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# Historical changes in the phenology of British Odonata are related to climate

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## Abstract

**Responses of biota to climate change take a number of forms including distributional shifts, behavioural changes and life history changes. This study examined an extensive set of biological records to investigate changes in the timing of life history transitions (specifically emergence) in British Odonata between 1960 and 2004. The results show that there has been a significant, consistent advance in phenology in the taxon as a whole over the period of warming that is mediated by life history traits. British odonates significantly advanced the leading edge (first quartile date) of the flight period by a mean of 1.51 ± 0.060 (SEM, $n = 17$) days per decade or 3.08 ± 1.16 (SEM, $n = 17$) days per degree rise in temperature when phylogeny is controlled for. This study represents the first review of changes in odonate phenology in relation to climate change. The results suggest that the damped temperature oscillations experienced by aquatic organisms compared with terrestrial organisms are sufficient to evoke phenological responses similar to those of purely terrestrial taxa.**

*Keywords:* biological records, climate change, diapause, flight period, global warming, life-history, Odonata, phenology, population dynamics, temperature

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## Introduction

A trend in environmental warming is now undeniable (Karl & Trenberth, 2003). Whether anthropogenic or natural, the effects on a wide range of global flora and fauna are significant and startling (Hughes, 2000; Parmesan & Yohe, 2003; Root *et al*., 2003). Physiological limits for temperature tolerance place restrictions on the persistence of organisms in the face of consistent changing temperature.

Coope (1995) has highlighted three potential responses to persistent climate change: (i) the species can become extinct, (ii) the species can adapt *in situ*, (iii) the species can migrate to areas with a more tolerable climate. There are examples of species that may have succumbed to the pressures of contemporary climate change (e.g. Pounds *et al*., 2006). Evolution appears to play a very minor role in faunal responses to climate change (Coope, 1978), although selection may have a more significant effect in plants (Davis *et al*., 2005). Large-scale distributional changes have been recorded numerous times (Parmesan *et al*., 1999; Hickling *et al*., 2006; Mieszkowska *et al*., 2006). However, flexibility inherent in an organism's life cycle may buffer against the impacts of climate change, thus altering the threshold at which the organism must resort to one of those responses.

In order to cope with seasonal fluctuations in climate, complex life histories have evolved in insects which permit maximum exploitation of warmer seasons while cooler seasons are survived by more resistant forms (Butterfield & Coulson, 1997). The mechanism for seasonal regulation most commonly involves the use of cues such as environmental temperature and photoperiod to determine when to undergo life-history transitions (Lutz, 1974). The issue of photoperiod has received attention in a variety of taxa (Vaz Nunes & Saunders, 1999). Critical photoperiods (the day lengths that result in the commencement of diapause) have been shown to vary latitudinally within the same species (Norling, 1984b) and there is evidence that critical

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photoperiods are changing with time as environmental warming increases amenable growth season (Harada *et al.*, 2005).

Photoperiod also acts at the end of the flight season to create a 'time stress', resulting in accelerated development in individuals exposed to photoperiods characteristic of later in the season (Johansson & Rowe, 1999; Norling, 1984a). This increase in developmental rate serves to restrict the trailing edge of the flight period. However, because of the reliance of this effect on photoperiods, it is unlikely that environmental warming will affect the latter part of the odonate flight period.

The Odonata are an ancient order, with all active stages of the life cycle being voracious carnivores. Distributional responses of some Odonata to environmental warming have been noted in some anecdotal studies (Ott, 1996; Aoki, 1997) and recently Hickling *et al.* (2005) produced a far more conclusive review of the British species. This study showed that there was a trend towards a northward shift in those range margins that occurred in Britain. With changes in mean environmental temperature over the past century, it seems reasonable to suppose that there will also be concurrent changes in the timing of life-history transitions. Such changes in phenology have been documented using biological records in a variety of British animals, including Lepidoptera (Sparks & Yates, 1997; Roy & Sparks, 2000), Homoptera (Fleming & Tatchell, 1995) and birds (Crick *et al.*, 1997), as well as flowering plants (Sparks *et al.*, 2000).

The long-term phenological response of Odonata to changing environmental temperature has not been investigated. This study seeks to examine an extensive collection of biological records in an attempt to discern patterns in flight period for British Odonata over the recent period of warming. Part of the flexibility in the odonate life cycle that permits variation in emergence phenology is due to periods of diapause which, depending upon species, can exist in the egg (Ando, 1962) or the larva (e.g. Corbet *et al.*, 1989) with hibernation (e.g. *Sympetrum striolatum*; Jödicke & Thomas, 1993) or aestivation (e.g. *S. striolatum*; Parr, in Pritchard, 1992, p.11) in the adult. Periods of diapause either occur over autumn/winter in temperate-centred species or, in the case of aestivation, through summer dry periods in tropical species.

Temperature can influence a variety of aspects of odonate biology. In the egg stage, both diapause development (Sawchyn & Church, 1973) and hatching (Sawchyn & Gillott, 1974a, b) are temperature dependent. In the larval stage, feeding rates (Thompson, 1978), development time (Pritchard, 1989) and larval ecdysis (Corbet, 1957; Lutz, 1974) are controlled by temperature. In the adult stage, flight periods (Hilfert-Rüppell, 1998) and colour change (Sternberg, 1996) are affected by temperature. Of the effects mentioned above, egg hatching, larval ecdysis and larval development time are most relevant to phenology.

Were environmental temperatures to increase, it would be expected that egg-hatching dates would occur earlier in the year. In 'summer species' (Corbet, 1954) where lower temperature thresholds (LTTs) for ecdysis occur (Corbet, 1957), these would be reached earlier in the year under conditions of environmental warming leading to advances in phenology. Similar advances in phenology would be expected for species that overwinter in the final instar ('spring species'; Corbet, 1954) due to threshold temperatures (which, along with long photoperiods, constitute permissive conditions for metamorphosis (Corbet, 1999)) occurring earlier. Impacts on larval development times are more complex in temperate regions due to the presence of semi- and partivoltine species. Norling's (1984a) model of photoperiodic responses in seasonal regulation posits a 'winter critical size' (WCS) which, if exceeded by larvae in the winter, causes a reversal of the long photoperiod induced diapause during the next summer. This results in accelerated development during long photoperiods and emergence that year. If temperatures increase, it is logical to suggest that larval development times will decrease and increasing proportions of individuals within a population will reach the WCS, leading to changes in voltinism. Such voltinism changes would alter peaks in emergence according to the varying proportions exhibiting different development times.

Some British species of Odonata exhibit a diapause in the egg stage which can take one of two forms: type 1 egg diapause where katatrepsis (the rotation of the embryo inside the egg) occurs after winter or type 2 egg diapause where katatrepsis occurs before winter (Ando, 1962). The egg diapause alters the exposure of the larvae to the low winter temperatures and prior exposure to low temperatures has been shown to affect photoperiodic responses in larvae (Ingram, 1975; Corbet *et al.*, 1989), so it may be that species exhibiting an egg diapause respond differently to changing spring temperatures than those that do not exhibit such a diapause. Advances in emergence dates may be expected to result from (i) threshold temperatures for metamorphosis occurring earlier for spring species, (ii) LTTs for ecdysis being reached earlier for summer species and (iii) variation in larval exposure to low temperatures between species that possess and lack an egg diapause.

Previous studies have shown patterns between purely terrestrial insect taxa and changes in ambient temperature (e.g. Fleming & Tatchell, 1995; Sparks & Yates, 1997). By contrast, this study investigates the impact of changing environmental temperature on the phenology of a taxon that has a sensitive period during an aquatic life-history stage and occupies a range of thermally varying habitats. Such work on phenology has come to the fore since changes in phenology were included in the UK government's indicators of climate change (Cannell *et al*., 1999).

## Materials and methods

### *The British Dragonfly Society database*

The British Dragonfly Society (BDS) maintains a database of sightings of Odonata from between 1807 and the present. At the time that the database was analysed (28 November 2005), it contained 448 547 records. These records included sightings of individuals (as larvae, adults and exuviae), as well as separate records for selected behaviours (emerging, copulating and ovipositing). However, only records of sightings of adults in Britain between 1960 and 2004 were included, since this period represents an anomalous period of warming (Jones & Mann, 2004) and increased recorder effort. Records were also excluded if they were deemed to be duplicates or if they did not have a precise date. This reduced the number of records to 268 772. Only records recorded between the latitudes of 50°N and 52°N were included to restrict latitudinal variation in flight periods, leaving 217 896 records for the analysis. This latitudinal band represented the greatest concentration of records, with higher latitudes having too few to produce reliable results.

Only established, nonmigratory British species were selected. According to the BDS species list (http://www.dragonflysoc.org.uk), *Aeshna mixta*, although formerly migratory, is now considered a British species. More recently *Erythromma viridulum* has been added to the list, but would be of no use in this study due to its relatively short history in the database. The *Sympetrum* spp. that migrate into Britain in waves before becoming extinct (*S. fonscolombii* and *S. flaveolum*) are classified as 'migrant/vagrant' and were excluded from the analysis. *S. nigrescens* was excluded on the basis that it most likely constitutes a melanic form of *S. striolatum* (Merritt & Vick, 1983). This selection process left 37 species.

The annual mean of the Central England Temperature (CET) index was used as a general indicator of British temperatures and was obtained from the Met Office's Hadley Centre. CET has been found to correlate with other regional temperatures and has been used in previous analyses of phenology (Sparks & Carey, 1995; Sparks & Yates, 1997). The annual mean CET between 1960 and 2004 was significantly correlated with spring (March, April and May; $r = 0.693$, $P < 0.001$), summer (June, July and August; $r = 0.701$, $P < 0.001$) and winter (December, January and February; $r = 0.731$, $P < 0.001$) mean temperatures and so was used as an indicator of general temperature change over the period.

### *Analysis*

For each species the records were divided into time periods. This was done in a species-specific way to maximize the resolution in each case. The longest time period was a decade, with the rarest species being grouped into 1960–1969, 1970–1979, 1980–1989, 1990–1999 and 2000–2004 when there were between 30 and 499 records in each period. Periods with fewer than 30 records were excluded. Where there were between 500 and 999 records in a decade, those records were divided into two groups for the first and second half of that decade. Where there were between 1000 and 4999 records in a decade, those records were divided into 3-year blocks (e.g. 1980–1982, 1983–1985, 1986–1988, etc.). In some cases, decades exceeded 5000 records and these were divided into 2-year blocks (e.g. 1980–1981, 1982–1983, 1984–1985, etc.). A conservative rule was required because records were not evenly distributed over the years and so care had to be taken to ensure that sufficient records were present in each period.

Species were excluded if they could not be split into five or more time periods to maintain the accuracy of the estimated slopes. This led to the omission of *Aeshna caerulea*, *A. isosceles*, *Brachytron pratense*, *Coenagrion hastulatum*, *C. mercuriale*, *C. pulchellum*, *Gomphus vulgatissimus*, *Ischnura pumilio*, *Lestes dryas*, *Leucorrhinia dubia*, *Libellula fulva* and *Somatochlora arctica*.

The date of each record was then converted into an ordinal date. The first quartile (Q1), median (Q2) and third quartile (Q3) were calculated from the distribution of ordinal dates for each time period. Owing to small sample sizes (5–11 points) nonparametric regression techniques were used. Kendall's robust line-fit method (Sokal & Rohlf, 1995) produced estimates of the slope of the line describing the relationship between date and temperature and each of the three flight date statistics. In addition, the relationships between the flight dates and the residuals of the regression of temperature on year were found in order to assess the impact of temperature anomalies on phenology. However, in averaging temperatures over a number of years in an attempt to maximize the accuracy of the flight date statistics, it is likely that the temperature anomalies will have been smoothed over. To test this, *Pyrrhosoma nymphula* (a highly recorded species) was analysed using records for individual years.

A *P*-value for each of the lines was obtained using Kendall's rank correlation. A Bonferroni's correction

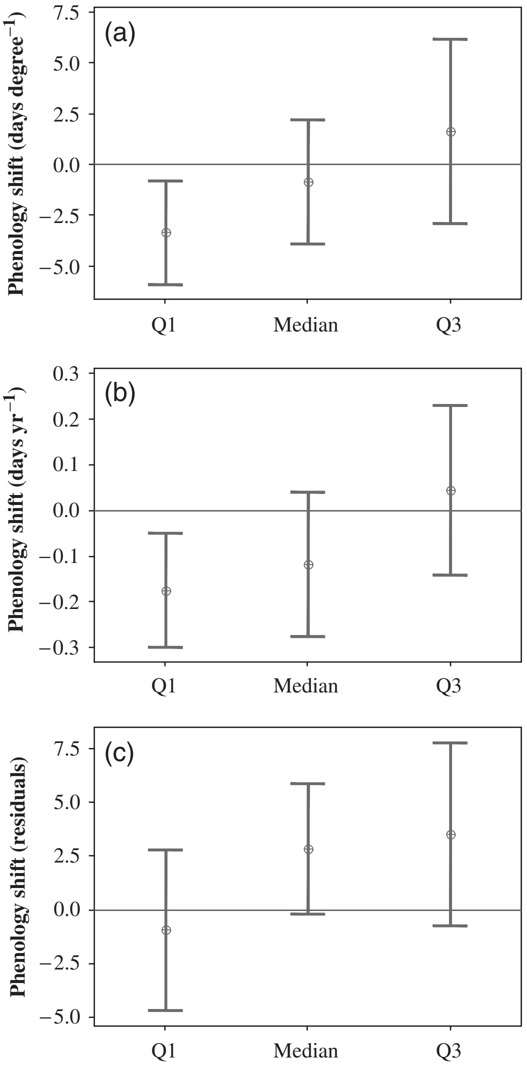

**Fig. 1** Rates of change in the phenology of Q1, median and Q3 flight dates in relation to (a) changing temperature, (b) year and (c) temperature anomalies (residuals of temperature on year) between 1960 and 2004. Bars are 95% confidence intervals.

was employed to correct for the number of tests (225) and this reduced the $\alpha$-level to 0.00022. Samples of slopes for each date-factor combination were analysed using two-tailed, one-sample $t$-tests with test means of zero. Samples of slopes for Q1 flight dates were further analysed with one-tailed, one-sample $t$-tests to test the hypothesis that these dates were advancing.

Felsenstein (1985) first highlighted the fact that phylogeny had to be taken into account when comparing species. However, 'all comparisons should start with a reliable phylogeny' (Stearns & Hoekstra, 2005, p. 349) and although much effort has been expended in attempting to elucidate both higher (Carle, 1982; Bechly, 1996; Trueman, 1996; Rehn, 2003) and deeper (Artiss *et al.*, 2001; May, 2002; von Ellenrieder, 2002; O'Grady & May, 2003) relationships within odonate phylogeny, a complete phylogeny for the British species is still lacking. In the absence of such a phylogeny, evolutionary relationships were partially controlled for by averaging across slopes from congeners in the analysis of samples of slopes (leaving 17 data).

In investigating factors affecting phenological response, phylogeny was controlled for using a GLM with type I (sequential) sum of squares with 'family' as the first term in the model (Hof *et al.*, 2006). All nine sets of slopes were checked for normality (Anderson–Darling test) and homoscedasticity before analysis. Factors analysed included presence/absence of egg diapause (using information in Merritt *et al.*, 1996; Corbet, 1999). Species defined as having an egg diapause were further divided into those with obligate and those with facultative egg diapause. Also investigated was the classification as 'spring' or 'summer' species (according to Corbet *et al.*, 1960). Corbet (1954) defined 'spring' species as those, which overwinter in late instars and emerge synchronously in the spring in response to temperature and photoperiodic cues. Summer species overwinter in earlier instars and undergo a number of moults before emerging asynchronously in the summer.

The distribution of records in the BDS database is temporally uneven. Statistics relating to the flight periods were tested for each species to assess the impact of increasing numbers of records at the latter end of the recording period. As there were three correlations per species and 25 species, a Bonferroni's adjustment was used to reduce the $\alpha$ level to that required for significance at 75 tests (new $\alpha = 0.00067$).

## Results

### *Recorder effort*

The number of records in the BDS database is biased temporally, with vastly more records in later periods. However, there were no significant correlations for any species between the number of records and Q1, median or Q3 flight dates at the reduced $\alpha$ level.

### *Changes in phenology*

There were no significant shifts in phenology that persisted after the reduction of the $\alpha$-value resulting from the Bonferroni correction (see Table 1). However, the samples of slopes for the Q1 flight date against both mean CET and date were found to be significantly different from zero in the two-tailed $t$-tests (Q1 and mean CET, $t = -2.69$, $P = 0.013$; Q1 and year, $t = -2.55$, $P = 0.018$; Fig. 1a and b), a result that persisted after

**Table 1** Slopes of relationships between year and mean CET and three flight period statistics (all figures are Kendall's $\tau$).

| | Residuals | | | Mean CET | | | Year | | |
|---|---|---|---|---|---|---|---|---|---|
| | Q1 | Q2 | Q3 | Q1 | Q2 | Q3 | Q1 | Q2 | Q3 |
| *Spring species* | | | | | | | | | |
| *Anax imperator* | 8.44 | 0 | −1.37 | −3.85 | 0 | −3.17 | −0.458 | −0.133 | −0.182 |
| *Calopteryx splendens* | −3.55 | 2.56 | 8.46 | −3.11 | 3.53 | 7.78 | −0.06 | 0.242 | 0.41 |
| *Calopteryx virgo* | −7.75 | 19.8 | 23.2 | 0.699 | 14.2 | 21.4 | 0.0397 | 0.397 | 0.67 |
| *Cordulegaster boltonii* | 5.64 | 4.92 | 7.38 | 3.96 | 4.46 | 8.49 | 0.0724 | 0.131 | 0.667 |
| *Cordulia aenea* | −8.7 | −10.4 | −17.5 | −1.95 | −7.59 | −16.9 | −0.0789 | −0.519 | −0.522 |
| *Erythromma najas* | 6.07 | 11.8 | 14 | −7.08 | −0.391 | 10.41 | −0.283 | −0.146 | 0.279 |
| *Libellula depressa* | −19.5 | −8.14 | −3.85 | −12.8 | −6.4 | −8.22 | −0.479 | −0.462 | −0.484 |
| *Libellula quadrimaculata* | −13.8 | −2.29 | 5.07 | −8.13 | −6.16 | −3.45 | −0.41 | −0.461 | −0.312 |
| *Orthetrum cancellatum* | 0 | 12 | 3.8 | −2 | 0 | 3.23 | −0.134 | −0.075 | 0.131 |
| *Orthetrum coerulescens* | 3.8 | −3.59 | 5.52 | −9.04 | −1.83 | 2.77 | −0.444 | −0.166 | 0.103 |
| *Platycnemis pennipes* | −3.09 | 3.09 | 11.7 | 0 | 2.06 | 12.36 | 0.0385 | 0.1 | 0.308 |
| *Pyrrhosoma nymphula* | −9.32 | 0 | −3.88 | −13.1 | −14.1 | −12.6 | −0.583 | −0.778 | −0.625 |
| *Somatochlora metallica*† | −22.6 | −40 | −12.4 | 1.59 | −1.08 | −1.35 | 0.226 | 0.509 | 0.113 |
| *Summer species* | | | | | | | | | |
| *Aeshna cyanea** | 5.61 | 10.3 | 5.04 | 2.83 | 1.82 | 0.57 | 0.127 | 0.0268 | 0.0233 |
| *Aeshna grandis** | 0 | −4.94 | −4.66 | −4.68 | −6.04 | −6.35 | −0.267 | −0.368 | −0.3333 |
| *Aeshna juncea** | 22.2 | 26.8 | 16.1 | 3.74 | 9.77 | 5.83 | 0.0192 | 0.535 | 0.46 |
| *Aeshna mixta** | −1.08 | 0 | −6.71 | −6.53 | −4.4 | −5.48 | −0.197 | −0.29 | −0.272 |
| *Ceriagrion tenellum* | −2.26 | −0.139 | 8.82 | −1.47 | 1.8 | 7.31 | −0.064 | −0.00081 | 0.158 |
| *Coenagrion puella* | −6.55 | 0 | 0 | −9.4 | −7.69 | 0 | −0.275 | −0.375 | 0.0543 |
| *Enallagma cyathigerum* | 4.36 | 3.7 | 3.7 | −2.38 | 1.96 | 1.81 | −0.359 | −0.0833 | 0 |
| *Ischnura elegans* | 0 | 3.71 | 0 | −4.53 | −3.37 | 0.974 | −0.333 | −0.214 | 0.0526 |
| *Lestes sponsa** | 2.9 | 2.9 | 8.62 | 2.22 | 3.33 | 4.96 | 0.1645 | 0.167 | 0.115 |
| *Sympetrum danae** | 14 | 27.1 | 16.6 | 3.49 | 9.19 | 1.39 | 0.136 | 0.351 | 0.119 |
| *Sympetrum sanguineum*† | −8.34 | −5.75 | −12.5 | 3.5 | 0.875 | 0 | 0.333 | 0.273 | 0.0909 |
| *Sympetrum striolatum*† | −2.07 | 2.14 | −0.535 | −0.81 | 2.04 | 4.41 | 0.0714 | 0.111 | 0.3 |

Although some relationships were significant at $\alpha = 0.05$, Bonferroni's correction resulted in all results being nonsignificant.

*Species with an obligate egg diapause.

†Species with a facultative egg diapause.

CET, Central England Temperature.

controlling for phylogeny (Q1 and mean CET, $t = -2.65$, $P = 0.017$; Q1 and year, $t = -2.54$, $P = 0.022$). This pattern was also seen in the one-tailed, one-sample *t*-tests when phylogeny was controlled for (Q1 and mean CET, $t = -2.81$, $P = 0.009$; Q1 and year, $t = -3.00$, $P = 0.011$).

Neither median nor Q3 flight statistics advanced significantly in the taxon as a whole with temperature or date. There were also no significant relationships between flight dates and the residuals of the regression of temperature on date (Fig. 1c). However, flight statistics for years in which more than 30 records had been taken (1978–2004) for *P. nymphula* were highly significantly and negatively correlated with the residuals (Q1, $r = -0.608$, $P = 0.001$; median, $r = -0.629$, $P < 0.001$; Q3, $r = -0.471$, $P = 0.013$), confirming the independent effect of temperature on the phenology of this species. Unfortunately, such large numbers of records were not available for other species.

### *Traits affecting response*

After controlling for phylogeny, spring and summer species were found to differ in the phenological responses at the Q1 flight date both in relation to year and temperature (Table 2). Spring species tended to exhibit a greater advance in phenology than summer species. Species with an egg diapause (either obligate or facultative) tended to advance their phenology to a lesser extent than species without an egg diapause. This was a significant effect in Q1 and Q2 in relation to year and approached significance in relation to CET.

Phylogeny appeared to have a significant effect on the response of species to temperature anomalies. However, this could result from a single family, the Corduliidae (represented only by *Somatochlora metallica* and *Cordulia aenea*), giving anomalously extreme slopes. Only five data were available for *S. metallica* and seven for

*C. aenea*, so error margins were relatively high for this group.

## Discussion

As a taxon, British Odonata have significantly advanced their phenology chronologically (on average by 1.75 days per decade) and with respect to temperature (on average by 3.37 days per 1 °C increase) over a 45-year period (1960–2004). This shift represents an extension to the preceding edge of the flight period (first quartile flight date) as opposed to a shift of the flight period as a whole. This is the first phenology study of a taxon that is restricted to freshwater bodies to breed and concurs with the findings of studies on terrestrial British invertebrates (Fleming & Tatchell, 1995; Sparks & Yates, 1997; Roy & Sparks, 2000).

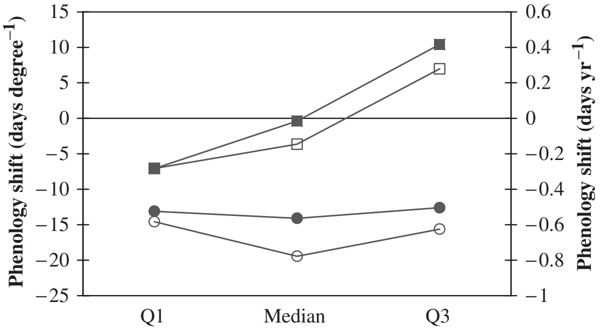

**Fig. 2** Shifts in the flight periods of *Pyrrhosoma nymphula* (circles) and *Erythromma najas* (squares). Open symbols indicate shifts in relation to year and closed symbols indicate shifts in relation to temperature.

In addition to being biased temporally, the records most likely represent sightings of mature individuals, rather than the full population demographic. During the prereproductive period, odonates possess a negative taxis towards reflective surfaces, causing them to disperse varying distances from their natal water body (Corbet, 1999). This is reversed during maturation to cause an aggregation of adults at water bodies at the start of the reproductive period. Many of the adults sighted will have been more mature individuals at water bodies where adults are at their highest concentrations and, hence, most noticeable. This means that the leading edge of the flight period (as indicated by the Q1 flight date) will slightly underestimate the actual date at which the species emerges, an effect that will be constant throughout the records.

Another factor that may influence results is the varying size of water body in which the different species live. The size of the water body affects the buffering of ambient temperature fluctuations and, therefore, the perception of temperature by aquatic organisms. However, odonates are known to seek out warmer microclimates within water bodies (e.g. *A. caerulea*, Sternberg, 1997), such as riparian vegetation, where such buffering is less effective. The data are not available to study this factor.

### *Phenology of the flight period*

The absence of a shift in the Q3 flight date is harder to explain. Having concluded that most species are advancing in phenology, it would be sensible to predict that the end to the flight season should either (i) advance in

**Table 2** Results of GLM to control for phylogeny (see text for details)

| | Family | | Spring/summer | | Family | | Egg diapause | |
|---|---|---|---|---|---|---|---|---|
| | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| *Residuals* | | | | | | | | |
| Q1 | 1.90 | 0.139 | 0.67 | 0.423 | 1.99 | 0.127 | 1.24 | 0.316 |
| Median | 2.27 | 0.086 | 0.43 | 0.522 | **3.13** | **0.032** | **4.01** | **0.039** |
| Q3 | 2.49 | 0.065 | 0.14 | 0.711 | **2.95** | **0.039** | 2.14 | 0.150 |
| *Mean CET* | | | | | | | | |
| Q1 | 1.21 | 0.350 | **6.23** | **0.023** | 1.21 | 0.353 | 3.60 | 0.051 |
| Median | 1.43 | 0.260 | 2.15 | 0.160 | 1.41 | 0.271 | 0.266 | 1.44 |
| Q3 | 2.38 | 0.074 | 0.16 | 0.698 | 2.49 | 0.068 | 0.94 | 0.410 |
| *Year* | | | | | | | | |
| Q1 | 1.39 | 0.275 | **8.58** | **0.009** | 2.01 | 0.124 | **10.53** | **0.001** |
| Median | 0.83 | 0.566 | 3.03 | 0.100 | 1.04 | 0.438 | **4.57** | **0.027** |
| Q3 | 1.97 | 0.128 | 1.60 | 0.222 | 2.13 | 0.107 | 2.06 | 0.160 |

Significant results are highlighted in bold.
CET, Central England Temperature.

a similar way or (ii) regress to mirror the advance of Q1 about the mean flight date.

In support of the former prediction, daily survivorship is constant throughout adult life in many species (e.g. *Coenagrion puella*; Banks & Thompson, 1985), with some studies showing an increased mortality at the beginning of the reproductive period (*Enallagma hageni*; Fincke, 1982). Therefore, if all individuals share the same cue for seasonal regulation, they should all emerge, live and die at earlier points through the year according to a type II survivorship curve. This pattern appears to be exhibited by *P. nymphula*, which shows similar advances in Q1, median and Q3 flight dates (Fig. 2).

The latter hypothesis is based on the assumption that insects die or become less active in winter due to abiotic factors such as falling ambient temperatures. If global warming is alleviating the temperature stress at the end of the flight season then it seems reasonable to expect that there will be more individuals on the wing at a later date (especially in those species with asynchronous emergence periods). *Erythromma najas* seems to follow this pattern, with shifts of similar magnitude but in opposite directions in the Q1 and Q3 flight dates and little change in the median (Fig. 2).

The fact that neither of these patterns is seen as a general pattern in the taxon as a whole suggests that either (i) neither hypothesis is correct and there are other factors governing the species–specific response of the latter part of the flight period, or (ii) that both factors are working antagonistically in odonates as a whole.

### Phenology and life-histories

As previously noted, Odonata possess a number of life-history traits which allow regulation of the life cycle in response to environmental conditions. One such trait is the egg diapause, which involves eggs overwintering and hatching in response to increasing temperatures (Corbet, 1956) (and sometimes increasing water levels; Sawchyn & Gillott, 1974b) in spring. In univoltine species the larvae then develop through the spring, emerging asynchronously in summer. In semi- or partivoltine species larval development continues through the year and the following winter is spent as a larva. Species which do not possess a diapause in the egg stage tend to overwinter as late-instar larvae and use warming temperatures and photoperiod in spring as a cue for metamorphosis (Corbet, 1999). The results of this study suggest that species without an egg diapause have flight periods which are more sensitive to increasing temperatures than species that do possess an egg diapause. This may be due to variations in exposure of larvae to low temperatures during winter.

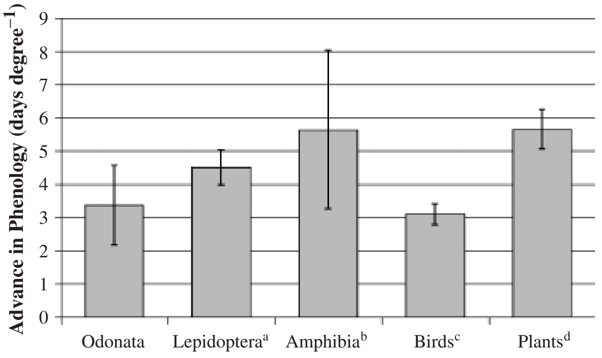

**Fig. 3** Comparison of shifts in phenology of Odonata with those of other taxa. a, Roy & Sparks (2000); b, Gibbs & Breisch (2001); c, Crick & Sparks (1999); d, Sparks *et al.* (2001).

The results also suggest that the variation in the use of rising vernal temperatures between spring and summer species results in a variation in response to environmental warming. The cause of this difference in response may stem from the fact that winter and spring temperatures are increasing faster than summer and autumn temperatures (Bonsal *et al*., 2001). Thus, spring species, which use only spring temperatures as a seasonal cue, would be more affected than summer species, which use a combination of spring and summer temperatures during their progression through LTTs.

## Conclusions

The Odonata are a warm-adapted taxon (Pritchard & Leggott, 1987) which may favour their chances of surviving climate change. This group has been shown to shift ranges poleward (Hickling *et al*., 2005) although this ability may be affected by changing distributions of freshwaters (Dawson *et al*., 2003), respond morphologically to variations in habitat configuration (Taylor & Merriam, 1995), adapt to external cues for seasonal regulation (Norling, 1984b) and, in the present study, take advantage of climatic warming to expand their flight period through changes in phenology. This response is of a similar magnitude to that of animals with a purely terrestrial life cycle and plants (Fig. 3), suggesting that aquatic and terrestrial life-history stages have a similar sensitivity to environmental warming despite that warming being slightly reduced in both rivers (Pilgrim *et al*., 1998) and lakes (Hostetler & Small, 1999). Patterns seen here in Odonata are likely to be seen in other insects with aquatic stages to their life cycles.

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