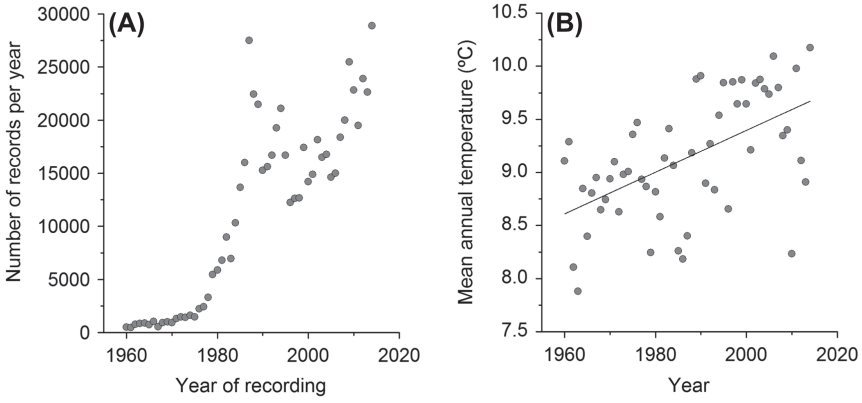

Figure 1. Changes in (A) the number of records in the Hoverfly Recording Scheme dataset and (B) mean annual temperature (from the central England temperature time series) over the course of the study period.

n = 6; mixed microorganisms/predators, n = 3; omnivorous, n = 2). Only species overwintering in the larval stage were present in the dataset after 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 yr^{-1}) 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 (Supplementary material Appendix 1, Table A2). 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 Supplementary material Appendix 1, Fig. A3 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 ($d°C^{-1}$) or year ($d\ yr^{-1}$). Additional results are shown in the supplementary materials for species with fewer than 20 yr 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). We then incorporated the phylogenetic data for the subset of species that were included in our Expert tree (Supplementary material Appendix 1; 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).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.v7g7d> (Hassall et al. 2016).

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; Fig. 2B). However, as shown in Fig. 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, Fig. 2C) and end (97 negative, 12 significant and negative, Fig. 2D) of the flight period. Data for the relationship between year and the flight dates show a similar pattern: the proportions of significant negative correlations

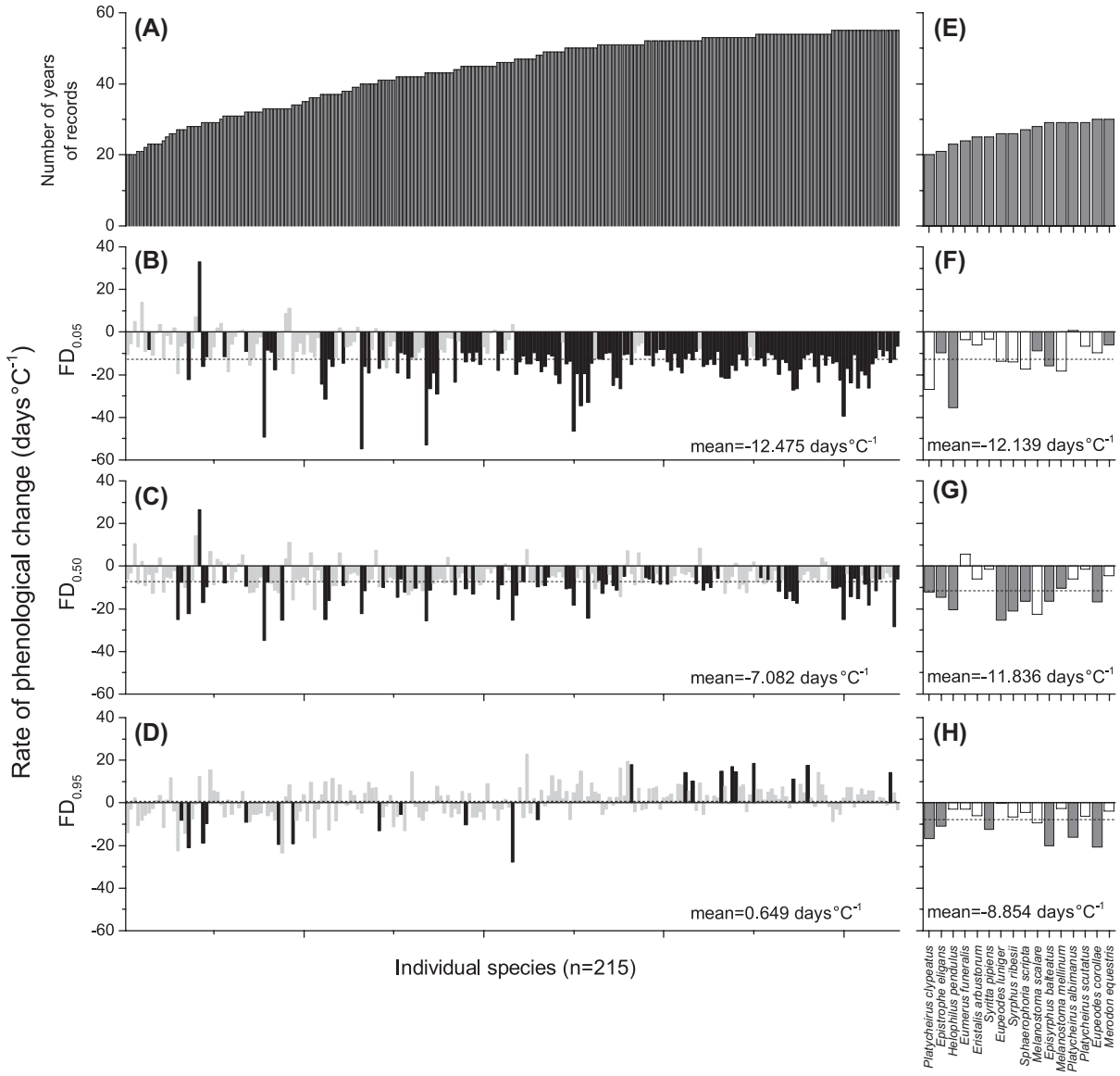

Figure 2. Phenological change in UK hoverflies (Diptera: Syrphidae) using two different datasets: biological records (A–D) and a 30-yr standardised monitoring dataset (E–H). (A) and (E) show the number of years of data used in the analysis for each species. For each species the remaining panels show 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 response to changing temperature. Rates of change are all measured in days per°C change in temperature. For (B–D) and (F–H), black bars represent $p < 0.05$, grey bars indicate $p \geq 0.05$.

between year and the flight dates decline substantially in the middle (151 negative, 50 significant and negative) and end (37 negative, 3 significant and negative) of the flight period (Supplementary material Appendix 1, Table A3). These patterns appear to indicate an advance of the beginning of the flight period under climate warming without an accompanying advance of the end of the flight period. Figure 2A also suggests that the most-recorded species (i.e. those with the greatest numbers of years of data included in the analysis) exhibit the strongest trends.

The extents of the phenological shifts also varied among the three sections of the flight period. The regression results show that the mean change in $FD_{0.05}$ in response to temperature was –12.475 d°C^{-1} (95%CI –13.818 to –11.132), while shifts of $FD_{0.50}$ were –7.082 d°C^{-1} (–6.074 to –8.090) and shifts of $FD_{0.95}$ were 0.649 d°C^{-1} (–0.475 to 1.773; data are summarised in Fig. 2 with full data for species-level responses to temperature and year in Supplementary material Appendix 1, Table A3). PGLS showed that the sample of Pearson correlations and regression coefficients were significantly different from zero after control for phylogenetic autocorrelation in $FD_{0.05}$ (correlation: $t = -16.355$, $p < 0.001$; regression: $t = -11.208$, $p < 0.001$) and $FD_{0.50}$ (correlation: $t = -10.965$, $p < 0.001$; regression: $t = -9.284$, $p < 0.001$) but not $FD_{0.95}$ (correlation: $t = 0.556$, $p = 0.579$; regression: $t = 0.981$, $p = 0.329$; $n = 117$ in all cases). Significance tests showed that there was no significant phylogenetic signal in mean species $FD_{0.05}$ ($\lambda = 0.219$,

$p = 0.312$) but a phylogenetic 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 evidence of a phylogenetic signal in the correlation or regression coefficients of temperature against any flight date ($\lambda < 0.001$, and $p \approx 1$ in all cases). Comprehensive analysis of phylogenetic signal and significance of community shifts using Bayesian and Expert trees can be found in Supplementary material Appendix 1, Table A4.

Measurement of shift: standardised recording

Of the 16 species for which there were sufficient records to perform the analysis, 15 (93.8%) showed negative correlations with temperature, with 5 significant negative correlations, and 13 species (81.3%) exhibited negative correlations between $FD_{0.05}$ and year of which 3 were significant negative relationships (Fig. 2F). The extents of the phenological shifts for the standardised monitoring did not vary among the three sections of the flight period as was the case in the HRS analysis. The mean change in $FD_{0.05}$ in response to temperature was –12.139 $d°C^{-1}$ (95%CI: –17.102 to –7.176, Fig. 2F), while shifts of $FD_{0.50}$ were –11.832 $d°C^{-1}$ (–16.55 to –7.114, Fig. 2G) and shifts of $FD_{0.95}$ were –8.854 $d°C^{-1}$ (–12.371 to –5.337, Fig. 2H; see Supplementary material Appendix 1, Table A6 for the full results). PGLS showed that the sample of Pearson correlations and regression coefficients were significantly different from zero after control for phylogenetic autocorrelation in $FD_{0.05}$ (correlation: $t = –7.100$, $p < 0.001$; regression: $t = –5.151$, $p < 0.001$), $FD_{0.50}$ (correlation: $t = –5.068$, $p < 0.001$; regression: $t = –4.978$, $p < 0.001$), and $FD_{0.95}$ (correlation: $t = –5.663$, $p < 0.001$; regression: $t = –5.185$, $p < 0.001$). These results suggest that the entire flight period of the species involved in the Owen analysis is shifting at approximately the same rate at the front, middle and end of the period. Comprehensive analysis of phylogenetic signal and significance of community shifts using Bayesian and Expert trees can be found in Supplementary material Appendix 1, Table A4.

Comparison of ad hoc and standardised recording datasets

There were significant correlations between the regression ($R = 0.470$, $p = 0.006$, $n = 32$, Fig. 5A) and correlation coefficients for the relationship between $FD_{0.05}$ and temperature ($R = 0.442$, $p = 0.011$, $n = 32$, Fig. 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 Fig. 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 2 × 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 temperature or year) was voltinism, where a greater number of generations per year were associated with stronger phenological advances (Fig. 3A, Table 1). A comprehensive traits analysis of phenological shifts using Bayesian and Expert trees can be found in Supplementary material Appendix 1, Table A5. Although an analysis of trait-dependence of shifts in the Owen dataset was carried out, the small sample sizes (16 species) led to weak statistical power. Results for these tests are shown in Supplementary material Appendix 1, Table A5 and show no convincing patterns after accounting for multiple tests.

Mechanisms of shift: developmental rates

The full dataset showed a strong relationship between development time and temperature when species were pooled for egg ($R = 0.523$, $p < 0.001$, $n = 352$), larval ($R = 0.283$, $p < 0.001$, $n = 565$), pupal ($R = 0.412$, $p < 0.001$, $n = 520$) and total development ($R = 0.341$, $p < 0.001$, $n = 240$). However, for those species that were well-represented in the literature (measurements taken at > 2 temperatures) there were inconsistent temperature–development relationships. *Episyrphus balteatus* showed a positive relationship but with substantial variability, *Eumerus vestitus* showed a strong relationship with low variability, and *Scaeva pyrastri* showed little change in development rate with temperature (Fig. 4). Model II regression showed no relationship between species' larval development rates and field measures of phenological shift (Fig. 3B), but there was a significant positive relationship between pupal development rate at 20–22°C and the correlation of $FD_{0.05}$ and temperature ($r = 0.661$, $p = 0.014$, $n = 13$, Fig. 3C), suggesting that slower development at those temperatures was associated with a stronger phenological response. Although there was evidence of a negative trend in the relationship between development–temperature regression coefficients and the rate of phenological change (indicating greater phenological advance in species for which there is a greater acceleration in development as temperature increases), the sample size does not allow any firm conclusions (Fig. 3D).

Discussion

Through the integration of multiple strands of biological evidence – laboratory rearing experiments, phylogenetics,

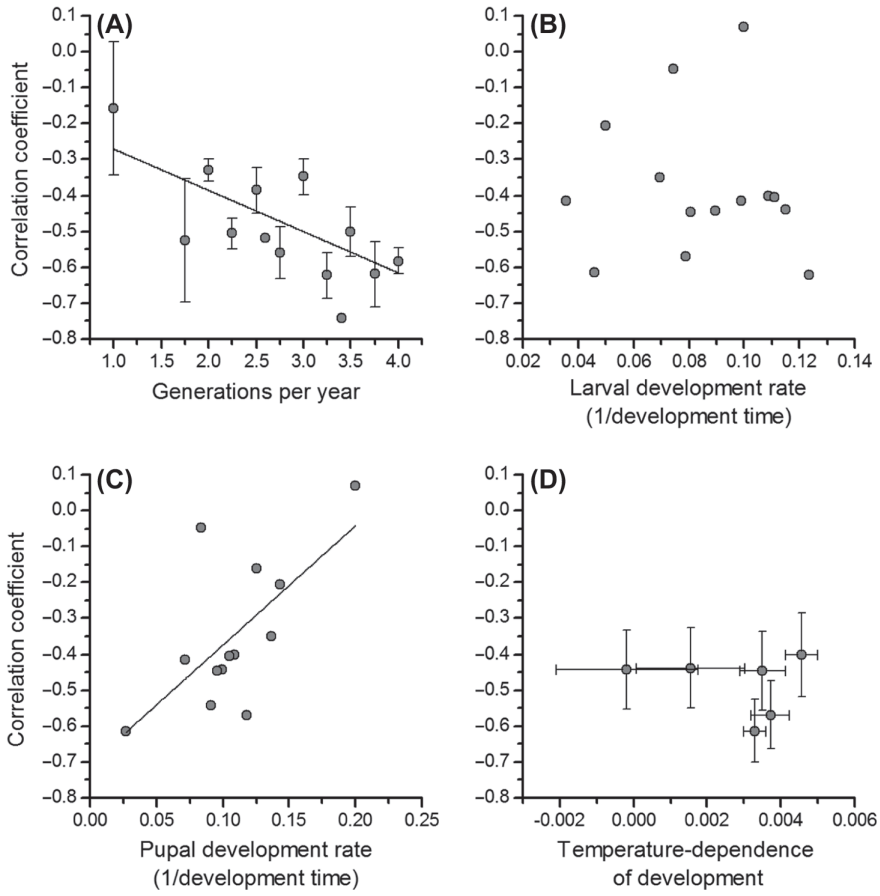

Figure 3. The relationship between phenological response from ad hoc recording (Pearson correlation between $FD_{0.05}$ and temperature) and species traits: (A) the number of generations per year (using fuzzy coding, see text for details), (B) laboratory larval development rate at 20–22°C, (C) laboratory pupal development at 20–22°C, and (D) the temperature dependence of development measured as the slope of the relationship between temperature and development rate. In (B–D), each point is a species. Error bars in (A) and (D) represent 1 SE.

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 d°C^{-1}, 95%CI: –17.102 to –7.176) and citizen science approaches (–12.475 d°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

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

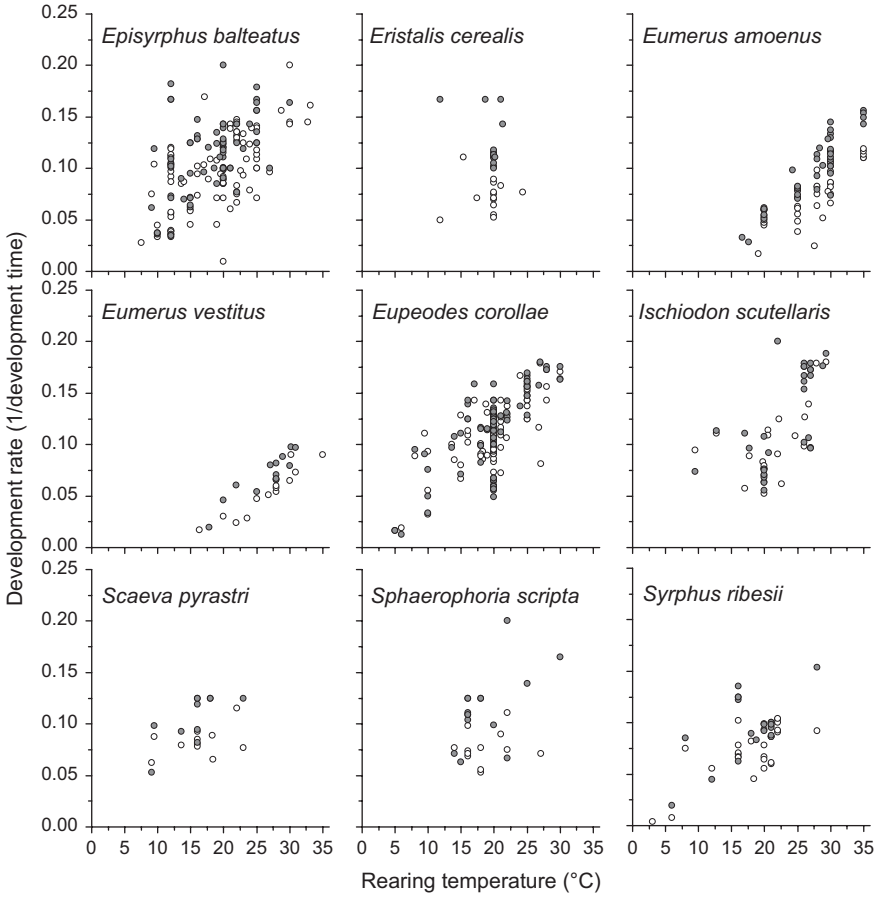

Figure 4. Laboratory estimates of interspecific variability in larval (open symbols) and pupal (filled symbols) development time in relation to temperature in nine well-studied species of hoverflies.

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 trend for the end of the flight period, suggesting an elongation of the period of activity. The only other study of syrphid phenology also provided results that were not focused on particular syrphid species' responses, rather expressing change in terms of date of snowmelt or degree day accumulation (Iler et al. 2013). However, again

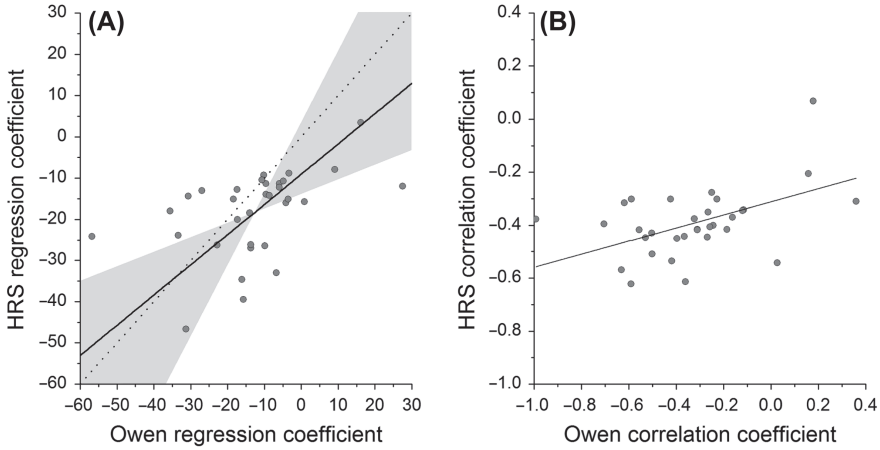

Figure 5. Relationships between (A) the extent (d°C^{-1}) and (B) the strength (Pearson correlation coefficient) of the phenological response in $FD_{0.05}$ to temperature in ad hoc (HRS) and standardised (Owen) analyses. Solid line in (A) indicates the RMA regression line and shaded area is the 95%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

there is a strong climatic signal in Iler et al.'s data that corresponds with the strength of the results observed in the present study. Taking the change in phenology per year from Supplementary material Appendix 1, Table A3, we see that the mean shift in $FD_{0.05}$ is 0.601 (± 0.057 SE) d yr^{-1}, which is similar to the 0.531 d yr^{-1} reported by Graham-Taylor et al. (2009), and both of which are considerably higher than the 0.25 d yr^{-1} reported in the meta-analysis of Menzel et al. (2006). However, it is worth noting that the durations of the studies and metrics used are different in all three cases. We present our raw results in the supplementary information such that future researchers are able to provide a clearer comparison with our findings. The observed advances in the start of the flight period were around 12 d$°C^{-1}$. This is considerably greater than the shifts recorded in UK flowering plants of between 1.7 and 6.0 d$°C^{-1}$ (Fitter and Fitter 2002), 4 d$°C^{-1}$ (Fitter et al. 1995), or 2–10 d$°C^{-1}$ (Sparks et al. 2000), in line with previous studies showing greater rates of advance in insects than in plants (Gordo and Sanz 2005, Visser and Both 2005).

Phylogenetic correlation in phenology has been shown to be inconsistent across other taxa. Large-scale analyses of plant phenology suggest that there is a strong phylogenetic pattern in the cues to which plants are responding (Davies et al. 2013). Some more focused studies have also detected a phylogenetic signal in phenological shifts both through time and with increasing temperature (Willis et al. 2008), while others have found a pattern with temperature but no shift over time (Davis et al. 2010). In line with our findings, plant communities across the northern hemisphere have been shown to exhibit strong phylogenetic signals in the timing of flowering, but not in the response of those flowering dates to temperature (Wolkovich et al. 2013). Other studies have shown that only the first flowering period and peak flowering period were phylogenetically-correlated, while last flowering and length of flowering period were not (CaraDonna and Inouye 2014). Insect phenology shows a degree of phylogenetic correlation where groups of related species share traits that impede responses to climate change (e.g. the egg diapause in Odonata, Hassall et al. 2007). However, it may be that where traits are more labile the phylogenetic signal can be lost and the traits themselves constitute the main predictor of species responses to climate (e.g. butterflies, Diamond et al. 2011). Our observation that the flight period itself is phylogenetically correlated but the response to change is not suggests that the flight period under relatively stable conditions is cemented in place by an accumulation of other traits that are not temperature sensitive. Under the highly dynamic conditions of contemporary climate change, only those species that have not accumulated additional phenological cues can respond rapidly. Hence, there may be an antagonistic effect between evolutionary inertia represented by an accumulation of non-thermal phenological cues during periods of relative climatic stasis (e.g. glacial maxima and minima), and the ecological plasticity that enables species to shift rapidly when climate begins to change (e.g. relatively rapid climate shifts during glacial transitions).

The data collected from a large, ad hoc recording network as a part of the Hoverfly Recording Scheme are shown to correlate with data from a standardised survey spanning 30 yr, although interesting differences are present. The fact that the end of the flight period does not show a significant advance in the HRS data, but does show a significant advance in the systematic recording, supports suggestions that recorders focus on early sightings in recording schemes (Bishop et al. 2013). That the end of the flight in the systematic dataset appears to be advancing to the same degree as the beginning of the flight period suggests that phenological decoupling in syrphid-plant pollinator networks may not be mitigated by greater overall activity periods (as suggested by Iler et al. 2013). While a growing number of computational and statistical techniques have evolved to deal with the complexities of varying recorder effort in heterogeneous biological record datasets (Isaac et al. 2014), more reassuring is the fact that in this analysis there is evidence of congruence between the ad hoc data and a standardised dataset. What is unclear is to what extent the single standardised dataset is a 'true' reflection of the biological signal, and hence the validation of biological records would certainly benefit from multiple, independent comparisons. Because effort in citizen science programs is often expended to check data validity at point of collection (Newman et al. 2003), it seems reasonable to suggest that each long-term citizen science initiative dedicate a small portion of its resources to these 'anchors' against which the larger datasets can be compared. It would be of great interest to see whether other long-term, standardised monitoring sites (e.g. moth, suction, or Malaise traps) correlate with complementary ad hoc data for the same taxa. If this were the case then perhaps the problems associated with ad hoc biological recording have been overstated.

The diversity of feeding traits, overwintering stages, and patterns of habitat use within the Syrphidae produce opportunities for interspecific variation in exposure to ambient temperatures that might mediate phenological shifts. However, despite a comprehensive analysis of available data, both in traits databases and derived from experimental studies of development, there were far fewer patterns than might have been predicted. First, the laboratory-derived measures of development produced only very equivocal correlations with field measures of phenology. It is clear that either 1) the mechanisms underlying phenological variation in the field cannot be grasped using reductive laboratory studies, or 2) the data-mining of studies has not produced a dataset of sufficient detail or quality to reveal those mechanisms. More reassuring is the evidence that a greater number of generations in a year is associated with stronger phenological advances. Although climate change has been shown to increase voltinism (Altermatt 2010), it is unclear what the link might be between a given number of generations per year and phenological advance. The answer may lie in the more rapid embryological development in multivoltine species which has been shown in aquatic insects (Gillooly and Dodson 2000). This pattern is also seen in the present study in the egg development times at 20–22°C which are negatively correlated with voltinism ($R = -0.553$, $p = 0.050$, $n = 13$). This more rapid development time may allow greater exploitation of warmer springs.

This study provides a nuanced view of the measurement and mechanisms underlying large-scale ecological change through the integration of ecology, physiology, phylogenetics, and citizen science. Taken together, the results suggest that the common hoverflies in general are advancing the

beginning of their flight periods at a greater rate than many other taxa. Ad hoc recording suggests that hoverflies are expanding their flight periods, while standardised recording suggests that the end of the flight period is also responding (although not to the same extent). As such, there is no reason based on phenological shifts to believe that the function of this taxon as biocontrol agents and pollinators is at risk under current climate change. Although rare species are unlikely to have been included in this analysis, the ecosystem services provided by Syrphidae (and, indeed, many other taxa) are generated mainly by the small number of very common species and are only supplemented by the rarer species (Kleijn et al. 2015). The results demonstrate the utility of ad hoc recording data, particularly when supported by data from standardised monitoring, for the detection of large scale ecological trends. Despite many candidate traits that may be predicted to influence the phenological response, only voltinism appears to correlate with variation in phenological shifts, with species exhibiting greater numbers of generations per year showing stronger phenological advances. We suggest that higher numbers of generations per year may be associated with higher egg development rates, and these may allow a subset of species to exploit ephemeral microclimates in early spring. However, there are equivocal relationships between laboratory-derived measures of development rate under varying temperature, and how species are responding to changes in environmental temperature under climate change. This weak link between existing laboratory and field data on syrphid development suggests that experiments geared specifically towards studying phenology may be required to reveal the mechanism underlying phenological shifts in this group.

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Supplementary material (Appendix ECOG-02623 at <www.ecography.org/appendix/ecog-02623>). Appendix 1.