

# Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin

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## Abstract

Phenological changes in response to climatic warming have been detected across a wide range of organisms. Butterflies stand out as one of the most popular groups of indicators of climatic change, given that, firstly, they are poikilothermic and, secondly, have been the subject of thorough monitoring programmes in several countries for a number of decades. Here we provide for the first time strong evidence of phenological change as a consequence of recent climatic warming in butterflies at a Spanish site in the northwest Mediterranean Basin. By means of the widely used Butterfly Monitoring Scheme methodology, three different phenological parameters were analysed for the most common species to test for trends over time and relationships with temperature and precipitation. Between 1988 and 2002, there was a tendency for earlier first appearance dates in all 17 butterfly species tested, and significant advances in mean flight dates in 8 out of 19 species. On the other hand, the shape of the curve of adult emergence did not show any regular pattern. These changes paralleled an increase of 1–1.5 °C in mean February, March and June temperatures. Likewise, a correlation analysis indicated the strong negative effect of spring temperature on phenological parameters (i.e. higher temperatures tended to produce phenological advances), and the opposite effect of precipitation in certain months. In addition, there was some evidence to indicate that phenological responses may differ between taxonomic lineages or species with similar diets. We discuss the consequences that these changes may have on species' population abundances, especially given the expected increase in aridity in the Mediterranean Basin caused by current climatic warming. We predict that varying degrees of phenological flexibility may account for differences in species' responses and, for multivoltine species, predict strong selection favouring local seasonal adaptations such as diapause phenomena or migratory behaviour.

*Keywords:* butterflies, climate change, flight period, monitoring, NW Mediterranean Basin, phenology

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## Introduction

Changes in phenology stand out as some of the most conspicuous reactions by wildlife in response to recent climatic warming (reviews in Hughes, 2000; Peñuelas & Filella, 2001; Walther *et al.*, 2002). Despite some contradictory results, long-term phenological data sets have provided compelling evidence for significant temporal advances in several biological phenomena across a wide range of organisms and from many different regions (Parmesan & Yohe, 2003, Root *et al.*, 2003). The

consistency of this pattern is shown by the phenological advances found in plant growth and flowering dates (e.g. Menzel & Fabian, 1999; Fitter & Fitter, 2002; Peñuelas *et al.*, 2002), the timing of adult emergence in insects (Fleming & Tatchell, 1995; Zhou *et al.*, 1996; Ellis *et al.*, 1997; Woiwod, 1997), the timing of migratory events for both insects and birds (e.g. Zhou *et al.*, 1995; Sparks, 1999; Inouye *et al.*, 2000) and reproduction dates in amphibians and birds (e.g. Beebee, 1995; Crick *et al.*, 1997; Dunn & Winkler, 1999). In general, the strongest responses have been found for those phenophases timed to occur in the spring (cf. Walther *et al.*, 2002).

Among the most suitable data sets for looking at phenological changes in insects are those obtained by

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means of the Butterfly Monitoring Schemes (BMS) operating in several European countries (Pollard & Yates, 1993; van Swaay *et al.*, 1997; Kuussaari *et al.*, 2000; Stefanescu, 2000). BMS data are collected in a standardized manner (i.e. visual counts along fixed transects, under defined weather conditions, and repeated on a weekly basis in successive years) and enable the flight periods of butterflies to be carefully recorded and characterized by means of some basic statistic descriptors (Brakefield, 1987). Moreover, butterflies are an ideal group for studying the effects of climatic change because, as poikilothermic animals, their life-cycle is highly influenced by temperature (Pollard, 1988; Dennis, 1993).

A recent paper by Roy & Sparks (2000) examined the effect of temperature on the phenology of 35 British butterflies over the period 1976–1998, using data from the UK BMS. Their analysis indicated that the first appearance and mean flight date of most species have advanced over the last two decades (means of 7.98 and 6.6 days per decade, respectively, for significant relationships) and flight periods have become longer (7.59 days per decade). These changes paralleled an increase of 1–1.5 °C in spring and summer temperatures in central England.

Data from BMS transects outside the UK have not been used to investigate phenological patterns in the context of climatic change. However, the Catalan BMS (CBMS) is particularly interesting because it provides information from the Mediterranean Basin, one of the biologically richest regions in the world and one from which studies on the effects of climatic change on wildlife are much needed (cf. Peñuelas *et al.*, 2002). Indeed, most of the studies using butterflies as indicators of climatic change in the European continent have focussed on UK fauna (e.g. Roy *et al.*, 2001; Thomas *et al.*, 2001; Warren *et al.*, 2001; Hill *et al.*, 2002; but see Parmesan *et al.*, 1999) and, as a result, the responses shown in other parts of the continent remain largely unknown. As a first attempt to filling this gap, in the present paper we use data from the CBMS to analyse the phenological trends experienced between 1988 and 2002 by the butterflies inhabiting a Mediterranean site in NE Spain. Albeit encompassing a quite short period, our data show that phenological changes have been strong and provide further evidence that ecological responses to recent climatic change are occurring at a very fast rate.

## Materials and methods

### *Butterfly data*

Butterfly data were obtained at El Cortalet (42°13'N 3°05'E), a coastal site in NE Spain, from where there

exists the longest data series of all the CBMS stations (Stefanescu, 2000). The area is very flat and the mean altitude is just 1.5 m asl (range of <5 m). For a 15-year period (from 1988 to 2002, with the exception of 1990), weekly butterfly counts were made along a fixed route of 4343 m, from 1 March to 26 September (a total of 30 recording weeks per year). All individuals seen within 2.5 m on each side and 5 m in front of the recorder were counted, using the standard methodology of the UK BMS (cf. Pollard & Yates, 1993).

A total of 58 species were detected during the sampling period, although about half were vagrants recorded only occasionally (see Stefanescu *et al.*, 1996, for details). For analytical purposes, we considered only those species that regularly breed in the area with mean counts of more than four individuals per year (i.e. those for which a phenological pattern could be drawn). The final data set consisted of 19 species encompassing a wide range of life cycles and appearance dates (Table 1).

### *Flight-period parameters and butterfly phenology*

Three different parameters were calculated for each species and for every year: first appearance date, mean flight date and the standard deviation (SD) of this latter date. The mean flight date was calculated as the weighted mean date of the counts and gives an estimation of the date of mean abundance in the adult flight period. SD is a measure of the degree of synchronization of the flight period (Brakefield, 1987). As in Pollard (1991), the recording weeks were used as the unit of time rather than the day of the counts. In *Pieris* spp., the flight period was truncated in a few years so that the first appearance date and SD of mean flight date were not always obtainable; however, the effect of the missing data on the mean flight period was negligible and this measure was still calculated. SD of mean flight date was not calculated for *Lycaena phlaeas* and *Polygonia c-album* (which were very scarce in some years), *Leptotes pirithous* (whose flight period was truncated at the end) and *Celastrina argiolus* (whose flight period consisted of two overlapped generations; see below).

Excluding univoltine species (i.e. those with a single generation per year; Fig. 1a), butterflies in the Mediterranean region usually show a complex phenological pattern, consisting of the succession of a distinct first generation in the spring (i.e. corresponding to overwintered pupae or grown larvae) by one or, more commonly, several overlapping generations throughout the summer and beginning of autumn (Fig. 1b, c). In most cases, this makes it impossible from mid-May onwards to identify peaks of abundance corresponding

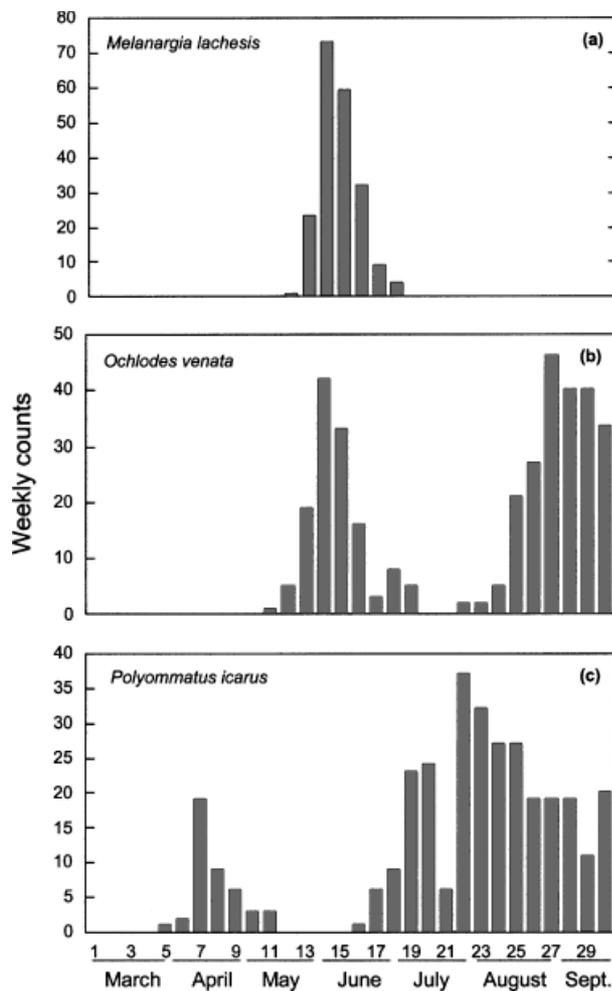
**Table 1** Ecological attributes and change (in weeks) for first appearance date and the standard deviation about this later date (SD), for the 19 butterfly species included in the analysis

Species	Family/ subfamily	Overwintering stage	Hostplant use	Migratory behaviour*	Mean first appearance			First appearance			Mean flight date			SD		
					date (weeks) <sup>†</sup>											
<i>Pieris brassicae</i>	P	Pupa	Herb	Dir	2.21	4.83	14	NS	-0.35	0.22	NS	-0.17	0.57	-	-	
<i>Pieris rapae</i>	P	Pupa	Herb	Dir	1.69	5.55	14	-	-	NS	NS	-0.13	0.66	-	-	
<i>Pieris napi</i>	P	Pupa	Herb	Non-dir	-	4.18	14	-	-	-1.77	-0.68	0.006	-	-	-	
<i>Colias crocea</i>	P	Und	Herb	Dir	3.64	6.14	14	NS	-0.44	0.12	NS	-0.34	0.26	1.4	0.60	
<i>Lycena phlaeas</i>	L	Larva	Herb	Non-dir	2.45	3.94	11	NS	-0.35	0.30	NS	0.16	0.64	-	-	
<i>Leptotes pirithous</i>	L	Und	Herb	Dir	20.64	25.86	14	NS	-0.27	0.35	NS	-0.38	0.19	-	-	
<i>Celastrina argiolus</i>	L	Pupa	Herb	Non-dir	12.93	20.78	14	-3.84	-0.59	0.024	-3.69	-0.70	0.004	-	-	
<i>Plebejus argus</i>	L	Egg	Herb	Sed	11.77	12.46	8	-2.93	-0.68	0.045	-1.88	-0.84	0.006	NS	0.42	
<i>Polyommatus icarus</i>	L	Larva	Herb	Sed	7.42	10.30	12	NS	-0.02	0.95	NS	0.14	0.68	NS	0.12	
<i>Cynthia cardui</i>	N	Und	Herb	Dir	8.64	14.34	14	NS	-0.15	0.61	NS	-0.39	0.17	NS	-0.07	
<i>Polygonia c-album</i>	N	Adult	Herb	Non-dir	2.21	3.83	14	NS	-0.16	0.60	NS	-0.33	0.26	-	-	
<i>Melanargia lachesis</i>	S	Larva	Grass	Sed	13.57	16.34	14	NS	-0.37	0.19	-2.23	-0.72	0.003	-0.98	-0.69	
<i>Pyronia tithonus</i>	S	Larva	Grass	Sed	18.64	21.61	14	NS	-0.28	0.34	NS	-0.13	0.67	NS	0.36	
<i>Pyronia cecilia</i>	S	Larva	Grass	Sed	20.14	21.78	14	NS	-0.37	0.21	-2.52	-0.57	0.034	NS	-0.12	
<i>Coenonympha pamphilus</i>	S	Larva	Grass	Sed	4.86	11.29	14	-6.15	-0.64	0.012	-2.29	-0.56	0.035	1.59	0.64	
<i>Lasionnata megera</i>	S	Larva	Grass	Sed	4.33	6.59	13	-5.71	-0.59	0.031	-3.96	-0.59	0.031	NS	0.46	
<i>Caracharodus alcae</i>	H	Larva	Herb	Sed	3.40	5.21	10	NS	-0.51	0.13	NS	-0.16	0.67	1.46	0.56	
<i>Thymelicus acteon</i>	H	Larva	Grass	Sed	12.86	16.67	14	NS	-0.35	0.22	NS	-0.29	0.32	NS	-0.05	
<i>Ochlodes venata</i>	H	Larva	Grass	Sed	10.64	14.65	14	-2.05	-0.53	0.048	-1.46	-0.64	0.013	NS	0.45	

Mean first appearance date, mean flight date, and the number of available years for each species are also included. Voltinism was determined from transect data (1988–2002), supplemented with BMS data from all over the country (Stefanescu, 2000). Overwintering stage, hostplant use and migratory behaviour were compiled either from the literature (mainly Tolman & Lewington, 1997) and from personal observations at the study area. Family/subfamily (P: Pieridae; L: Lycaenidae; N: Nymphalidae; S: Satyrinae; H: Hesperidae), Voltinism (U: univoltine; B: bivoltine; M: multivoltine), Overwintering stage (und undetermined, probably variable or non-existent). Significant changes are highlighted in bold type. NS: not significant.

\*Migratory behaviour: *sedentary* (sed), most of the population hatch and die within a discrete 'home area' in the range of 0.1–4 km; *non-directional* (non-dir), a substantial part of the population disperses in random and non-directional flights encompassing several kilometres; *directional* (dir), a large fraction of the population engages in seasonally predictable long distance movements encompassing several hundreds of kilometres.

<sup>†</sup>Starting on 1 March.



**Fig. 1** Representative flight-period patterns of butterflies at El Cortalet. Charts show transect counts of three species in single years for each week of the recording season (30 weeks, from 1 March to 26 September). (a) univoltine species: *Melanargia lachesis*, in 2001; (b) bivoltine species: *Ochlodes venata*, in 1998; (c) multivoltine species: *Polyommatus icarus*, in 1989. With a few exceptions, only the first and distinctive spring generation in multivoltine (and bivoltine) species was used for the calculation of flight-period parameters (see text for details).

to discrete generations (Stefanescu, 2000). To overcome this problem, with a few exceptions (see below) flight-period parameters in bivoltine and multivoltine species were calculated only for the spring generation.

In *C. argiolus*, a substantial part of the spring generation was unrecorded in most years because of adult emergence in February. Later in the season, this butterfly has two more additional greatly overlapping generations, peaking in mid-June and the end of July or beginning of August, respectively. Flight-period parameters were calculated for the pooled data of these two summer generations.

*P. c-album* was the only species overwintering in the adult stage that could be included in our data set. Overwintered individuals of this species appear in March–April and show a clear and distinct flight period in generations later on in the year, which appear from May to October in a complex pattern (S. Nylin and C. Stefanescu, unpublished results). We therefore restricted analysis to the early spring emergence.

Five long-distance migrants have been considered in this study (Table 1): *Pieris brassicae*, *Pieris rapae*, *Colias crocea*, *L. pirithous* and *Cynthia cardui*. The first three species regularly overwinter in the area and have a distinct spring generation in March–April before the arrival of a variable northward migrant population in May–July, which reinforces the local population (Stefanescu *et al.*, 1996; Stefanescu, 2000). For these species, flight-period parameters were calculated for the locally produced distinctive spring generation. On the other hand, *L. pirithous* and *C. cardui* cannot overwinter in the area and their regular occurrence in counts is exclusively due to yearly recolonization from Africa or the southern Iberian Peninsula. In *C. cardui*, northward migrants arrive in April–June, sometimes in great numbers (Stefanescu, 1997; Pollard *et al.*, 1998). Although these migrants breed in the area, their progeny remains highly inconspicuous, probably because emerging butterflies quickly emigrate when encountering dry summer conditions. This means that the distinctive peak of abundance occurring in late spring is followed by a period with virtually no counts, until some southward migrants of more northern European origin reappear in August–September while travelling back to their winter headquarters. In this paper, first appearance and mean flight dates were calculated only for spring migrants and thus represent a measure of the timing of the arrival of African butterflies each season. This species was therefore excluded from those analyses trying to relate the flight period parameters to local weather variables.

In *L. pirithous*, a few migrants are usually recorded by late June or early July and immediately give rise to a rapidly growing local population, consisting of a succession of overlapping generations that extend well into October. For this butterfly, we did not try to distinguish between migrants and locally born butterflies because the pattern of counts is often too complex. Instead, we calculated the flight-period parameters until 26 September using all available data, even though this meant that the part of the population flying after this date was wholly absent from the samples. The first appearance date thus gives an estimation of the timing of the arrival of northward migrants, while the mean flight date indicates the average date of abundance of locally produced individuals during the sampling period.

### Climate data

A meteorological station owned by the Instituto Nacional de Meteorología has provided weather data from El Cortalet since 1984. This station is located at the beginning of the butterfly transect and therefore gives a very precise estimation of the weather experienced by the butterflies.

Between 1984 and 2002, the average yearly temperature and precipitation were 15.2 °C and 624 mm, respectively. These figures fall well within the typical average found in the northwestern Mediterranean region (Grove & Rackham, 2001). The butterfly recording period included an exceptionally hot year (1994, with a mean summer temperature of 23.7 °C, 1.34 °C more than the average excluding that year) and a 5-year period of severe drought (1997–2001, with an average yearly rainfall of only 499 mm).

### Statistical analyses

Trends over time in first appearance, mean flight dates and SD were examined using regression with year as an explanatory variable. The number of advanced or delayed weeks for each phenophase (or the increase or decrease in the number of weeks, for SD) and species were calculated from linear regressions with time, as the difference between the timing of flight-period parameters at the onset and the end of the study. As a complement of the previous analysis, a two-tailed binomial test was used to check for a random distribution in the signs of regressions (whether significant or not), under the assumption that if there was no consistent change in phenology with time an equal number of positive and negative regressions would be expected. The relationships between phenological parameters were examined using correlation coefficients.

We also used the number of weeks of departure from the average phenophase date per species to calculate linear annual trends in a standardized way for all species together. The regression models were conducted with average values, and, therefore, with values having known associated variance. Thus, a model II regression was chosen (Coleman *et al.*, 1994) and the reduced major axis method was employed (Sokal & Rohlf, 1995).

ANOVA and Tukey–Kramer *post hoc* tests were subsequently conducted with the changes in phenophase timing as dependent variables and different ecological attributes of the butterfly species as independent variables (Table 1). Ecological attributes included taxonomic affiliation (to the family/subfamily level), voltinism (uni-, bi- or multivoltines), overwintering

stage (egg, larva, pupa, adult or non-existent), hostplant use (grasses vs. herbs) and migratory behaviour (sedentary, non-directional migrants, directional migrants).

Finally, a correlation analysis was conducted between the temperature and rainfall in previous months (of the current year) and the phenophase date. Both single months or subsets of months were entered as explanatory variables, and final models included only those combinations explaining most of the variance of the dependent variable.

## Results

### Temporal trends in temperature and rainfall

Between 1984 and 2002, the mean annual temperature and rainfall did not show any significant statistical trend in our study area (Fig. 2a). However, significant trends over time were found for temperature when the analyses were restricted to individual months (Fig. 2b). February, March and June have become warmer in the area during the last two decades, while November has become colder. No such trend was found for monthly rainfall.

### Temporal trends in butterfly phenology

Between 1988 and 2002, 5 out of 16 species showed significant advances of 1–7 weeks in their first appearance date (Fig. 3a; Table 1; excluding the migrant *C. cardui*, whose flight period was composed by non-locally bred individuals). For the remaining 11 species, the relationships between the first appearance date and years were also negative. Overall, the proportion between negative and positive regressions indicated a real tendency for earlier appearance in later years (binomial test, 16 negative regressions vs. 0 positive regressions,  $P < 0.0001$ ). The mean flight date advanced significantly for 1–5 weeks in 8 out of 18 species (Fig. 3b; Table 1). Again, the proportion between negative and positive regressions (16 vs. 2) strongly differed from the equality (binomial test,  $P < 0.001$ ). SD increased significantly for about 1.5 weeks in three cases, and diminished in nearly one week in one case (Table 1). Eight regressions were positive, and three were negative (binomial test,  $P = 0.08$ ).

First appearance and mean flight dates were positively correlated in all 17 species for which both measures could be calculated (Table 2). Both variables showed a strong relationship, as indicated by the high percentage of significant correlations (76% at  $P < 0.05$ ; 88% at  $P < 0.1$ ). SD showed different relationships with the other two variables. While it was strongly and

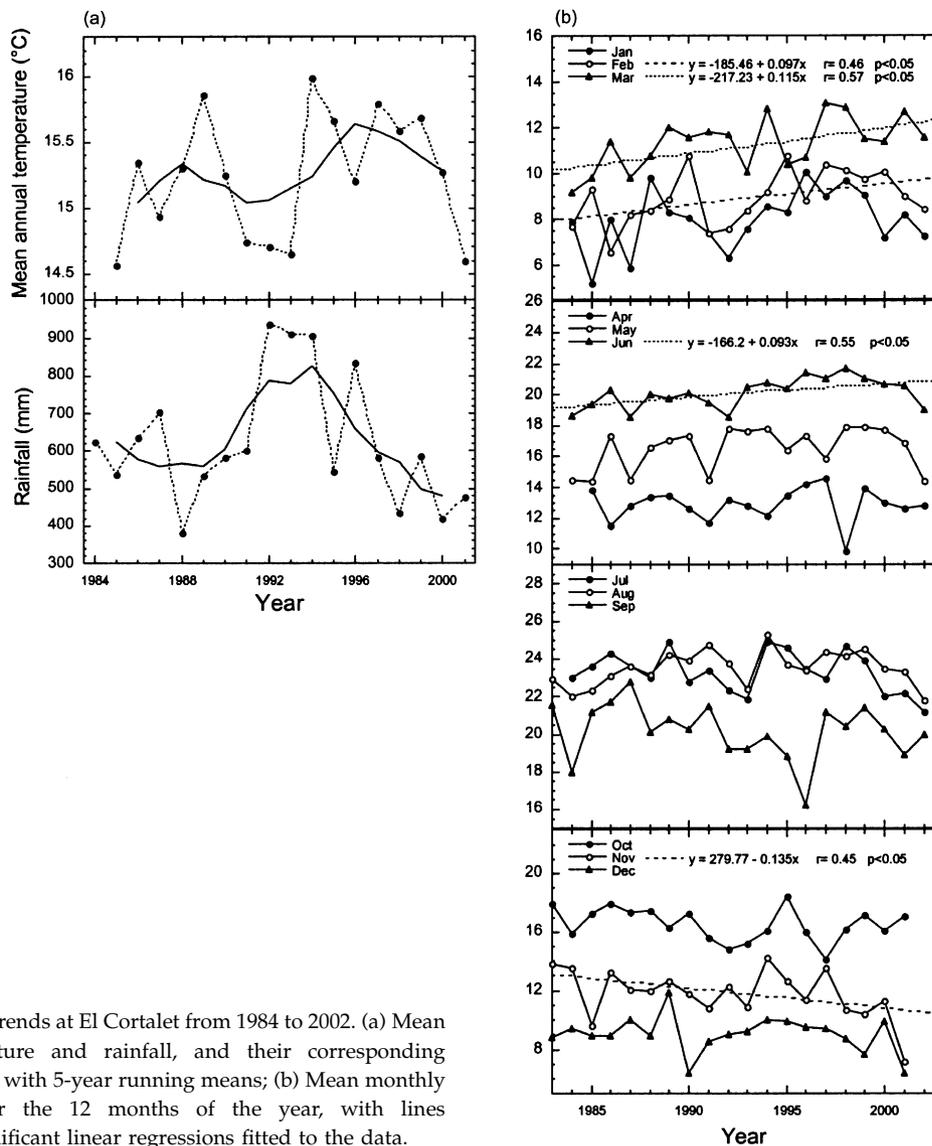


Fig. 2 Climate trends at El Cortalet from 1984 to 2002. (a) Mean annual temperature and rainfall, and their corresponding smoothed curves with 5-year running means; (b) Mean monthly temperatures for the 12 months of the year, with lines representing significant linear regressions fitted to the data.

negatively correlated with the first appearance date, no clear pattern was found with the peak of abundance date (Table 2).

The overall linear annual trends for each phenophase, combined for all species, are shown in Fig. 4. Linear regressions were highly significant for both first appearance and mean flight dates ( $P < 0.01$ ), indicating advances of 2.23 weeks and 1.5 weeks, respectively, in the last 15 years. A slight but significant ( $P < 0.05$ ) increase of 0.53 weeks in SD was also found.

#### *Differences in trends associated with ecological attributes*

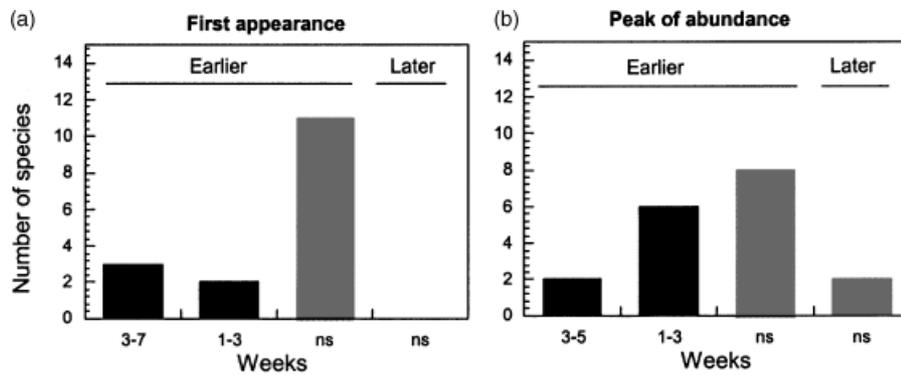
Significant differences in phenological trends among ecological groups were only found for mean flight date

in comparisons based on taxonomic affiliation and hostplant-use (Fig. 5). No significant differences were found to depend on voltinism, overwintering stage or migratory behaviour. It has to be noted, however, that several categories were represented by very few species and, thus, the power of the tests was much reduced.

Satyrinae species showed stronger advances than Pieridae, Nymphalinae and Hesperidae, but not more so than Lycaenidae. Also, species feeding on grasses showed stronger responses than those feeding on herbs (Fig. 5 and Table 1).

#### *Relationships with weather*

A summary of the regression models relating first appearance and mean flight dates to temperature and



**Fig. 3** Phenological changes in butterflies at El Cortalet from 1988 to 2002. The frequency distribution of the species with advancing and delaying trends in phenophases. (a) First appearance dates for 16 species; (b) mean flight dates for 18 species. Significant trends ( $P < 0.05$ ) are shown in black for advances; non-significant in grey.

**Table 2** Correlation coefficients between the studied phenological variables (first appearance date, mean flight date, standard deviation (SD) about this latter date) for the 19 butterfly species included in the analyses

Species	First appearance date-mean flight date	First appearance date-SD	Mean flight date-SD
<i>Pieris brassicae</i>	0.08(NS)	–	–
<i>Pieris rapae</i>	–	–	–
<i>Pieris napi</i>	–	–	–
<i>Colias crocea</i>	<b>0.54*</b>	<b>–0.83****</b>	0.00 (NS)
<i>Lycaena phlaeas</i>	0.17(NS)	–	–
<i>Leptotes pirithous</i>	<b>0.64***</b>	–	–
<i>Celastrina argiolus</i>	<b>0.50*</b>	–	–
<i>Plebejus argus</i>	<b>0.85****</b>	<b>–0.77****</b>	–0.04 (NS)
<i>Polyommatus icarus</i>	<b>0.74***</b>	<b>–0.86****</b>	–0.37 (NS)
<i>Cynthia cardui</i>	<b>0.57**</b>	<b>–0.86****</b>	–0.25 (NS)
<i>Polygonia c-album</i>	<b>0.53**</b>	–	–
<i>Melanargia lachesis</i>	<b>0.65**</b>	0.30 (NS)	<b>0.70***</b>
<i>Pyronia tithonus</i>	<b>0.56**</b>	<b>–0.85***</b>	<b>–0.74***</b>
<i>Pyronia cecilia</i>	<b>0.75***</b>	–0.35 (NS)	0.09 (NS)
<i>Coenonympha pamphilus</i>	<b>0.74***</b>	<b>–0.79***</b>	<b>–0.55**</b>
<i>Lasiommata megera</i>	<b>0.88***</b>	<b>–0.72**</b>	–0.34 (NS)
<i>Carcharodus alceae</i>	<b>0.74**</b>	<b>–0.74**</b>	–0.13 (NS)
<i>Thymelicus acteon</i>	<b>0.53*</b>	–0.34 (NS)	0.29 (NS)
<i>Ochlodes venata</i>	<b>0.73**</b>	<b>–0.77***</b>	–0.27 (NS)

Significant correlations are highlighted in bold type.

\* $P < 0.1$ ; \*\* $P < 0.05$ ; \*\*\* $P < 0.01$ ; \*\*\*\* $P < 0.001$ ; –: not available; NS: not significant.

precipitation data is presented in Table 3. Temperature appeared in most regressions, almost always with a negative influence (that is, higher temperatures tended to produce advances in the flight-period). February and March temperatures (i.e. those corresponding to the months preceding the flying dates in most first generations) were the most important in explaining the variance in phenology. April and June temperatures also had a strong influence in determining the appearance dates in several species.

Precipitation usually had an opposite effect to temperature, high values tending to produce delays in the phenology. Again, February was the most influential month, followed by May, January and March.

Weather variables were also correlated with the variation in SD in some cases, but not in a consistent manner (Table 3). For instance, high temperatures tended to produce longer flight periods in some species, but shorter in others.

Discussion

The climatological data from the studied site in NE Spain indicate that temperature has increased signifi-

cantly in February, March and June and decreased significantly in November over the last two decades, while precipitation has experienced no change. Recorded changes in temperature have been in the order of 2 °C. In spite of some divergences associated with the regional heterogeneity of climate data (IPCC, 2001), our findings are in accordance with an earlier analysis showing recent climate warming in the Mediterranean Basin (Jones *et al.*, 1999).

According to current knowledge, advances in the timing of butterfly emergence would be expected under this scenario (cf. Roy & Sparks, 2000). The existence of a 15 yr data series from the study site of the CBMS allowed us to test this prediction and confirm that, indeed, many butterfly species have significantly advanced their flight periods since 1988. For the whole butterfly community, this response can be summarized as an advance of 0.1 weeks per year in the adults' mean flight date.

Furthermore, the correlation analyses indicated significant negative relationships between flight-period parameters and the temperature of preceding months (i.e. higher temperatures tending to produce advances in the flight-period), particularly February and March. This result was predictable if we take into account the strong dependence of development rates of immature insects on temperature (Ratte, 1985), and the fact that postdiapause growth and development occurs by the end of winter and early spring in most of the studied species. We also found a frequent positive relationship between flight-period dates and precipitation in February and May. In this case, the most plausible explanation is an indirect relationship with temperature since rainfall has a negative effect on daily temperatures (and, thus, on larval and pupal development), through the reduction of insolation levels associated with cloudy skies. Evidence in favour of this explanation was given by the negative correlation between temperature and precipitation for both February ( $r_p = -0.548$ ,  $p = 0.018$ ,  $n = 18$ ) and May ( $r_p = -0.530$ ,  $p = 0.024$ ,  $n = 18$ ).

Besides a general advance in the flight period, the calculation of the SD of the mean flight date allowed us

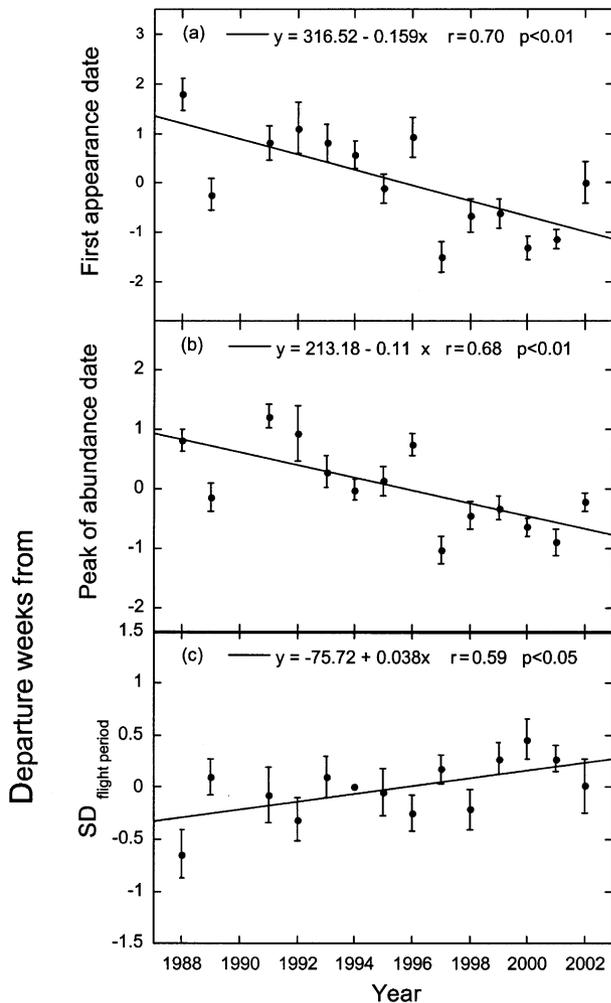


Fig. 4 Temporal trends of (a) first appearance date, (b) mean flight date, and (c) standard deviation of the flight period for all the studied butterflies. Data have been reduced to a single mean value per year, and used in the calculation of a model II regression (see text).

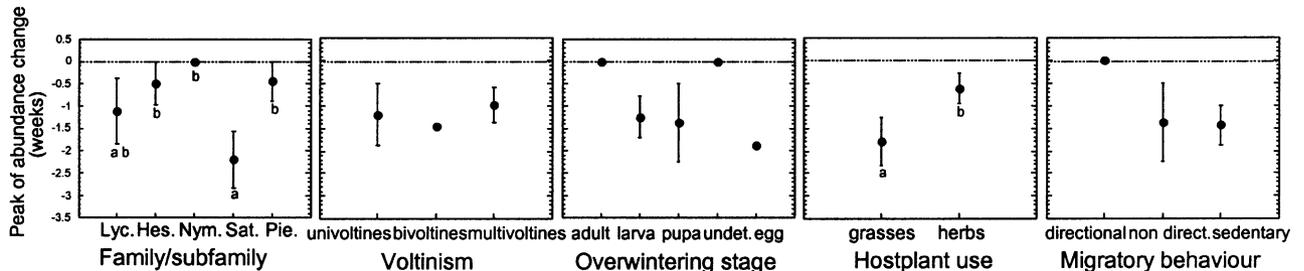


Fig. 5 Mean values of changes in peak of abundance date for groups of species showing different ecological attributes. Bars are standard errors ( $n$  in Table 1). Different letters refer to significant differences ( $P < 0.05$ , Tukey/Kramer *post hoc* tests) among groups.

**Table 3** Most correlated climate variables with first appearance date, peak of abundance date and standard deviation about this later date (SD of flight period) for each species included in the analysis; correlation coefficients and their significance are also indicated

Species	<i>n</i>		First appearance date			Mean flight date			SD of flight period		
			Most correlated variable	<i>r</i>	<i>p</i>	Most correlated variable	<i>r</i>	<i>p</i>	Most correlated variable	<i>r</i>	<i>p</i>
<i>Pieris brassicae</i>	14	Temperature	TFeb–Mar	–0.73	0.002	–	–	–	–	–	–
		Precipitation	–	–	–	–	–	–	–	–	–
<i>Pieris rapae</i>	14	Temperature	–	–	–	TMar	–0.67	0.007	–	–	–
		Precipitation	–	–	–	PMar	0.54	0.048	–	–	–
<i>Pieris napi</i>	14	Temperature	–	–	–	TFeb–Mar	–0.78	0.0006	–	–	–
		Precipitation	–	–	–	PMar	0.65	0.011	–	–	–
<i>Colias crocea</i>	14	Temperature	–	–	–	TFeb	–0.57	0.041	TJan	–0.52	0.067
		Precipitation	–	–	–	PJan–Feb	0.58	0.038	–	–	–
<i>Lycaena phlaeas</i>	11	Temperature	–	–	–	TFeb–Apr	0.77	0.004	–	–	–
		Precipitation	–	–	–	PFeb	–0.69	0.016	–	–	–
<i>Leptotes pirithous</i>	14	Temperature	TJun	–0.82	0.0001	TJun	–0.67	0.007	–	–	–
		Precipitation	PMay	0.72	0.003	PMay	0.65	0.011	–	–	–
<i>Celastrina argiolus</i>	14	Temperature	TFeb–Apr	–0.54	0.045	TJun	–0.51	0.059	–	–	–
		Precipitation	–	–	–	PJun	0.53	0.049	–	–	–
<i>Plebejus argus</i>	8	Temperature	TFeb–Mar	–0.70	0.036	–	–	–	TMay–Jun	0.76	0.015
		Precipitation	–	–	–	–	–	–	PApr	–0.63	0.072
<i>Polyommatus icarus</i>	12	Temperature	–	–	–	TFeb–Apr	–0.73	0.005	TJan	–0.52	0.087
		Precipitation	–	–	–	PFeb	0.53	0.079	–	–	–
<i>Polygonia c-album</i>	14	Temperature	–	–	–	TFeb–Mar	–0.71	0.003	–	–	–
		Precipitation	–	–	–	PMar	0.56	0.036	–	–	–
<i>Melanargia lachesis</i>	14	Temperature	TFeb–Mar	–0.60	0.022	TFeb–Apr	–0.68	0.006	TFeb–Apr	–0.57	0.034
		Precipitation	–	–	–	–	–	–	–	–	–
<i>Pyronia tithonus</i>	14	Temperature	TApr	–0.50	–	–	–	–	TFeb–Apr	0.55	0.039
		Precipitation	–	–	–	–	–	–	PFeb	–0.54	0.046
<i>Pyronia cecilia</i>	14	Temperature	TFeb–Mar	–0.54	0.043	TMar	–0.59	0.026	TJul	0.58	0.046
		Precipitation	PMay	0.53	0.051	PMay	0.48	0.085	PApr	0.55	0.067
<i>Coenonympha pamphilus</i>	14	Temperature	TFeb–Mar	–0.86	<0.0001	TFeb	–0.71	0.003	TFeb–Mar	0.76	0.001
		Precipitation	PFeb	0.56	0.036	PFeb	0.73	0.002	–	–	–
<i>Lasiommata megera</i>	13	Temperature	TFeb–Mar	–0.51	0.076	TFeb	–0.72	0.004	–	–	–
		Precipitation	–	–	–	–	–	–	–	–	–
<i>Carcharodus alceae</i>	10	Temperature	–	–	–	–	–	–	TJan	–0.71	0.018
		Precipitation	PFeb	0.68	0.028	–	–	–	PFeb	–0.61	0.062
<i>Thymelicus acteon</i>	14	Temperature	TFeb	–0.61	0.019	–	–	–	TJan	0.51	0.064
		Precipitation	PJan–Feb	0.53	0.053	–	–	–	–	–	–
<i>Ochlodes venata</i>	14	Temperature	TMar	–0.58	0.028	TFeb–Apr	–0.68	0.006	TMay	–0.50	0.066
		Precipitation	–	–	–	–	–	–	–	–	–

–: no significantly correlated climate variable.

to test for the possible changes in the shape of the curves of adult emergence. Most species showed non-significant responses, however, and in only two cases did a significant advance in the mean flight date coincide with a significant change in SD. While in *Melanargia lachesis* this was a decrease, indicating a tendency for a more synchronized emergence, in *Coenonympha pamphilus* the opposite trend was found.

Apparently, this result is not in agreement with the general lengthening and the more asymmetrical flight periods reported by Roy & Sparks (2000) for British butterflies. However, the strongly negative correlation that we found between the first appearance date and SD, together with the general pattern of earlier flight periods, suggests a tendency for less synchronized emergences that may have remained undetected

because the available time series are still too short. This tendency was further confirmed by a slight, but significant, overall linear annual trend in species for the increase of SD.

Albeit based on a limited dataset, our results suggest that phenological responses may differ between taxonomic lineages. In particular, Satyrinae species showed the strongest advance in the flight period in comparison with other taxonomic groups (but the difference was not significant when compared with the Lycaenidae). However, this may reflect instead the major effect of a confounding factor, namely the larval hostplant, which differentiates the Satyrinae and two species of Hesperiiidae, whose larvae feed on grasses, from the rest of the species (whose larvae feed on herbs). On the contrary, other ecological traits that might have seemed influential (e.g. the overwintering stage and the voltinism; Dennis, 1993) were apparently unimportant. Further analysis of more datasets, together with laboratory experiments, will be necessary to identify the roles played by each of the factors considered.

It is broadly accepted that changes in the timing of flight periods may have important consequences on species' population abundances, through alterations of phenological patterns and disruptions in the synchrony of plant–insect or host–parasitoid interactions (e.g. Hassell *et al.*, 1993; Visser & Holleman, 2001). Although in our study a few species have shown trends in population size (as measured by an annual index of relative abundance that correlates with absolute population estimates; see Pollard & Yates, 1993), these may have been mainly a consequence of changes in management practices at some parts of the transect route. Thus, significant increases in *Plebejus argus*, *C. pamphilus* and *Ochlodes venata* populations have coincided with the colonization of former arable crops that were converted to pasture meadows in the course of the recording period. On the other hand, a negative trend in *M. lachesis* and *Pyronia cecilia* may be attributable to severe population reductions following the increasingly wet conditions experienced by two dry meadows where the species were particularly common. We believe that, at least at the studied site and during this short period of 15 years, habitat changes related to management practices have been more influential for butterfly populations than phenological advances. In the long term, however, this last factor may play a fundamental role in some cases. In this respect, a varying degree of phenological flexibility may allow certain species, but not others, to undergo adaptive responses under the new conditions created by climatic warming. The ability to undergo such responses may prove essential for the survival of those populations subject to the most severe changes.

Our dataset included four univoltine species and 15 multivoltine species that strongly differ in their phenological flexibility. Thus, while the four single-brooded butterflies are characterized by a fixed phenological pattern (i.e. their voltinism remains invariable throughout their geographical distribution), latitudinal and altitudinal shifts in voltinism exist among most of the other species in response to varying climatological conditions.

For the four univoltine species included in our analysis, the first instar larva corresponds to the longest stage in the biological cycle. In the Mediterranean region, immediately after hatching in early or mid-summer, first-instar larvae enter an aestivation phase that is followed by an overwintering phase that lasts several months (E. García-Barros, personal communication). In this way, they not only reduce the risk of starvation when grasses are no longer suitable as larval food plants because of the summer drought but can also cope with the unfavourable winter season, in which temperatures are too low for larval activity and growth. An advance in the adult flight period means that eggs and larvae would appear earlier in the season, which, in turn, would lead to a lengthening of the larval aestivation period. Although no reliable information exists on this subject, it seems highly likely that this would impose progressively greater and detrimental mortality rates on populations. In this respect, two alternative phenologies shown by some of the most common univoltine Satyrinae inhabiting the Mediterranean Basin may have evolved to cope with high mortality experienced by young larvae aestivating for long periods: an arrested ovarian maturation coupled with total or partial adult summer inactivity that leads to a delay in the onset of oviposition, and an aestivation phase in the egg stage (García-Barros, 1988, 2000). Both strategies enable these species to reduce greatly how much of the period of summer drought is spent as a first instar larva, and predominate in those areas subject to more severe Mediterranean climates.

Contrasting with previous species, the rest of the butterflies analysed in this paper are potentially multivoltine (Tolman & Lewington, 1997) and all have more than one brood per season at the study site. Moreover, in common with many other European multivoltine butterflies (e.g. Nylin *et al.*, 1993), they show an increase in the number of broods from northern to southern latitudes (and from high altitudes to lower ones) as ambient temperatures promoting larval and pupal development become less of a limiting factor. In the northwest Mediterranean Basin, the existence of two moderated adverse periods (i.e. the cool winter and the dry summer) prevents a continuously multivoltine cycle and means that development is usually comple-

tely arrested during part of the season (E. García-Barros, personal communication; see also Yela & Herrera, 1993, for a paper dealing with Noctuid moths). Even in this case, the multivoltine cycle in this region is always completed and, depending on the species and such factors as the larval hostplant's phenology and nutritional value, consists of 2–5 generations (cf. Materials and methods).

Therefore, in the study area, a forward shift in the first brood of potentially multivoltine species would not lead to an increase in the frequency with which multivoltinism occurs, as predicted by Roy & Sparks (2000) for British butterflies. However, it may result in a further advance of subsequent generations (as shown for *C. argiolus* in this paper) and, eventually, in an increase in the number of generations per year (Yamamura & Kiritani, 1998). In multivoltine species, this is one of the most important factors affecting population abundance, even though the complexity of the interactions with other species means that no reliable predictions can be made about the nature of population changes (e.g. Davis *et al.*, 1998).

Predictions are further complicated by the fact that changes other than an increase of ambient temperature are expected to occur in the Mediterranean Basin under climatic warming. For instance, climate models point to a very likely increase in precipitation variability (Easterling *et al.*, 2000), a factor which has recently been shown to hasten population extinctions in a Californian butterfly (McLaughlin *et al.*, 2002). Also, because significant changes in rainfall have not been observed so far in the Mediterranean Basin, it is generally recognized that the region will become more arid in the future due to increased potential evapotranspiration rates (Piñol *et al.*, 1998). Most likely, the increasingly adverse conditions (i.e. a longer and drier summer period) will interfere with a multivoltine cycle and impose a strong selection on some broods and favour local seasonal adaptations such as diapause or dormancy phenomena (see Held & Spieth, 1999, for an example concerning *P. brassicae* in southern Spain) or migratory behaviour (e.g. Shapiro, 1980; Dingle *et al.*, 2000). Alternatively, severe declines or even extinctions may be the most likely outcome if climatic change occurs too fast or if the amount of genetic variability is not great enough to allow these evolutionary changes to occur.

In conclusion, together with other recent studies (Peñuelas *et al.*, 2002), the present work demonstrates that changes in the timing of biological events as a consequence of climatic warming are not limited to northern latitudes, but are also taking place at a fast rate in the Mediterranean Basin. Moreover, in agreement with the findings of Peñuelas *et al.* (2002), it shows that

species representing a wide range of phenological patterns are being affected, and, also, that the strength of the responses varies widely according to species.

Although this makes it difficult to predict the outcome of increasing temperatures on butterfly communities, further comparative analyses based on the abundant phenological data provided by both the CBMS and other European Butterfly Monitoring Schemes would reveal some regular patterns in this popular group of indicators of climatic change.

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