

Changing temperature regimes have advanced the phenology of Odonata in the Netherlands

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Abstract. 1. Responses of biota to climate change have been well documented for a restricted number of taxa. This study examined shifts in phenology of 37 species of the aquatic insect order Odonata in the Netherlands over the last decade.

2. The present study shows that adults of the Dutch dragonflies and damselflies have advanced their flight dates over recent years due to complex effects of changing temperature regimes on the timing of adult flight dates.

3. Flight dates did not respond to changes in autumn/winter temperatures, advanced with increases in spring temperatures of the focal and previous year, and delayed with increases in summer temperatures of the previous year. Climate change consequently advanced the flight dates of the Odonata because only spring temperatures have increased during the study period.

4. The findings imply that climate change can evoke strong phenological responses in aquatic insects. Moreover, shifts in phenology due to climate change are likely to vary both spatially or temporally, depending on the exact nature of climate change.

Key words. Aquatic insects, biological records, climate change, flight period, global warming, larval development, life history, Odonata, phenology, temperature.

Introduction

The phenology of a variety of plant and animal species has shifted due to climate change (Hughes, 2000; Parmesan & Yole, 2003; Root *et al.*, 2003; Menzel *et al.*, 2006). Understanding the proximate mechanisms causing these shifts is becoming increasingly urgent now that accumulating evidence is showing that climate change can have strong negative effects on population numbers and survival of certain types of species (e.g. Both *et al.*, 2006; Pounds *et al.*, 2006; WallisdeVries & Van Swaay, 2006). To date, work on climate change has largely focused on strictly terrestrial species, such as butterflies, migratory birds, or arctic plants (Hughes, 2000). Few studies have, however, examined phenological shifts of species with (partial) aquatic life-history phases (Hickling *et al.*, 2005), despite growing awareness that climate change may affect both the distribution and characteristics of freshwater habitats (Hostetler & Small, 1999; Dawson *et al.*, 2003; Blenckner *et al.*, 2007). The present study

makes use of a large fine-scale data set on an exemplar group of aquatic insects, dragonflies and damselflies (order Odonata), to assess whether the phenology of insects with aquatic larval stages is affected by temperature regimes and climate change.

In a recent paper, Hassall *et al.* (2007) hypothesised that increased environmental temperatures would advance the phenology of adult Odonata, based both on documented shifts in the phenology of other insect taxa (Fleming & Tatchell, 1995; Sparks & Yates, 1997; Roy & Sparks, 2000) and on a large body of experimental work on Odonata showing that developmental rates of eggs and larvae increase with increased temperatures over a large range of environmental temperatures (reviewed by Pilon & Masseur, 1984; Pritchard & Leggot, 1987; Pritchard *et al.*, 1996; Corbet, 1999). In agreement with this notion, Hassall *et al.* (2007) showed that the leading edge of the flight date of the average British odonate had advanced over the last 40 years. This advancement correlated significantly with the annual mean of the Central England Temperature (CET) index, tentatively suggesting that the shifts in phenology were caused by climate change. None of the flight date statistics were, however, significantly related to the CET index when (linear) effects of year were controlled for, implying that an unequivocal link between

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phenology and temperature could not be shown. Hassall *et al.* (2007) suggested that the shifts in phenology were nevertheless caused by climate change but that the effects of temperature were *smoothed over* by averaging data from different years to deal with low sample sizes. We suggest, in contrast, that annual mean temperature indexes may not adequately capture those aspects of temperature regimes that affect flight dates of adult Odonata.

We start our argument with the notion that the environmental temperatures of temperate regions vary qualitatively between the seasons. Temperature, furthermore, causally affects both the timing and the duration of all odonate life-history phases (egg, larvae, adult) by affecting growth rates of eggs and larvae (Pilon & Masseur, 1984; Pritchard & Leggot, 1987; Pritchard *et al.*, 1996; Corbet, 1999), the duration of ecdysis (Corbet, 1957; Lutz, 1974), and reproductive decisions and survival of adults (Thompson, 1990; Uéda, 1993; Kery & Juillerat, 2004). Importantly, effects of temperature are often non-linear. Egg and larval developmental rates of Odonata are largely arrested at low temperatures, increase with temperature at intermediate temperatures, but are then followed by a decrease with temperature at relatively high temperatures (Boehms, 1971; Krishnaraj & Pritchard, 1995; Van Doorslaer & Stoks, 2005). It would therefore be expected that the relationship between adult flight dates and temperature differs both quantitatively and qualitatively between seasons. If temperature indeed advances the timing of oviposition (Hassall *et al.*, 2007), we further expect that spring and summer temperatures have carry-over effects over years as the timing of oviposition sets a lower date to the onset of egg (and larval) development.

Making use of a large dataset on the Dutch odonates, this study examines shifts in phenology of 37 species of Odonata in the Netherlands over the last decade (1995 through 2004). This study quantifies the relationship between various aspects of the adult flight period (minimum, maximum, mean, and median date, and length of flight period) and five temperature variables (spring temperature of the previous year, summer temperature of the previous year, autumn/winter temperature of the previous year, spring temperature, and summer temperature) and assesses whether observed shifts in phenology are caused by shifts in these temperature variables over recent time.

Materials and methods

Dutch dragonfly database

Phenological data of adult dragonflies and damselflies were obtained from the Dutch Dragonfly Databank managed by the Dutch Dragonfly Society, Dutch Butterfly Conservation, and the European Invertebrate Survey – the Netherlands. This databank holds over 390 000 records of all species of Odonata recorded in the Netherlands from 1849 onwards (one record consists of all observations of a species per date and locality; for a description of the databank see Nederlandse Vereniging voor Libellenstudie, 2002). Phenological data were analysed for a 10-year period (1995 through 2004) that coincides with a period of rapid climate warming both globally (Jones & Mann, 2004)

and in the Netherlands (Verbeek, 2003; see Results), and for which large numbers of records exist in the Dutch Dragonfly Databank. Selected for data analyses were all species for which ≥ 30 records of adults with a precise date were available for each year in the databank (version 16 November 2005). This criterion was chosen to maximise the number of species available for analyses whilst setting a lower limit to the annual number of records per species, resulting in the inclusion of 53% (37 of 70; listed in the Appendix) of all species recorded from the Netherlands (mean \pm SE number of records per species per year was 614 ± 91). The set criterion effectively resulted in the exclusion of species that were either rare and/or irregularly recorded as migrants, because 95.6% of all records (227 288 of 237 664 records) were included in these analyses.

Flight period characteristics

Five characteristics of the flight period that altogether provide a detailed description of its shape and timing were calculated for each species and year: the 10th, 50th, and 90th percentile (hereafter called minimum, median, and maximum flight date respectively), the arithmetic average (hereafter called mean flight date), and the number of days between the 10th and the 90th percentile (hereafter called length of the flight period).

Temperature data

Monthly mean air temperatures of the Royal Netherlands Meteorological Institute (weather station De Bilt, central Netherlands; data available on <http://www.knmi.nl/klimatologie/maandgegevens/index.html>) were used to calculate the average temperature of the (i) previous spring (April through June of the previous year), (ii) previous summer (July through September of the previous year), (iii) previous autumn/winter (October of the previous year through March of the focal year), (iv) spring (April through June of the focal year), and (v) summer (July through September of the focal year), for each year separately.

Statistical analyses

For each species and flight period characteristic separately, multiple regression analysis was used to estimate the slope of the relationship between the flight period characteristic of interest and year. This slope represents the average annual change in the flight period characteristic over the 10-year period due to the combined effect of all environmental factors that have changed over the years and is hereafter referred to as *overall annual change* in the flight period characteristic. The log-transformed annual number of all odonate records (hereafter called intensity of observation) was simultaneously fitted to control for any potential bias introduced by the behaviour of observers (see Hassall *et al.*, 2007 for a similar approach). Notably, intensity of observation was not correlated with year (Pearson's $r = 0.128$, $P = 0.725$, $n = 10$) and therefore did not bias estimates of phenology shifts in the present study.

For each species and flight period characteristic separately, multiple regression analysis was also used to estimate the slope of the relationship between the flight period characteristic and year while simultaneously fitting not only the intensity of observation (see above) but also the five temperature variables (temperature of previous spring, previous summer, previous winter, spring, and summer). Here, the slope of the relationship between the flight period characteristic, and year thus represents the average annual change in the flight period characteristic over the 10-year period due to the combined effect of all *unknown* environmental factors that have changed over these years. Importantly, this slope is not due to the combined effect of the five temperature variables (because they were included as explanatory variables in the model and their effects were therefore statistically controlled for) and is hereafter referred to as *residual annual change* in the flight period characteristic. The *overall annual change* minus the *residual annual change* thus represents the average annual change in flight period characteristic explained by the combined effect of the five temperature variables, and is hereafter referred to as *temperature-induced annual change* in flight period characteristic. The slopes of the relationships between the flight period characteristics and each temperature variable (representing the change in flight period characteristic in days per °C) were used in further analyses to reveal how the temperature variables led to temperature-induced annual changes in flight period characteristics.

Phylogenetic effects need to be taken into account while comparing species (Felsenstein, 1985). A complete phylogeny of the Dutch odonates is still, however, lacking. A highly conservative approach was therefore used to avoid pseudo-replicated results. That is, family (instead of genus or species) was

used as the unit of analyses to avoid spurious findings that might result from the non-independence of species within genera and/or genera within families. For each flight period characteristic separately, we therefore averaged each species-specific estimate (see above) per genus, and then averaged these means per family, resulting in seven data points (families) for further statistical analyses. A series of one-sample *t*-tests were then used to assess whether the distribution of these seven data points differed from zero (Tables 1 and 2). To check for any sign of phylogenetic effects, it was assessed whether heterogeneity in the estimates existed either among families or among genera within families using general linear models (GLM) with both family and genus (nested within family) fitted as random effects, where species was the unit of analysis (Table 3). Neither genus nor family explained significant variation in phenological shifts, suggesting that phylogenetic effects were either absent or at best very small.

We further checked for three statistical artefacts that might result from the multiple regression analyses outlined above. Firstly, we checked whether the significance of the estimated change in flight period characteristics over years (Table 1) was biased by outliers. To do so, Spearman rank correlations were calculated between year and each flight period characteristic (for each species separately), and then the data were summarised as outlined above (averaging over genera then families followed by series of one-sample *t*-tests). These non-parametric analyses produced reassuringly similar values of *P* (results not shown), implying that the analyses were not biased by outliers. Secondly, it was confirmed that the parameter estimates of temperature variables (Table 2) derived from the multiple regression analyses were not biased by over-parametrisation of the multiple regression models. To do so, the regression analyses

Table 1. Phenology shifts of Dutch Odonata between 1995 and 2004. For each of five flight period characteristics (minimum, median, mean, maximum, and length of the flight period), the mean change over years (the slope of the relationship between the flight period characteristic and year) is given. Overall annual change, annual change induced by temperature variables (listed in Table 2), and residual annual change (not caused by the combined effect of the five temperature variables) are shown. Slopes were calculated separately for each of 37 species and then averaged per genus and family (see Methods). It was tested whether the distribution of these family-mean slopes differed from zero, where family is the unit of analyses ($n = 7$). Values of *P* that were significant after Bonferroni correction are highlighted in bold.

Variable	Mean change ± SE (days per year)	t_6	<i>P</i>	Experimental error rate
<i>Overall annual change in</i>				
Minimum	-0.874 ± 0.140	-6.261	<0.001	0.017
Median	-0.984 ± 0.134	-7.329	<0.001	0.013
Mean	-0.881 ± 0.063	-13.957	<0.001	0.010
Maximum	-0.575 ± 0.133	-4.320	0.005	0.025
Length	0.299 ± 0.228	1.308	0.239	0.050
<i>Temperature-induced annual change in</i>				
Minimum	-1.497 ± 0.193	-7.738	<0.001	0.013
Median	-1.942 ± 0.257	-7.564	<0.001	0.017
Mean	-1.555 ± 0.159	-9.802	<0.001	0.010
Maximum	-1.043 ± 0.319	-3.265	0.017	0.025
Length	0.454 ± 0.374	1.213	0.271	0.050
<i>Residual annual change in</i>				
Minimum	0.623 ± 0.230	2.711	0.035	0.017
Median	0.957 ± 0.327	2.929	0.026	0.013
Mean	0.675 ± 0.180	3.746	0.009	0.010
Maximum	0.468 ± 0.354	1.323	0.234	0.025
Length	-0.155 ± 0.319	-0.488	0.643	0.050

Table 2. Effects of temperature variables on the phenology of Dutch Odonata. For each of five temperature variables (spring, summer, and autumn/winter temperature of the previous year, and spring and summer temperature of the focal year), the slope of the relationship between the flight period characteristic and temperature is given. Slopes were calculated separately for each of 37 species, and then averaged per genus and family (see Materials and methods). It was tested whether the distribution of these family-mean slopes differed from zero, where family is unit of analyses ($n = 7$). Values of P that were significant after Bonferroni correction are highlighted in bold.

Variable	Mean change \pm SE (days per °C)	t_6	P	Experimental error rate
<i>Spring temperature previous year</i>				
Minimum	-1.792 \pm 1.163	-1.540	0.174	0.017
Median	-3.517 \pm 1.670	-2.106	0.080	0.013
Mean	-2.652 \pm 0.639	-4.152	0.006	0.010
Maximum	-2.288 \pm 1.728	-1.324	0.234	0.025
Length	-0.496 \pm 1.860	-0.267	0.799	0.050
<i>Summer temperature previous year</i>				
Minimum	1.940 \pm 0.381	5.086	0.002	0.010
Median	2.921 \pm 1.005	2.905	0.027	0.025
Mean	2.542 \pm 0.665	3.826	0.009	0.013
Maximum	1.890 \pm 0.632	2.989	0.024	0.017
Length	-0.050 \pm 0.602	-0.083	0.936	0.050
<i>Autumn/winter temperature previous year</i>				
Minimum	-0.127 \pm 0.587	-0.216	0.836	0.017
Median	-1.511 \pm 0.483	-3.129	0.020	0.010
Mean	-0.677 \pm 0.364	-1.859	0.112	0.013
Maximum	-0.093 \pm 0.571	-0.163	0.876	0.025
Length	0.034 \pm 0.300	0.114	0.913	0.050
<i>Spring temperature</i>				
Minimum	-9.793 \pm 1.237	-10.511	<0.001	0.017
Median	-10.753 \pm 0.473	-8.515	<0.001	0.025
Mean	-8.956 \pm 0.613	-14.604	<0.001	0.010
Maximum	-5.175 \pm 1.263	-10.945	<0.001	0.013
Length	4.618 \pm 0.932	3.733	0.010	0.050
<i>Summer temperature</i>				
Minimum	0.170 \pm 0.836	0.203	0.846	0.050
Median	0.990 \pm 0.614	1.612	0.158	0.010
Mean	0.702 \pm 0.513	1.369	0.220	0.013
Maximum	-0.387 \pm 0.486	-0.796	0.456	0.017
Length	-0.557 \pm 0.992	-0.561	0.595	0.025

were re-ran for each temperature variable separately but now included only year and the temperature variable of interest (instead of all temperature variables and intensity of observation) as explanatory variables. These simpler models produced reassuringly similar outcomes (results not shown), implying that over-parametrisation of the regression models did not bias the results. Thirdly, none of the temperature variables were significantly correlated (all $P > 0.076$), implying that issues connected to colinearity of explanatory variables did not bias the results.

Sequential Bonferroni adjustment of experimental error rates was applied to account for multiple testing (Sokal & Rohlf, 1995) in all cases where *families of tests* were conducted to evaluate the same hypothesis (Chandler, 1995). Thus the Bonferroni adjustment was applied to account for conducting each set of analyses five times (i.e. for each of the five flight period characteristics). We give the appropriate experimental error rate for each statistical test shown in Tables 1–3. The data were analysed using spss version 13.0. All tests were two-tailed and a critical value of $P = 0.05$ is applied throughout.

Results

Annual changes in flight period characteristics

The overall annual change in flight period characteristics was significant for four out of five flight period characteristics (Table 1). The average species within the average genus within the average family (hereafter called *the average odonate*) showed an overall advancement of the minimum (8.7 days), median (9.8 days), mean (8.8 days), and maximum flight date (5.7 days) over the 10-year period. Because these four flight period characteristics showed quantitatively similar advancements, no significant change was observed in the length of the flight period: the timing – not the shape – of the odonate flight periods had changed over the years.

These overall annual changes in flight period characteristics were primarily caused by the combined effect of the temperature variables: the overall and the temperature-induced annual changes were both significant and qualitatively similar for the same four flight period characteristics (Table 1). The average odonate showed a temperature-induced advancement of both

Table 3. Sources of among-species variation in phenology shifts. For each of five flight period characteristics (minimum, median, mean, maximum, and length of the flight period), we test for variation among genera and families in the slope of the relationship between the flight period characteristic and year (see Table 1 for average slopes). Overall annual change, annual change induced by temperature variables (listed in Table 2), and residual annual change (not caused by the combined effects of the five temperature variables) are given. Results are from series of general linear models where genus ($n = 18$) was nested with family ($n = 7$). Neither genus nor family explained significant variation after applying Bonferroni correction for multiple testing.

Variable	Family			Genus		
	$F_{6,11}$	P	Experimental error rate	$F_{11,19}$	P	Experimental error rate
<i>Overall annual change in</i>						
Minimum	1.220	0.364	0.010	0.422	0.928	0.050
Median	0.377	0.879	0.025	2.491	0.039	0.010
Mean	0.262	0.944	0.050	1.807	0.124	0.017
Maximum	0.440	0.838	0.017	2.321	0.052	0.013
Length	0.930	0.510	0.013	1.213	0.343	0.025
<i>Temperature-induced annual change in</i>						
Minimum	1.346	0.315	0.013	0.705	0.720	0.025
Median	1.092	0.423	0.017	0.585	0.818	0.050
Mean	0.310	0.919	0.025	0.941	0.525	0.013
Maximum	0.246	0.951	0.050	1.605	0.176	0.010
Length	2.020	0.147	0.010	0.795	0.643	0.017
<i>Residual annual change in</i>						
Minimum	0.464	0.822	0.017	0.749	0.682	0.010
Median	0.676	0.672	0.013	1.467	0.223	0.013
Mean	0.195	0.972	0.050	1.130	0.392	0.017
Maximum	0.224	0.961	0.025	1.104	0.249	0.025
Length	0.893	0.532	0.010	1.810	0.123	0.050

minimum (14.9 days), median (19.4 days), mean (15.5 days), and maximum flight date (10.4 days) over the 10-year period. Because these four flight period characteristics showed quantitatively similar advancements, no temperature-induced change was observed in the length of the flight period. Annual changes in temperature regimes thus affected the timing – not the shape – of odonate flight periods over the years.

The residual annual change (the change over the years not caused by changes in the temperature variables) was significant for only one out of five flight period characteristics (Table 1). The average odonate showed a residual delay of mean flight date (6.7 days) over the 10-year period. Although non-significant, minimum, median, and maximum flight date also showed a residual delay over the years, explaining the quantitative mismatch between the overall and the temperature-induced changes in flight period characteristics (see above). The length of the flight period also did show a residual delay over the years.

None of the (overall, temperature-induced, or residual) annual changes in any of the flight period characteristic differed between families or between genera within families (Table 3), suggesting that the observed shifts in phenology did not relate to phylogeny. Estimates of average annual changes for the average odonate, as given in Table 1, therefore appeared to be truly representative of the average Dutch odonate.

Temperature effects on flight period characteristics

Temperature affected the flight period characteristics of the average odonate, but the five temperature variables differed

both quantitatively and qualitatively in their effects (Table 2; Fig. 1).

Increased spring temperatures advanced the minimum (9.7 days per °C), median (10.7 days per °C), mean (8.9 days per °C), and maximum flight date (5.1 days per °C) (Fig. 2). Because increased spring temperatures led to a greater advancement of minimum compared to maximum flight dates, the length of the flight period also increased with increasing temperature (4.6 days per °C). Spring temperature also had a comparatively weak but significant carry-over effect over years: the mean flight date was also advanced by increased spring temperature of the previous year (2.6 days per °C). Spring temperature thus appeared to have relatively strong direct effects and somewhat weaker carry-over effects on the shape and the timing of the flight period.

Summer temperature only had carry-over effects over years: increased summer temperature of the previous year delayed both the minimum (1.9 days per °C) and the mean flight date (2.5 days per °C). Increased summer temperature of the previous year also delayed median (2.9 days per °C) and maximum flight date (1.8 days per °C) but these results were not significant when correcting for multiple testing and should therefore be regarded less than definitive. Summer temperature of the previous year, nevertheless, had quantitatively similar effects on minimum, median, mean, and maximum flight period and did therefore not affect the length of the flight period. Increased summer temperatures thus appeared to affect the timing – not the shape – of the odonate flight periods in the following year. Autumn/winter temperatures did not affect any of the flight period characteristics.

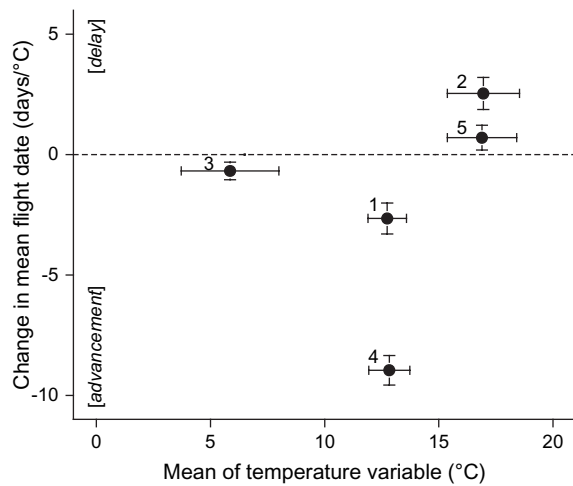


Fig. 1. Overview of the main results. The relationship between phenology and temperature differs qualitatively and quantitatively between five temperature variables. The change in mean flight date (in days per $^{\circ}\text{C} \pm \text{SE}$), for the average species, is plotted against the average temperature (1995 through 2004) for each of the temperature variables: 1, spring temperature of the previous year; 2, summer temperature of the previous year; 3, autumn/winter temperature of the previous year; 4, spring temperature; and 5, summer temperature. Positive changes correspond to delaying effects of increased temperature, negative changes to advancing effects (see Table 2 for statistical analyses). Horizontal bars give the range (minimum–maximum) of observed yearly temperatures.

The reported responses to spring and summer temperatures (Table 2) were not caused by some species (genera or families) reacting strongly to temperature while others did not respond, thereby biasing the results. In contrast, the responses were qualitatively consistent when comparing among species, genera, and families. The slopes of mean flight date versus spring temperature of the previous year were negative for 28 of the 37 species (75%), and on average negative for 15 of the 18 genera (83%) and for all seven families (100%). Similarly, the slopes of mean flight date versus summer temperature of the previous year were positive for 32 of the 37 species (86%), and on average positive for 17 of the 18 genera (94%) and for all seven families (100%). Finally, the slopes of mean flight date versus spring temperature were negative for all 37 species (100%).

Change in temperature variables over time

The existence of temperature-induced annual changes in flight period characteristics (Table 1) implied that (certain components of) temperature regimes had changed over the years included in this study. Temperatures did, however, not show similar changes over the years (1995–2004) when comparing among the different periods of the year: spring temperatures had increased with year (linear regression; $F_{1,9} = 7.360$, $P = 0.024$, $r^2 = 0.450$; change $\pm \text{SE} = 0.129 \pm 0.048$ $^{\circ}\text{C}$ per year), but summer ($F_{1,9} = 0.050$, $P = 0.829$, $r^2 = 0.074$; change $\pm \text{SE} = -0.019 \pm 0.084$ $^{\circ}\text{C}$ per year) and autumn/winter temperatures ($F_{1,9} = 0.718$, $P = 0.419$, $r^2 = 0.272$; change \pm

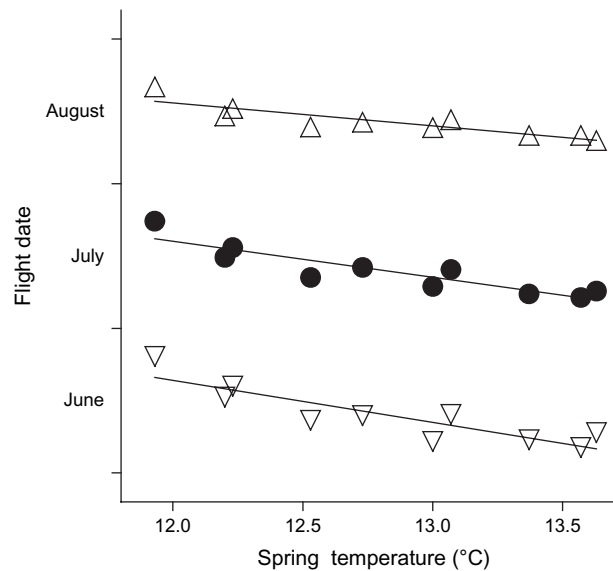


Fig. 2. The relationship between the phenology and spring temperature. The yearly mean (filled circles), minimum, and maximum (10th and 90th percentile respectively; triangles) flight dates are plotted against spring temperature, where each circle represents the average estimate of all 37 species listed in the Appendix. Increased spring temperatures advanced the flight period of the Dutch Odonata (see Table 2 for statistical analyses).

$\text{SE} = 0.082 \pm 0.096$ $^{\circ}\text{C}$ per year) had not. These changes in temperature variables were not specific to the study period, but genuinely reflected observable shifts over the last 25 years (1980 through 2004; spring temperatures: $F_{1,23} = 9.740$, $P = 0.005$, $r^2 = 0.267$; summer temperatures: $F_{1,23} = 2.613$, $P = 0.120$, $r^2 = 0.063$; autumn/winter temperatures: $F_{1,23} = 3.686$, $P = 0.067$, $r^2 = 0.101$). The temperature-induced change in the timing of odonate flight periods (Table 1) was thus primarily caused by increased spring temperatures over the 10-year period.

Discussion

The Dutch dragonflies and damselflies have advanced their phenology over recent years (1995–2004; Table 1). This advancement appears to have been caused by the interplay of complex effects of temperature regimes on the timing of the flight dates of adult Odonata and complex changes in the temperature regimes of the Netherlands. Effects of temperature regimes were complex because spring, summer, and autumn/winter temperatures had both quantitatively and qualitatively different effects on the phenology of the Dutch Odonata (Table 2; Fig. 1). Increased spring temperatures advanced the flight period of adult Odonata in both the focal (Fig. 2) and the following year, increased summer temperatures delayed the flight period of the following year, and autumn/winter temperatures did not affect any of the flight periods characteristics. Notably, those variable responses to temperature did not differ between genera or families (Table 3), implying that they were characteristic for the insect order as a whole. Changes in temperature regimes were

complex because only spring temperatures advanced over the past decade, and climate change was thus characterised by a decoupling of temperature regimes in different periods of the year rather than a general rise in temperature over all seasons (see also Bonsal *et al.*, 2001). The observed advancement in phenology therefore appears to be caused neither by a *general* increase in the overall temperature over the years nor by a *general* response of these insects to temperature, but instead by changes in *specific* temperature regimes (spring temperatures) in combination with a *specific* response (advancement) towards this particular environmental variable. The findings of the present study therefore imply that shifts in phenology due to climate change may well vary qualitatively between years and/or geographical areas depending on the nature of climate change.

Other factors not included in this study counteracted the temperature-induced annual advancement in phenology to some extent (Table 1). The estimated advancement of minimum, median, mean, and maximum flight date (range of advancement: 10.4–19.4 days per decade) caused by the combined effects of all temperature variables included in the analyses was substantially greater than the observed overall advancement of these flight period characteristics (range of advancement: 5.7–9.8 days per decade), implying that simultaneously occurring shifts in other (unknown) environmental factors delayed – rather than advanced – the phenology of the adult Odonata (range of delay: 4.6–9.5 days per decade). Such factors might well relate to other aspects of climate change not captured by the analyses. For instance, weather condition (like cloud cover and rain) is known to affect emergence dates (Bennett & Hill, 1993) and longevity of adult damselflies (Thompson, 1990). Likewise, the odonate phenology might partly be influenced by other components of temperature regimes not included in the present analyses. For instance, threshold temperatures are likely exist below and above which developing eggs or larvae do not grow (Corbet, 1999). Alternatively, shifts in other biotic and abiotic factors that influence larval development and/or adult survival may also have caused the (residual) delay in phenology not caused by the combined effect of the five temperature variables (Blenckner *et al.*, 2007). A variety of factors thus appears to affect the phenology of the adult Odonata (see also Danks, 1991; Corbet, 1999), implying that seasonal regulation of this insect order is extremely flexible.

Proximate explanations for variable responses to temperature

In a recent paper, Hassall *et al.* (2007) postulated that increased *environmental temperatures* would generally result in the advancement of the phenology of adult Odonata (see Introduction). The findings of the present study do not agree with this general prediction, because the effect of ambient temperature in different seasons of the year had quantitatively and qualitatively different effects on the phenology of the Dutch Odonata (Table 2). Autumn/winter temperatures did not affect their phenology, increased spring temperatures advanced their phenology and carried over to the next year, and increased summer temperatures delayed the phenology in the following year (Fig. 1).

These qualitatively and quantitatively different effects of the five temperature variables on the phenology of the Odonata may well have resulted from a non-linear relationship between temperature and developmental rates of eggs or larvae. The existence of such a non-linear relationship has indeed been shown by various laboratory studies (Boehms, 1971; Krishnaraj & Pritchard, 1995; Van Doorslaer & Stoks, 2005): egg and larval developmental rates of Odonata are often largely arrested at low temperatures, increase with temperature at intermediate temperatures, but are then followed by a decrease with temperature at higher temperatures. Hence, because the eggs and larvae of most species that in the Netherlands are inactive when temperatures drop below a certain threshold (Nederlandse Vereniging voor Libellenstudie, 2002), autumn and winter temperatures might thus not impact on the phenology of their adult stage. In contrast, the advancement of phenology with spring temperature (Fig. 2) is likely to have resulted from increased spring temperatures speeding up larval development (as well as shortening the duration of ecdysis; Corbet, 1999) at these intermediate temperatures, consequently allowing the larvae to emergence from the water at an earlier date. The observed carry-over effect of spring temperatures thus likely exists because increased spring temperatures result in advanced egg deposition dates (Hassall *et al.*, 2007), hence allowing more time for the development of eggs (and larvae hatched from these eggs) before the onset of winter, resulting in advanced emergence dates in the following year. Summer temperatures, in contrast, might not directly affect the phenology in the focal year because most emerging larvae will have reached their final larval stage before July, whereas high summer temperatures might hamper developmental rates of eggs deposited in the focal year (and larvae hatched from these eggs), thus delaying their emergence dates in the following year. Hence, the complex findings of this study are consistent with a general, but non-linear, relationship between temperature and phenology (Fig. 1).

Various alternatives scenarios can be put forward to explain the variable effects of the five temperature variables on the phenology of the Odonata. Effects of temperature may, for instance, be date-specific *per se* if the duration of the different life-history phases (egg, larvae, adult) is differentially affected by temperature. The timing and duration of the various life-history phases differs substantially among species, genera, and families occurring in the Netherlands (Nederlandse Vereniging voor Libellenstudie, 2002). It is therefore unlikely that this scenario would produce the highly consistent patterns reported in this paper: all seven families showed advanced flight dates in response to increased spring temperatures, and delayed flight dates in response to increased summer temperatures. Changes in voltinism (the number of generations produced per year) are also unlikely to result in such highly consistent patterns as the reported shifts were also observed in families that have only one generation per year.

Conclusions

The Dutch dragonflies and damselflies have significantly advanced their phenology over recent years. The observed

advancement in phenology was caused by changes in *specific* temperature regimes (spring temperatures) in combination with a *specific* response (advancement). The Odonata of temperate regions have been suggested to respond *positively* to climate change by shifting their ranges poleward (Hickling *et al.*, 2005) and expanding their reproductive season (Hassall *et al.*, 2007). The findings of the present study imply that such a generalisation should be treated with caution: detrimental effects of high temperatures on the survival and development of eggs and larvae have been shown experimentally (Pilon & Masseur, 1984; Lutz & Rogers, 1991; Pilon *et al.*, 1992; Corbet, 1999; references cited above), and may explain why increased summer temperatures delayed rather than advanced the phenology of this taxon. Shifts in species abundance and phenology of damselflies and dragonflies are therefore likely to vary geographically, depending on the exact nature of climate change.

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Appendix. Species included for data analyses. The total number of records (1995–2004; sample size), and the minimum–maximum number of records per year are given.

Family	Species	Sample size	Minimum–maximum
Calopterygidae	<i>Calopteryx splendens</i> (Harris, 1782)	5361	328–1109
Lestidae	<i>Lestes barbarus</i> (Fabricius, 1798)	1763	104–249
Lestidae	<i>Lestes dryas</i> Kirby, 1890	1185	44–246
Lestidae	<i>Lestes sponsa</i> (Hansemann, 1823)	8677	630–1300
Lestidae	<i>Lestes virens</i> (Charpentier, 1825)	1144	49–227
Lestidae	<i>Lestes viridis</i> (Vander Linden, 1825)	8172	443–1225
Coenagrionidae	<i>Ceriagrion tenellum</i> (de Villers, 1789)	2575	64–918
Coenagrionidae	<i>Coenagrion lunulatum</i> (Charpentier, 1840)	875	40–177
Coenagrionidae	<i>Coenagrion puella</i> (Linnaeus, 1758)	9658	778–1364
Coenagrionidae	<i>Coenagrion pulchellum</i> (Vander Linden, 1825)	8201	517–1138
Coenagrionidae	<i>Enallagma cyathigerum</i> (Charpentier, 1840)	13 054	948–2215
Coenagrionidae	<i>Erythromma najas</i> (Hansemann, 1823)	6146	322–945
Coenagrionidae	<i>Erythromma viridulum</i> (Charpentier, 1840)	5027	239–1051
Coenagrionidae	<i>Ischnura elegans</i> (Vander Linden, 1820)	29 092	1871–4504
Coenagrionidae	<i>Ischnura pumilio</i> (Charpentier, 1825)	577	33–116
Coenagrionidae	<i>Pyrrhosoma nymphula</i> (Sulzer, 1776)	8275	450–1423
Platycnemididae	<i>Platycnemis pennipes</i> (Pallas, 1771)	3575	209–800
Aeshnidae	<i>Aeshna cyanea</i> (Müller, 1764)	5725	311–901
Aeshnidae	<i>Aeshna grandis</i> (Linnaeus, 1758)	4794	180–764
Aeshnidae	<i>Aeshna isoceles</i> (Müller, 1767)	2022	90–332
Aeshnidae	<i>Aeshna juncea</i> (Linnaeus, 1758)	1220	52–206
Aeshnidae	<i>Aeshna mixta</i> Latreille, 1805	11 864	575–1774
Aeshnidae	<i>Anax imperator</i> Leach, 1815	9489	576–1750
Aeshnidae	<i>Brachytron pratense</i> (Müller, 1764)	2784	171–387
Corduliidae	<i>Cordulia aenea</i> (Linnaeus, 1758)	2792	184–511
Corduliidae	<i>Somatochlora metallica</i> (Vander Linden, 1825)	1230	40–240
Libellulidae	<i>Leucorrhinia dubia</i> (Vander Linden, 1825)	1062	60–262
Libellulidae	<i>Leucorrhinia rubicunda</i> (Linnaeus, 1758)	3175	97–814
Libellulidae	<i>Libellula depressa</i> Linnaeus, 1758	4438	298–687
Libellulidae	<i>Libellula fulva</i> Müller, 1764	1216	79–212
Libellulidae	<i>Libellula quadrimaculata</i> Linnaeus, 1758	10 531	766–1846
Libellulidae	<i>Orthetrum cancellatum</i> (Linnaeus, 1758)	16 824	1015–3006
Libellulidae	<i>Sympetrum danae</i> (Sulzer, 1776)	8382	564–1260
Libellulidae	<i>Sympetrum flaveolum</i> (Linnaeus, 1758)	3190	35–806
Libellulidae	<i>Sympetrum sanguineum</i> (Müller, 1764)	9657	570–1697
Libellulidae	<i>Sympetrum striolatum</i> (Charpentier, 1840)	6473	426–1031
Libellulidae	<i>Sympetrum vulgatum</i> (Linnaeus, 1758)	7063	459–1095