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Phenology of British butterflies and climate change

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Abstract

Data from a national butterfly monitoring scheme were analysed to test for relationships between temperature and three phenological measures, duration of flight period and timing of both first and peak appearance. First appearances of most British butterflies has advanced in the last two decades and is strongly related to earlier peak appearance and, for multibrooded species, longer flight period. Mean dates of first and peak appearance are examined in relation to Manley's central England temperatures, using regression techniques. We predict that, in the absence of confounding factors, such as interactions with other organisms and land-use change, climate warming of the order of 1 °C could advance first and peak appearance of most butterflies by 2–10 days.

Keywords: butterflies, climate change, emergence, flight period, monitoring, phenology

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Introduction

Since the late 18th Century, the timing of biological events has been enthusiastically recorded (Clarke 1936). With increasing evidence for human-induced global climate change (Houghton *et al*. 1996), phenology has taken on greater importance as an indicator of species' response to the changing environment. In order to predict future responses of species to a changed climate we first need to discover how species have responded to climate in the past. Studies covering a diverse range of taxonomic groups and biological events have demonstrated strong relationships between phenological events and climate. Analyses of long-term datasets have shown earlier nesting and arrival from migration for birds (Crick *et al*. 1997; Sparks 1999), an extended growing season across Europe (Menzel & Fabian 1999) and advanced first flowering of plants (Fitter *et al*. 1995). Although invertebrates make up a large fraction of terrestrial biodiversity (Groombridge 1992), datasets on their phenology are limited. However, analyses of long-term phenological records have shown that climate warming of the order of 3 °C could advance butterfly appearance by two to three weeks (Sparks & Carey 1995; Sparks & Yates 1997).

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Butterflies are good organisms for studying the effects of environmental change. As poikilothermic animals their activity is closely controlled by weather and many species are constrained by climate (Pollard 1979, 1988; Turner *et al*. 1987; Dennis 1993), mostly occupying a small part of the range of their host plants (Dennis & Shreeve 1991; Quinn *et al*. 1998). They are fecund, have high dispersal ability and an annual or more frequent life cycle, so changes in abundance and distribution can be detected over a relatively short time-scale (Pollard & Yates 1993; Parmesan 1996). Butterflies are also an ideal group for phenological recording, as they are conspicuous and have a high public profile. Also, there is a large amount of data on the flight-periods of butterflies in the British Butterfly Monitoring Scheme (BMS), a national monitoring network.

A previous study has used data from the BMS to demonstrate the effects of spring temperatures on the timing of first and mean appearance for 12 species of British butterflies (Sparks & Yates 1997) between 1976 and 1993. In the current paper, we examine the effects of temperature on the phenology of 35 British butterflies over a longer time period 1976–98, using data from the BMS. The main aims of this study are: (i) to detect temporal trends in timing of first and peak appearance and flight-period length; (ii) to examine inter-relationships between timing of first and peak appearance and flight-period length; and (iii) to predict the effects of

Table 1 Trends over time (1976–98) for mean first appearance, peak flight date and length of flight period. Table reports R^2 and significance values from regressions of flight period characteristics on year. Values for change per decade are number of days.

		Mean first appearance			Mean peak appearance			Mean length of flight period		
		R^2 (%)	sig.	Change (+10 y)	R^2 (%)	sig.	Change (+10 y)	R^2 (%)	sig.	Change (+10 y)
(a) species with one flight period each year										
Thymelicus sylvestris (Poda.)	small skipper	0	ns	−1.4	0	ns	−1.6	0	ns	−0.9
Ochlodes venata (Br. & Grey)	large skipper	11	ns	−3.7	1	ns	−2.3	31	**	4.4
Erynnis tages (L.)	dingy skipper	17	*	−5.1	6	ns	−3.4	18	*	4.3
Pyrgus malvae (L.)	grizzled skipper	28	**	−6.0	11	ns	−4.4	12	ns	3.4
Anthocharis cardamines (L.)	orange tip	50	***	−7.6	39	**	−7.0	1	ns	1.2
Callophrys rubi (L.)	green hairstreak	23	*	−4.3	21	*	−4.7	0	ns	−0.2
Quercusia quercus (L.)	purple hairstreak	0	ns	−1.7	7	ns	−3.8	0	ns	−0.4
Lysandra coridon (Poda.)	chalk-hill blue	0	ns	0.0	0	ns	−0.3	0	ns	0.0
Limenitis camilla (L.)	white admiral	7	ns	−3.1	4	ns	−2.5	0	ns	0.4
Clossiana selene (D. & S.)	small pearl-bordered fritillary	0	ns	−1.8	0	ns	−0.5	0	ns	1.6
Clossiana euphrosyne (L.)	pearl-bordered fritillary	27	**	−6.7	11	ns	−4.7	0	ns	1.8
Argynnis aglaja (L.)	dark green fritillary	0	ns	0.0	0	ns	−0.5	0	ns	−1.8
Argynnis paphia (L.)	silver-washed fritillary	12	ns	−4.4	0	ns	−2.3	14	*	3.5
Melanargia galathea (L.)	marbled white	23	*	−4.6	9	ns	−3.2	6	ns	1.7
Hipparchia semele (L.)	grayling	0	ns	0.4	4	ns	−2.7	30	**	−4.6
Pyronia tithonus (L.)	hedge brown (gatekeeper)	0	ns	−1.6	2	ns	−2.0	0	ns	−1.1
Maniola jurtina (L.)	meadow brown	1	ns	−2.0	0	ns	−0.8	6	ns	2.1
Aphantopus hyperantus (L.)	ringlet	23	*	−4.6	10	ns	−3.2	28	**	4.6
(b) species with two flight periods, but only one generation										
Gonepteryx rhamni (L.)	brimstone	24	*	−5.3	0	ns	−2.6	20	*	5.7
Inachis io (L.)	peacock	36	**	−12.8	15	*	−8.1	18	*	10.4
(c) species with two or more flight periods representing different generations										
Pieris brassicae (L.)	large white	0	ns	3.7	8	ns	5.2	0	ns	−1.9
Pieris napi (L.)	green-veined white	32	**	−6.6	0	ns	0.6	45	***	10.2
Pieris rapae (L.)	small white	3	ns	3.6	13	ns	5.6	0	ns	−2.1
Lycaena phlaeas (L.)	small copper	0	ns	0.1	0	ns	0.3	0	ns	1.1
Aricia agestis (D. & S.)	brown argus	0	ns	2.2	0	ns	0.9	0	ns	−2.4
Polyommatus icarus (Rott.)	common blue	0	ns	0.2	0	ns	1.3	0	ns	0.1
Lysandra bellargus (Rott.)	Adonis blue	15	*	−11.2	2	ns	−5.0	15	*	13.3
Celastrina argiolus (L.)	holly blue	0	ns	−2.9	0	ns	−4.1	0	ns	3.6
Vanessa atalanta (L.)	red admiral	40	***	−15.8	0	ns	−1.6	38	**	17.3
Cynthia cardui (L.)	painted lady	5	ns	−8.3	0	ns	−2.3	5	ns	9.8
Aglais urticae (L.)	small tortoiseshell	0	ns	−2.5	0	ns	−0.7	0	ns	1.8
Polygonia c-album (L.)	comma	36	**	−13.2	0	ns	−1.2	24	*	13.1
Pararge aegeria (L.)	speckled wood	13	ns	−5.2	6	ns	5.2	26	**	8.9
Lasiommata megera (L.)	wall brown	0	ns	2.9	4	ns	−3.4	7	ns	−6.1
Coenonympha pamphilus (L.)	small heath	0	ns	−1.0	0	ns	1.6	0	ns	1.2

ns $P > 0.05$, * $0.05 > P > 0.01$, ** $0.01 > P > 0.001$, *** $0.001 > P$

temperature on first and peak appearance. Latin names have been used throughout this paper; common English names are listed in Table 1.

Methods

Butterfly Monitoring Scheme (BMS)

The BMS was established in 1976 to monitor the abundance of butterflies in the British Isles (Pollard 1977). The methods used in the BMS have been described in detail elsewhere (Pollard & Yates 1993). Briefly, at over 100 sites throughout the country, observations are taken at least weekly from April until September each year. Butterflies are counted on fixed transect routes under defined weather conditions. We have abstracted data on 35 out of a total of 51 species covered by the BMS for the years 1976 until 1998. Species present in less than 20 years or with a mean of less than five sites recorded per year were excluded. Data for each species have been summarized for each year to provide simple parameters to describe flight-period characteristics. The following measures have been derived across all sites: mean first appearance date, mean peak abundance date, mean length of flight period and mean number of sites. Parameters were calculated for 30,710 individual flight periods. For individual species, the number of flight periods ranges from 115 for *Lysandra bellargus* to over 1700 for *Maniola jurtina*.

To simplify comparison between species and because we do not want to make any distributional assumptions, we measure duration of flight period as the interval between the first and last counts. Previous studies used the standard deviation of flight days as a measure of the length of the flight period (Brakefield 1987; Pollard 1991). They suggested that the interval between first and last counts, as used in this analysis, was variable and liable to distortion by a single individual which lived a week or more longer than the rest of its cohort. However, this is unlikely to seriously affect the estimates derived from the large number of flight periods used here.

Butterfly species that are migrant in the UK such as *Vanessa atalanta* and *Cynthia cardui* have been included in the following analyses. Although they do not emerge from pupae in this country, timing of first and peak appearance and duration of flight period at BMS sites is of interest. Trends over time and temperature effects have been demonstrated in timing and patterns of migrating birds in Britain (Sparks 1999).

Temperature data

The Central England Temperature (CET) series constructed by Manley (Manley 1974), provides monthly mean surface air temperatures for a region representative of central England for each year from 1659 to 1973. The series was extended to 1991 by Parker *et al*. (1992) and is now regularly updated by the Meterological Office Hadley Centre (http://www.cru.uea.ac.uk/mikeh/datasets/uk/cet.htm). Data from the CET series have been shown to be broadly representative of temperature in other parts of the UK (Duncan 1991).

Analysis

Trends over time in mean first appearance, peak appearance and length of flight period were examined using regression with year as the explanatory variable. The relationship between mean first appearance date and other measures of flight periods (mean flight date and length of flight period) were examined using correlation coefficients to test for linear trends.

A stepwise regression approach was used to relate changes in first and peak appearance to temperature data. Potential explanatory variables included monthly temperatures for the year preceding overall mean first and peak appearance dates and a year index (for unexplained changes over time). For example, for a species such as *M. jurtina* with a mean first appearance month of June, monthly temperature for July–December of the previous year and January–June of the current year

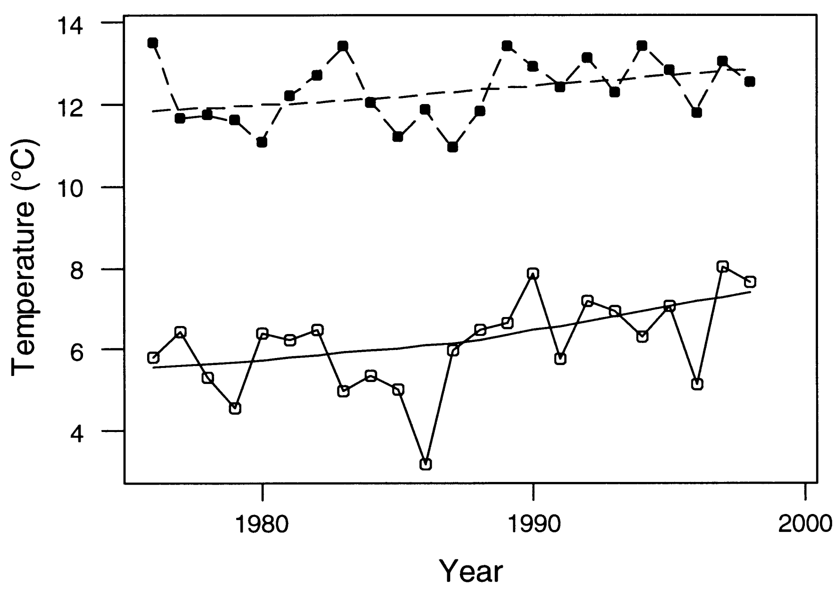

Fig. 1. Time trends in spring and summer Central England Temperature (CET) 1976–98. Open circles are spring temperatures (mean February–April CET) and solid circles are summer temperatures (mean May–July CET).

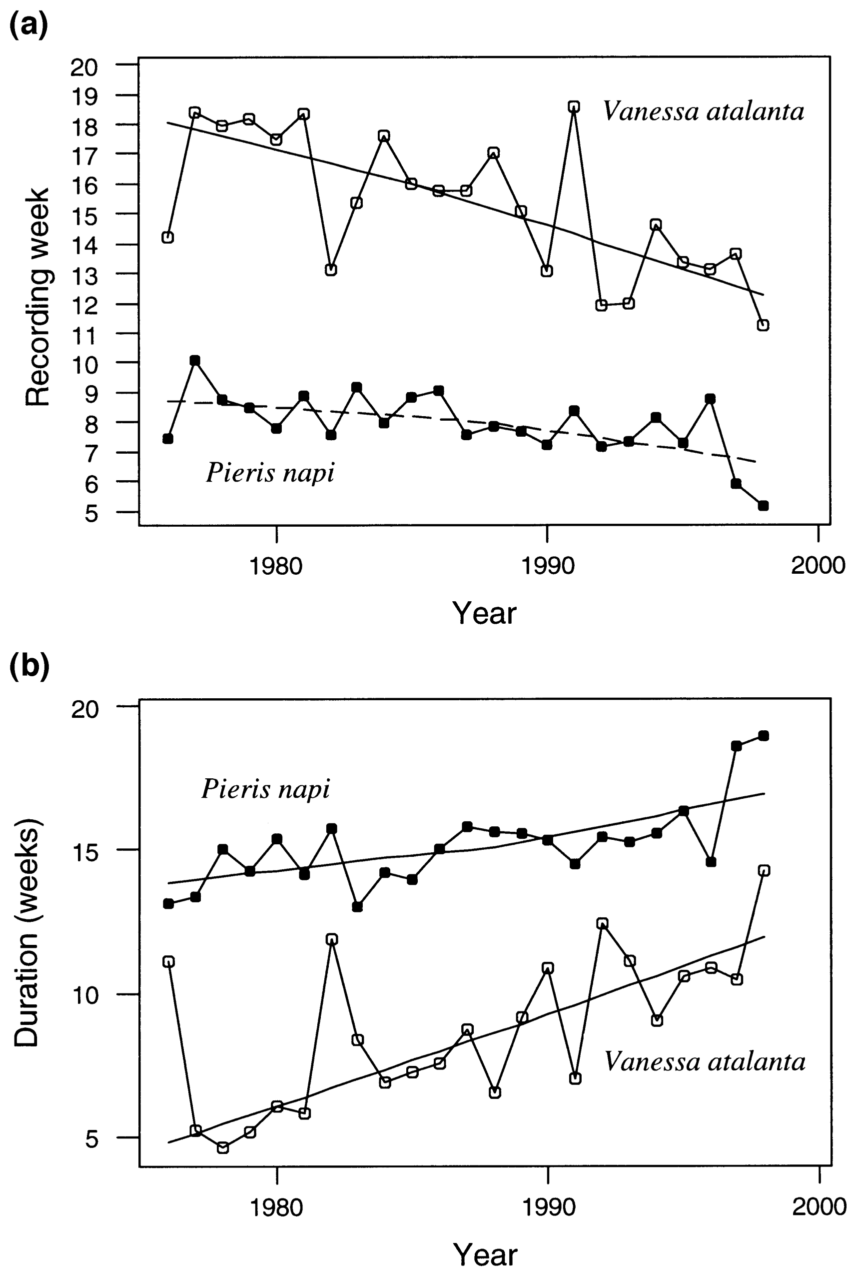

Fig. 2 Time trends for (a) first appearance and (b) duration of flight period for *Vanessa atalanta* and *Pieris napi*. Week 1 is the first week in April.

were included. Only significant months were included in the final model. Weather in both the current and previous year may be important for the timing of appearance of butterfly species. Pollard (1988) has shown a positive association between temperature in the previous summer and current butterfly numbers, particularly for spring-flying species such as *Erynnis tages* and *Pyrgus malvae*. Smoothed lines on figures are produced using the LOWESS (LOcally WEighted Scatterplot Smoother) process.

Results

Trends over time

Between 1976 and 1998 central England spring temperature increased by approximately 1.5 °C and summer temperature by approximately 1 °C (Fig. 1), even though 1976 was the warmest summer. Table 1 summarizes trends in mean first appearance date, peak flight date and length of flight period over the same time period.

Table 2 Correlation between mean first appearance 1976–98 and (i) peak flight date (ii) mean length of flight period.

	Peak flight date		Length of flight period	
(a) species with one flight period each year				
Thymelicus sylvestris	0.92	***	0.08	ns
Ochlodes venata	0.93	***	−0.43	*
Erynnis tages	0.94	***	−0.66	***
Pyrgus malvae	0.87	***	−0.21	ns
Anthocharis cardamines	0.96	***	−0.13	ns
Callophrys rubi	0.93	***	0.08	ns
Quercusia quercus	0.90	***	−0.36	ns
Lysandra coridon	0.91	***	−0.69	***
Limenitis camilla	0.95	***	0.01	ns
Clossiana selene	0.91	***	−0.24	ns
Clossiana euphrosyne	0.90	***	−0.34	ns
Argynnis aglaja	0.82	***	−0.46	*
Argynnis paphia	0.90	***	−0.13	ns
Melanargia galathea	0.93	***	−0.17	ns
Hipparchia semele	0.88	***	−0.35	ns
Pyronia tithonus	0.89	***	−0.14	ns
Maniola jurtina	0.85	***	−0.73	***
Aphantopus hyperantus	0.95	***	−0.54	**
(b) species with two flight periods, but only one generation				
Gonepteryx rhamni	0.59	**	−0.55	**
Inachis io	0.67	***	−0.93	***
(c) species with two or more flight periods representing different generations				
Pieris brassicae	0.61	**	−0.90	***
Pieris napi	0.41	*	−0.83	***
Pieris rapae	0.60	**	−0.88	***
Lycaena phlaeas	0.57	**	−0.90	***
Aricia agestis	0.72	***	−0.91	***
Polyommatus icarus	0.51	*	−0.91	***
Lysandra bellargus	0.34	ns	−0.83	***
Celastrina argiolus	0.77	***	−0.67	***
Vanessa atalanta	0.54	**	−0.96	***
Cynthia cardui	0.76	***	−0.91	***
Aglais urticae	0.61	**	−0.86	***
Polygonia c-album	0.54	**	−0.87	***
Pararge aegeria	0.26	ns	−0.93	***
Lasiommata megera	0.58	**	−0.87	***
Coenonympha pamphilus	0.39	ns	−0.76	***

ns $P > 0.05$, * $0.05 > P > 0.01$, ** $0.01 > P > 0.001$, *** $0.001 > P$.

The first appearance of most species (26 species) is earlier in recent years. This relationship is significant for 13 species, most notably *Anthocharis cardamines* and *V. atalanta* where appearance has advanced by 17.5 and 36.3 days, respectively, over the period 1976–98 (Fig. 2). Mean peak appearance is also earlier in recent years for most species (27 species), but the relationship is significant for only three species. Twelve species have a significant relationship with mean flight period length over time. With the exception of *Hipparchia semele*, this relationship is for a longer flight period in recent years. The most marked increases in duration of flight period over the period 1976–98 are for *V. atalanta* (39.8 days), *Pieris napi* (23.5 days), *L. bellargus* (30.6 days) and *Polygonia c-album* (30.1 days).

From the significant relationships of mean first appearance and mean length of flight period over time, a number of species show the same pattern: earlier first appearance and longer flight period (Table 1). This effect is strongest in *P. napi* and *V. atalanta* (Fig. 2), but is also apparent in *L. bellargus*, *Gonepteryx rhamni*, *P. c-album*, *Erynnis tages*, *Inachis io* and *Aphantopus hyperantus*.

Relationships with first appearance

All 35 species analysed have a positive correlation coefficient between mean first appearance date and mean peak flight date (Table 2). With the exception of *L. bellargus*, *Coenonympha pamphilus* and *Pararge aegeria*, the relationship is significant: for all univoltines the relationship is highly significant. Almost all species (32) also have a negative relationship between mean first appearance date and length of flight period. Early first appearance results in an extended flight period and for the majority of species the relationship is significant: for all multivoltine species the relationship is highly significant.

There is a clear relationship between three attributes of flight period: dates of first and peak appearance and length of the flight period. For single-brooded species such as *Thymelicus sylvestris*, *Limenitis camilla* and *Callophrys rubi* early first appearance results in an early peak flight date, but no lengthening of the flight period. For multibrooded species such as *P. aegeria*, *L. bellargus* and *P. napi* early first appearance results in a longer flight period, but not a significantly earlier peak flight date (Fig. 3).

Relationships with weather

Table 3 gives a summary of regression models relating mean first appearance and mean peak flight date to temperature. For almost all species, there is a highly significant relationship with weather of both first appearance date and peak flight date. Almost all temperature components had a negative effect; warmer weather tended to produce earlier first and peak appearance. The most striking result is that many species showed earlier first and peak appearance with warm spring temperature, particularly in February (e.g. *A. cardamines* and *Polyommatus icarus*, Fig. 4), or with summer temperature (e.g. *Melanargia galathea* and *M. jurtina*, Fig. 4). Trend with calendar year was

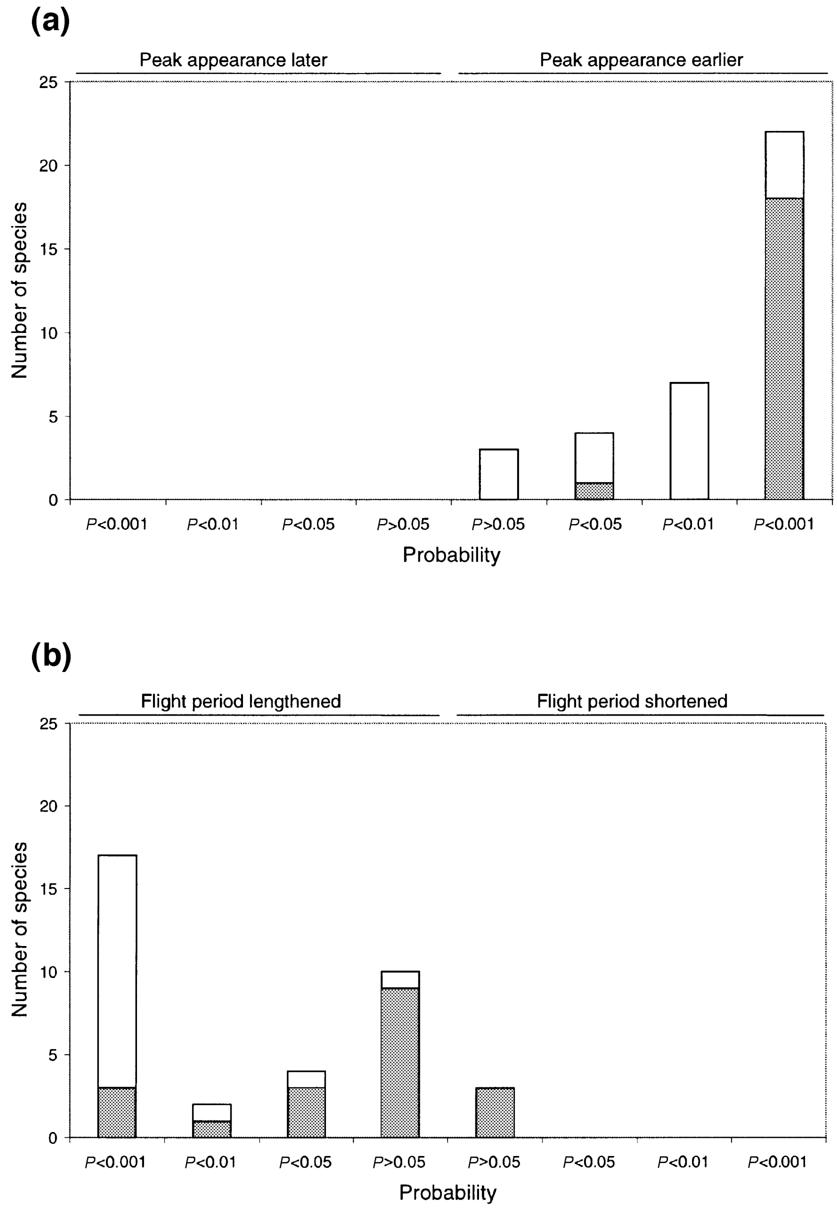

Fig. 3 Correlations with first appearance. Frequency distribution of *P*-values of correlation between first appearance and (a) peak appearance and (b) length of flight period. Univoltine species are shown in grey, multivoltine in white.

apparent for a number of species, reflecting changes over time not accounted for by the examined temperature variables. Where trend over time was apparent, the effect was negative, suggesting that these species have appeared earlier. In the absence of trend the more reliable models suggest that a 1 °C rise in temperature could advance both mean first and peak appearance by 2–10 days.

Discussion

The foregoing analyses support recent research suggesting that the timing of many natural events is occurring earlier in recent years (e.g. Crick *et al*. 1997; Menzel & Fabian 1999) and that climate is the most likely cause of change (Beebee 1995; Sparks *et al*. 1997; Sparks & Crick 1999; Sparks 1999). We have demonstrated that first appearance of most British butterflies has advanced over the last two decades and that there is a strong relationship between these changes and temperature. The Butterfly Monitoring Scheme is probably the longest running scheme of its sort in the World. However, while 23 years is still a relatively short time-series with which to detect change, we are excited by the consistency of results reported herein.

Together with early emergence, there is a concurrent advancement of peak appearance and longer flight duration. Therefore, advanced first appearance results

Table 3 Summary of regression models relating mean first appearance and mean peak flight date to temperature data. Terms are included in the order they entered the model; values represent CET month number with those from the previous year being negative, i.e. 2 = February of current year, −11 = November of previous year. All coefficients with temperature are negative, except those marked with +. The figures in parenthesis adjacent to 'Yr' indicate the per year coefficient associated with the significant trend over time. Values for change per + 1 °C are number of days. Number of years in all models, $n = 23$.

	First appearance date				Peak flight date			
	Terms included	R^2 (%)	sig.	Change (+1 °C)	Terms included	R^2(%)	sig.	Change (+1 °C)
(a) species with one flight period each year								
Thymelicus sylvestris	6,2	82	***	−4.9	6,7,2,1+	85	***	−6.7
Ochlodes venata	2,6	79	***	−5.1	6,2	73	***	−5.0
Erynnis tages	2,4,1	78	***	−6.2	4,5	73	***	−8.7
Pyrgus malvae	2,Yr(0.05),-9+	69	***	0.7	2,-9+	67	***	0.1
Anthocharis cardamines	Yr(−0.08),2	75	***	−1.7	2,Yr(−0.05),-11+,4,1,5	91	***	−5.7
Callophrys rubi	2,Yr(−0.04),-8+	83	***	−1.8	2,Yr(−0.04),-7	79	***	−2.7
Quercusia quercus	6,2	62	***	−2.1	2,6	51	**	−4.9
Lysandra coridon	6,3	73	***	−7.7	6,8	68	***	−7.3
Limenitis camilla	6,2	65	***	−4.8	6,2	63	***	−4.5
Clossiana selene	2	36	**	−1.9	2,6	46	**	−3.7
Clossiana euphrosyne	2,Yr(−0.07)	54	***	−1.9	2	56	***	−2.9
Argynnis aglaja	2,3+	47	**	−0.3	6,2	45	**	−3.1
Argynnis paphia	2,7,6	58	**	−5.9	2,7	63	***	−5.5
Melanargia galathea	5,6,Yr(−0.05)	77	***	−4.7	6,5,7,4	86	***	−8.7
Hipparchia semele	6,2	46	**	−3.3	2,6	40	**	−3.5
Pyronia tithonus	6,7,5,4	91	***	−7.0	6,7,2	88	***	−5.7
Maniola jurtina	2,6	83	***	−4.7	6,2,7	79	***	−5.4
Aphantopus hyperantus	6,Yr(−0.05),-10+,2	77	***	−3.0	6,2,-10+,Yr(−0.03)	78	***	−2.1
(b) species with two flight periods, but only one generation								
Gonepteryx rhamni	Yr(−0.08)	28	**	−4.4	2	31	**	−3.4
Inachis io	Yr(−0.15),-8	55	***	−6.6	2,-12,6	34	***	−9.9
(c) species with two or more flight periods representing different generations								
Pieris brassicae	5,Yr(0.09),-7+,-11,-6	90	***	−9.3	6,Yr(0.11),2	56	**	−2.4
Pieris napi	2,Yr(−0.08),-6+	69	***	−0.4	6	22	*	−2.8
Pieris rapae	5,3+	56	***	−3.9	6,Yr(0.11),2	59	**	−5.8
Lycaena phlaeas	2	23	*	−2.4	7+,6	37	**	1.0
Aricia agestis	−8	23	*	−3.7	5	21	*	−5.2
Polyommatus icarus	2	42	**	−2.5	7+,2	43	**	1.3
Lysandra bellargus	3,-8	54	***	−11.8	5	19	*	−9.2
Celastrina argiolus					7+	39	**	8.5
Vanessa atalanta	Yr(−0.19),6,2	77	***	−9.2	6	27	*	−3.7
Cynthia cardui	none				none			
Aglais urticae	2	21	*	−1.9	1	26	*	−3.0
Polygonia c-album	Yr(−0.26),-9,3+	65	***	−5.4	none			
Pararge aegeria	5,4	77	***	−10.2	none			
Lasiommata megera	2,6,Yr(0.10)	60	***	−8.2	2	55	***	−2.8
Coenonympha pamphilus	2	60	***	−2.5	7+,5	54	***	1.8

ns $P > 0.05$, * $0.05 > P > 0.01$, ** $0.01 > P > 0.001$, *** $0.001 > P$

in a more asymmetrical flight period distribution rather than a forward shift: for univoltine species the tail of the flight period is lengthened; for multivoltine species extra generations per year may be produced. As well as increasing the duration of each generation, earlier appearance may allow those species capable of multivoltinism to increase the frequency with which this occurs. Voltinism of several butterfly species can change in response to artificial selection (Lees 1962, 1965; Lees & Archer 1980; Pullin 1986), and it is likely that similar changes would occur with climate change. Species such as *P. icarus* and *C. pamphilus* have flexible voltinism in

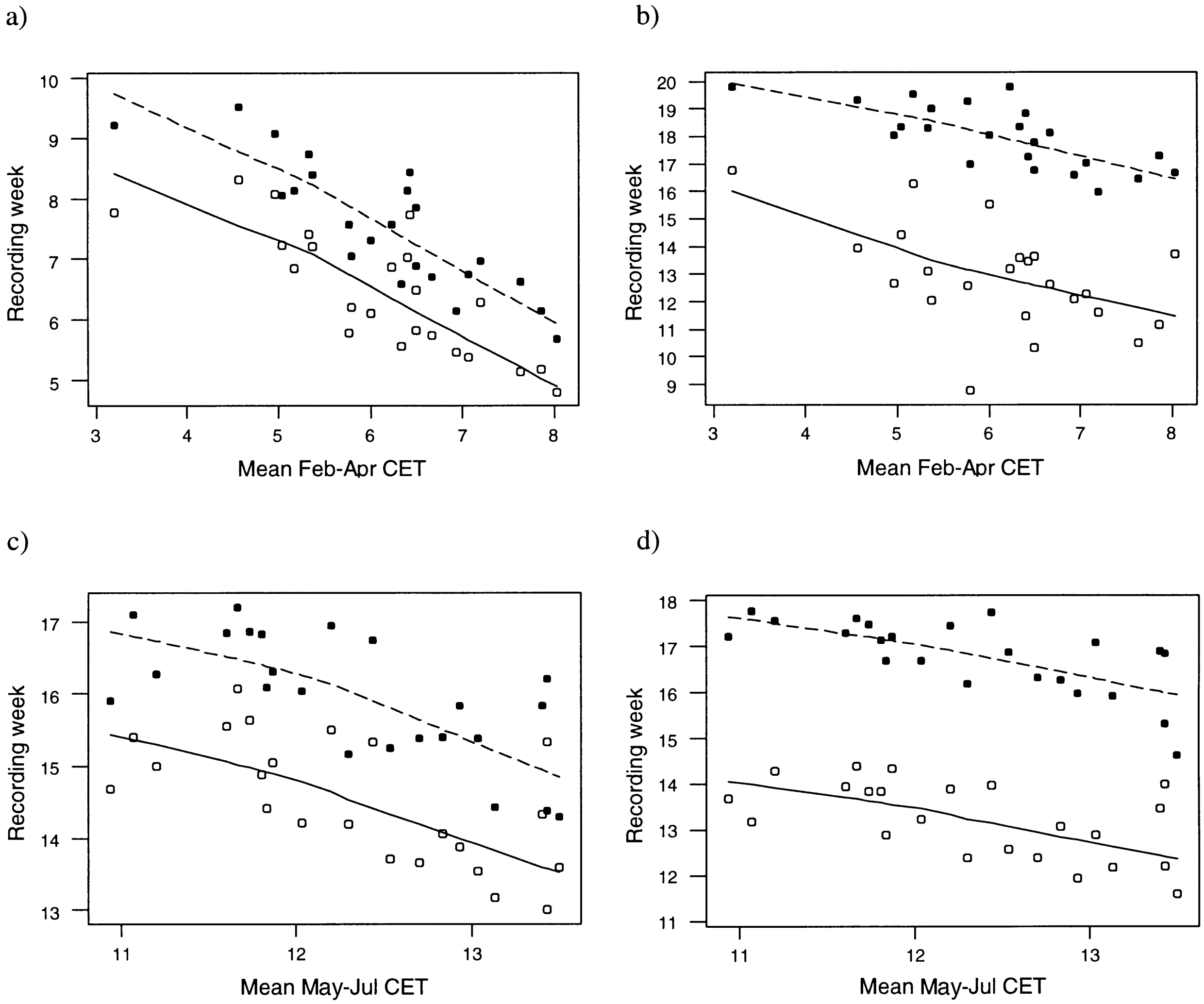

Fig. 4 Relationships between mean first and mean peak appearance dates and temperature. Open circles are first appearance dates, solid circle are peak appearance and are related to mean spring temperature (mean February–April Central England Temperature, CET) for (a) *Anthocharis cardamines* and (b) *Polyommatus icarus* and summer temperature (mean May–July Central England Temperature, CET) for (c) *Melanargia galathea* and (d) *Maniola jurtina*. Week 1 is the first week of April.

southern Britain; in warm years there are two generations. Certain species which are univoltine in Britain, have more than one generation in warmer parts of their range, e.g. *I. io* has two generations in central Europe (Pullin 1986). Duration of flight-period has also been shown to be longer in open (grassland) compared to closed (woodland) biotopes for *M. jurtina* and *C. pamphilus* (Pollard & Greatorex-Davies 1997). Other implications of earlier emergence of British butterflies may include increased abundance and range expansion northward for species currently restricted geographically by climate (Pollard *et al*. 1995). Pollard (1991) has shown a longer flight period and earlier mean flight date for the *Pyronia tithonus* during a period of range expansion.

Clearly, early emergence is an effective measure of other flight period characteristics, but it is not clear how advanced first appearance is related to population abundance. This question is complicated by the probabilistic argument that increased abundance in a given year may lead to first appearance being observed earlier, i.e. less chance of an isolated, early individual being overlooked. This is only likely to be a problem with less apparent species undergoing large annual population changes. Resolving the link between population size and first observation is not trivial and is probably best approached through simulation studies.

Regression analyses suggest a relationship between temperature and timing of first and peak appearance for most species. In particular, a positive effect of February temperature on first appearance was detected for the majority of species. Over the last 20 years, this month has shown greatest variation in temperature in the UK compared to other periods of the year. Although this may increase the likelihood of detecting an effect, spring is a critical time for larval development for many species and increased temperatures over this period are likely to advance emergence. Whilst some of the effects reported may be spurious due to the large number of comparisons being made, the dominance of negative relationships with spring temperatures (warmer springs linked to earlier appearance) cannot be denied. Predictions of advanced timing of appearance of British butterflies mostly vary between 1 and 10 days per °C. The advanced nesting of long-tailed tit, *Aegithalos caudatus* (by 4.1 days), the early arrival of blackcap, *Sylvia atricapilla*, from migration (by 2.3 days), and the early leafing of oak, *Quercus robur* (by 7.8 days), with each additional °C, as reported by Sparks & Crick (1999), also fall within this range. However, there are clearly a large number of confounding factors such as food supply, desiccation, predation, and possibly most strongly land-use change, which will modify the impact of climate change as suggested here.

The effects of temperature on other aspects of butterfly ecology such as diversity, range and abundance are well recognized (Turner *et al*. 1987; Pollard 1988; Dennis 1993). Most predicted effects of climate change on butterflies are likely to be positive, mainly through the increase in flight-dependant activities such as mate-location, egg laying, nectaring, predator-evasion and dispersal (Dennis & Shreeve 1991). However, the propensity for drought associated with climate change predictions may have negative effects on some butterfly species. Dry summers are likely to affect egg survival, host plant growth and habitat structure (Pollard 1988; Dennis & Shreeve 1991).

Interactions with other organisms as well as abiotic factors add further complexity to prediction of the response of individual butterfly species to increased temperatures (Harrington *et al*. 1999). A driving force for climate warming is elevated levels of 'greenhouse gases', notably CO_2. As well as indirectly raising temperature, increased levels of this gas have been shown to raise photosynthetic activity (Keeling *et al*. 1996). This in turn can affect plant–insect herbivore interactions (Bazzaz 1990; Bezemer & Jones 1998). Studies of Lepidoptera, however, have shown that *A. cardamines* is likely to remain synchronized with one of its foodplants, garlic mustard *Alliaria petiolata* (Sparks & Yates 1997); a similar synchrony is apparent between winter moth *Operophtera brumata* (L.) larvae and oak budburst (Buse & Good 1996).

Most studies of the effects of climate change on the timing of biological events have utilized avian and botanical datasets. This paper has shown that historical change in the phenology of butterfly species demonstrate an impressive response to only two decades of climate change.

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