

Climatic trends and advancing spring flight of butterflies in lowland California

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Abstract

Many studies, largely from cool-temperate latitudes, have investigated the relationship between the timing of biological events and changes in climatic conditions during the past few decades. Relatively little is known about the response of plants and animals at lower latitudes. Here we show that the average first spring flight of 23 butterfly species in the Central Valley of California has advanced to an earlier date over the past 31 years. Among the species that have appeared significantly earlier, the average shift is 24 days. Climatic conditions (largely winter temperature and precipitation) are found to explain a large part of the variation in changing date of first flight. These results suggest a strong ecological influence of changing climatic conditions on a suite of animals from a mid-latitude, Mediterranean climate.

Keywords: butterflies, climate change, emergence, overwintering, phenology

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Introduction

Many published studies on the ecology of climate change, particularly those involving large suites of terrestrial plants and animals, are from cool-temperate latitudes (Sparks & Carey, 1995; Ellis *et al.*, 1997; Crick & Sparks, 1999; Hofgaard *et al.*, 1999; Post & Stenseth, 1999; Roy & Sparks, 2000; Roy *et al.*, 2001; Warren *et al.*, 2001; Fitter & Fitter, 2002; Walther *et al.*, 2002). Organisms at high latitudes, such as Scandinavia and the British Isles, are often near the northern limit of their geographical ranges, where slight changes in climate can have dramatic biological influence (Thomas *et al.*, 1994; Root *et al.*, 2003), including range expansion or contraction and the altered timing of ecological phenomena (Parmesan *et al.*, 1999; Walther *et al.*, 2002; Parmesan & Yohe, 2003). While climatic conditions appear to be changing globally (IPCC, 2001), we know comparatively little about the response of biota at lower latitudes, where very different patterns of seasonality may produce different biological effects. A few studies of large groups of plants and animals have recently been published from lower latitudes (Pounds *et al.*, 1999; Peñuelas *et al.*, 2002),

but more examples are needed before we can understand the global impact of changing climatic conditions (Root *et al.*, 2003).

In this study, we present an analysis of the phenology of a group of butterflies from the mid-latitude, Mediterranean climate of lowland California (characterized by hot, dry summers and wet, mild winters). Butterflies are highly sensitive to changing abiotic conditions (Pollard, 1988; Dennis, 1993), and their ubiquity in ecological studies facilitates comparisons among disparate geographical regions. Our objectives in the present study are: (i) to document trends in the dates of first spring appearance of 23 butterfly species over 31 years, (ii) to analyze the relationship between climatic conditions and butterfly appearance, (iii) to examine specific differences in butterfly appearance and how they relate to differences in life history traits, and (iv) in conclusion, we compare our results to other phenological studies from different regions.

Materials and methods

Butterfly monitoring and weather data

The date of first spring flight of 23 butterfly species was recorded in the Central Valley portions of three counties in Northern California (Yolo, Sacramento, and Solano, all

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below 65 m elevation) for 31 years by one of us (A.M.S). The date of first flight (DFF) refers to the date that the first adult of a species is observed in the field in a given calendar year. A.M.S. has three permanent sites within the study area, which are visited only during 'good butterfly weather' at roughly two-week intervals all year, as well as two sites, which are visited at three- to four-day intervals only in late winter and spring. Most of the data are generated by visits to these five sites, but if a given species is observed elsewhere within the study area before it is seen at one of the five sites, that data is used as well. Fewer than 10% of the dates considered in this study have resulted from such casual observations, and they are scattered haphazardly across the 31 years of record. The probability of seeing a given species on a given day at a given place is related to its abundance. However, this is a problem which affects all phenological studies and which we are unable to address here.

Weather data were obtained from the University of California/National Oceanic and Atmospheric Administration climate station in Davis, California: 38 32 07N, 121 46 30 W, elevation 18.29 m (a World Meteorological Organization station centrally located to our study sites).

Analyses

Temporal trends in DFF were analyzed first for each species individually, and then for all species collectively (to ask if the biota as a whole has been appearing earlier through time). Individual analyses, with year as the explanatory variable and DFF as the response, are presented in Table 1. The collective analyses of trends in appearance dates (Fig. 1) is based on rank transformed data (Conover & Iman, 1981; Zar, 1999). Within each species, the DFF were ranked from 1 to 31, with the earliest year receiving the rank of one, and so on. Rank transformation is an effective way of removing variation due to species-specific differences in DFF, and facilitates a collective analysis of the fauna.

For our analysis of climatic factors and changing DFF, 12 weather variables were considered: total precipitation, average daily maximum temperature, and average daily minimum temperature for winter and spring of the year in question, and summer and fall of the previous year. Because they were highly correlated with other weather variables, four weather variables were excluded from further analyses (a correlation of greater than 0.50 was used as a threshold for exclusion): summer minimum temperature, winter minimum temperature, spring minimum temperature and spring precipitation. Summer minimum temperature was correlated with summer maximum temperature (Pearson correlation = 0.51), winter minimum temperature was correlated with winter maximum temperatures (0.74), and both spring minimum

temperature and spring precipitation were correlated with spring maximum temperature (0.74 and 0.63, respectively). In all cases where variables were highly correlated with each other, we have retained the variable that was most highly correlated with mean DFF. The remaining eight weather variables were used in stepwise multiple regression models, both for each species individually (Table 1) and for the biota as a whole, using mean, rank DFF as the response variable. All data entering multiple regression models (DFF and weather variables) were detrended using first-order differencing, a process which reduces the likelihood of inferring spurious relationships produced by similar but unrelated long-term trends by comparing interannual differences in data (Box & Jenkins, 1976).

In investigating the relationship between the seasonal order of appearance of the butterfly species and their tendency to appear earlier over the 31 years, we have used Spearman's nonparametric rank correlation calculated for two sets of values. The first is the average order that a species emerges in any year (i.e. a value of five indicates that a species is on average the fifth butterfly to be seen in a year). The second is Spearman's rank correlation calculated independently for each species between emergence date and years (used as an index of behaviour over 31 years, with larger negative values corresponding to species that have shifted their DFF to an earlier date). Nonparametric correlations are appropriate for these interspecific comparisons because they make no assumptions about the equivalency of behaviour among species that emerge at different times of the year under different seasonal conditions. Similarly, the relationship between mode of overwintering and tendency to appear earlier was tested with a Kruskal-Wallis nonparametric analysis with two modes of overwintering as categories (larvae and pupae) and Spearman's rank correlation for each species (described above) as the response. All statistics were done with both JMP IN 4.0.2 (SAS Institute, 2001) and SYSTAT 9 (SPSS, 1999) software.

Results and discussion

Temporal trends

The mean DFF for the entire fauna has been shifting towards an earlier date over the course of the past 31 years (Fig. 1). Sixteen species (70% of the total fauna) show a trend toward earlier appearance when DFF is regressed on years; four of these regressions are significant ($P < 0.05$) (Table 1). Seven species (30%) show the opposite trend, later appearance; none of these regressions are significant (Table 1). The distribution of species-specific responses (with the majority of species showing significant or nonsignificant tendencies to appear earlier

Table 1 Behaviour of 23 species over 31 years: trends in date of first flight (DFF) through time and relationship of DFF to weather variables

Species	Trends over time in DFF				Relation of weather to DFF			
	Slope	R ²	F _{df}	P	Terms	R ²	F _{df}	P
Hesperiidae								
<i>Atalopedes campestris</i> P,21	-0.88	0.28	11.18 _{1,29}	< 0.01	6 ⁻ ,7 ⁺	0.49	15.01 _{2,27}	< 0.001
<i>Erynnis tristis</i> L,18	0.34	0.02	0.61 _{1,29}	0.44	6 ⁻ ,7 ⁺	0.22	5.10 _{2,27}	0.01
<i>Hylephila phyleus</i> P,19	-0.36	0.06	1.73 _{1,29}	0.20	6 ⁻ ,2 ⁺	0.40	10.71 _{2,27}	< 0.001
<i>Pholisora catullus</i> L,15	0.52	0.11	3.51 _{1,29}	0.07	6 ⁻ ,7 ⁺	0.39	10.24 _{2,27}	< 0.001
<i>Polites sabuleti</i> P,20	-0.46	0.10	3.01 _{1,29}	0.10	6 ⁻ ,3 ⁻	0.55	18.71 _{2,27}	< 0.001
<i>Pyrgus communis</i> L,14	-0.52	0.08	2.65 _{1,29}	0.11	6 ⁻ ,8 ⁻ ,7 ⁺	0.61	16.12 _{3,26}	< 0.001
<i>Pyrgus scriptura</i> P,8	-0.62	0.23	8.62 _{1,29}	0.01	6 ⁻ ,7 ⁺ ,1 ⁻ ,2 ⁺	0.79	27.61 _{4,25}	< 0.001
Lycaenidae								
<i>Everes comyntas</i> L,12	0.22	0.02	0.70 _{1,29}	0.41	6 ⁻ ,7 ⁺ ,2 ⁺	0.40	7.47 _{3,26}	< 0.001
<i>Lycaena helloides</i> E,23	0.87	0.10	3.12 _{1,29}	0.09	6 ⁻ ,7 ⁺	0.21	4.89 _{2,27}	0.02
<i>Plebejus acmon</i> L,17	0.27	0.01	0.29 _{1,29}	0.60	7 ⁺ ,6 ⁻ ,2 ⁺	0.73	23.89 _{3,26}	< 0.001
<i>Strymon melinus</i> P,6	-0.18	0.03	0.78 _{1,29}	0.38	6 ⁻ ,8 ⁺ ,3 ⁺ ,7 ⁺	0.28	3.84 _{4,25}	0.01
Nymphalidae								
<i>Danaus plexippus</i> I,13	0.51	0.05	1.53 _{1,29}	0.23	6 ⁻ ,2 ⁻	0.29	6.95 _{2,27}	< 0.01
<i>Nymphalis antiopa</i> A,4	-0.39	0.08	2.38 _{1,29}	0.13	1 ⁺ ,2 ⁺	0.24	5.22 _{2,25}	0.01
<i>Phyciodes campestris</i> L,22	0.14	< 0.01	0.05 _{1,29}	0.82	7 ⁺ ,8 ⁻ ,1 ⁺ ,3 ⁺ ,4 ⁻ ,5 ⁺	0.65	9.94 _{6,23}	< 0.001
<i>Phyciodes mylitta</i> L,10	-0.40	0.05	1.59 _{1,29}	0.22	7 ⁺ ,1 ⁺ ,6 ⁻ ,3 ⁺	0.65	14.32 _{4,25}	< 0.001
<i>Vanessa annabella</i> A,1	-0.17	0.01	0.26 _{1,29}	0.61	3 ⁻ ,4 ⁻	0.28	6.23 _{2,25}	0.01
<i>Vanessa atalanta</i> A,3	-0.91	0.16	5.25 _{1,29}	0.03	None			
<i>Vanessa cardui</i> I,9	-0.05	< 0.01	0.01 _{1,29}	0.92	2 ⁺ ,1 ⁺ ,4 ⁻ ,7 ⁺	0.49	8.06 _{4,25}	< 0.001
Pieridae								
<i>Colias eurytheme</i> L,5	-0.72	0.07	2.07 _{1,29}	0.16	6 ⁻ ,1 ⁺ ,3 ⁻	0.28	4.59 _{3,24}	0.01
<i>Euchloe ausonides</i> P,7	-0.15	0.02	0.51 _{1,29}	0.48	6 ⁻ ,2 ⁺	0.41	10.98 _{2,27}	< 0.001
<i>Pieris rapae</i> P,2	-0.63	0.20	6.68 _{1,29}	0.02	5 ⁻ ,7 ⁺ ,1 ⁺	0.36	4.22 _{3,23}	0.02
Papilionidae								
<i>Papilio rutulus</i> P,16	-0.16	0.02	0.49 _{1,29}	0.49	6 ⁻ ,4 ⁻ ,1 ⁺	0.58	14.60 _{3,26}	< 0.001
<i>Papilio zelicaon</i> P,11	-0.14	0.01	0.39 _{1,29}	0.54	6 ⁻ ,7 ⁺	0.41	11.08 _{2,27}	< 0.001

Subscripts after species names indicate mode of overwintering (A = adult, I = immigrant, E = egg, P = pupae, L = larvae), and average order of emergence within any one season. Slope, R², F, and P-values for trends over time represent the results of individual regressions of DFF vs years. Statistics reported for weather analyses are the results of multiple regressions of eight weather variables vs DFF (for multiple regression, both DFF and weather variables were detrended by first-order differencing). Terms are listed in the order in which they entered the model, negative and positive signs in superscript indicate the sign of the regression coefficient (legend for term numbers is presented below). Terms included in multiple regression analyses:

- 1 = average daily maximum temperature for summer preceding DFF
- 2 = total precipitation for summer preceding DFF
- 3 = average daily maximum temperature for fall preceding DFF
- 4 = average daily minimum temperature for fall preceding DFF
- 5 = total precipitation for fall preceding DFF
- 6 = average daily maximum temperature for winter of DFF
- 7 = total precipitation for winter of DFF
- 8 = average daily maximum temperature for spring of DFF.

over time) is significantly different from that which would be expected by chance ($\chi^2 = 81.41$, $P < 0.001$; Fisher's combination procedure compares the distribution of independently attained P-values with a χ^2 distribution (Sachs, 1982)).

Among the species that have been appearing earlier, two have shifted their DFF by approximately a month over the past 31 years (*Atalopedes campestris*, 27.28 days, and *Vanessa atalanta*, 28.21 days), and two have shifted their DFF by almost three weeks (*Pyrgus scriptura*,

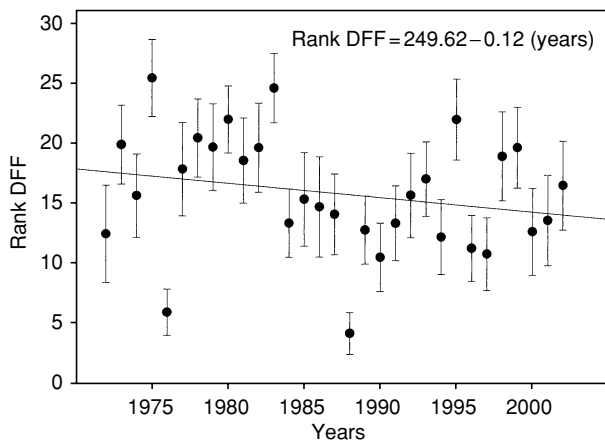


Fig. 1 Dates of first flight (DFF) for 23 butterfly species for the years 1972–2002. The average DFF has been shifting to an earlier date over the course of the 31 years ($F_{1,705} = 10.03$, $P = 0.002$, $R^2 = 0.01$). Dates were standardized by rank transformation within each species. For example, a mean value of 10 on the y -axis for a given year indicates that that year was on average ranked 10th earliest within each of the butterflies for 31 years. Error bars represent 95% confidence intervals.

19.22 days, and *Pieris rapae*, 19.53 days) (phenological shifts for individual species were calculated by multiplying the slopes of the regressions of DFF vs years (from Table 1) by 31 years). One of the species that has responded most dramatically, *A. campestris*, has also been expanding the northern limit of its range in the western United States, and this expansion has been linked to warmer temperatures (Crozier, 2002).

Relationships with climate

All of North America has experienced warmer temperatures over the past 30 years (Waple *et al.*, 2002), and the Central Valley of California has been getting hotter and drier over the same period (EPA, 1997). We have analyzed 31 years of weather data from a weather station in Davis, California, and found no trend in annual precipitation, but a significant increase in both annual daily maximum temperatures ($F_{1,29} = 7.74$, $P = 0.01$), and annual daily minimum temperatures ($F_{1,29} = 7.40$, $P = 0.01$). Annual maximum temperatures in the region of our study sites have been going up by 0.04°C per year (1.24 degrees in 31 years), and annual minimum temperatures have been increasing by 0.03°C per year (0.93 degrees in 31 years).

To investigate the role of climate in the changing mean DFF in California, we have used weather data from the Davis weather station in a stepwise multiple regression model that explains 83.6% of the variation in mean DFF ($F_{4,25} = 37.84$, $P < 0.0001$) (Sokal & Rohlf, 1997). Four variables were retained in the model (numbers following

model terms represent the contribution of that variable to the total R^2): average winter daily maximum temperature (0.62), total winter precipitation (0.18), average summer daily maximum temperature (0.02), and average daily fall minimum temperature (0.03) (the individual contributions do not sum exactly to 83.6%, which is the R^2 adjusted for the number of terms in the model – the unadjusted figure is 85%). Winter conditions, temperature and rainfall, made the greatest contribution to the multiple regression model. These results are consistent with the individual analyses presented in Table 1, in which the DFF for 15 of 23 species are most strongly associated with winter temperatures, and winter precipitation was either the first or second term to enter the model for 11 of 23 species.

Higher winter maximum temperatures and drier winter conditions are associated with earlier butterfly appearance (Fig. 2). Warmer temperatures advance larval growth and promote earlier adult emergence (Ratte, 1984). Rain can affect emergence in two ways, by being correlated with greater cloud cover and less insolation,

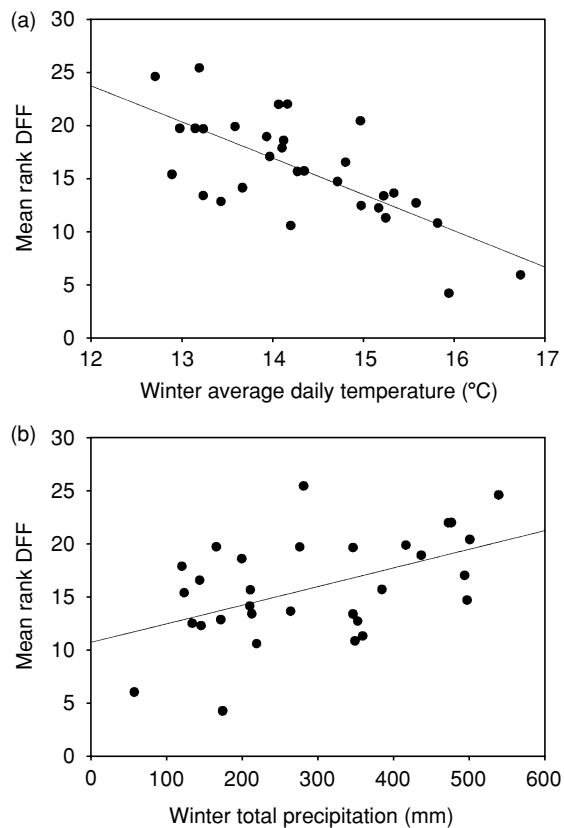


Fig. 2 Regressions of mean rank date of first flight (DFF) on weather variables. (a) Mean rank DFF vs winter average daily temperature ($F_{1,29} = 28.21$, $P < 0.0001$, $R^2 = 0.49$). (b) Mean rank DFF vs winter total precipitation ($F_{1,29} = 9.81$, $P = 0.004$, $R^2 = 0.25$).

and through the production of fog and low clouds that result from water that is held by the clay soils of the Central Valley for many days after a rain (leaving the air cold and damp even with afternoon clearing).

Species-specific patterns over time

Beyond documenting the pattern of shifting phenologies, it remains to be investigated why some species respond to a changing climate and some do not. We tested two hypotheses: (i) butterflies that fly earlier in the spring may be most sensitive to changing winter temperatures, (ii) the life history stage in which a species spends the winter (as larvae, pupae, etc.) may influence how it responds to changing temperatures. There is a nonsignificant, positive correlation between order of appearance (within any season) and changing DFF over 31 years (Spearman's rank correlation; 0.27, $P=0.21$) (Sokal & Rohlf, 1997). Though the relationship is nonsignificant, the correlation is in the predicted direction: early spring butterflies appear to make up the majority of those species that have exhibited a negative shift in their DFF (i.e. towards an earlier date over 31 years). Other studies have found that the timing of biological events that happen earlier in the year are more likely to change in response to changing temperatures (Bradley *et al.*, 1999; Post & Stenseth, 1999; Menzel *et al.*, 2001).

The butterflies in our study sites overwinter in different life history stages, as eggs (1 species), larvae (8 species), pupae (9 species), and adults (3 species); two more species immigrate in the spring from distant overwintering sites. We wished to test the hypothesis that mode of overwintering is related to change in DFF. Because three of the modes (eggs, adults, and immigrants) are represented each by a small number of species, we have excluded them and asked if pupae and larvae have behaved similarly over the 31 years. Butterflies that overwinter as pupae have tended to change their DFF more than those that spend the winter as larvae ($\chi^2=4.9$, $P=0.03$). Larvae that overwinter only feed posttorpor or postdiapause; prefeeding winter or early spring conditions cannot therefore accelerate metamorphosis since they are not yet growing. Species that overwinter as pupae generally do so in diapause. Postdiapause development in these species is temperature-dependent and tends to happen in a very narrow window. As a consequence, butterflies that overwinter as pupae may be more likely to be affected by winter or spring conditions.

Conclusion

Only one other study has been published in which long-term data from a Mediterranean climate (Cardedeu, Spain) are analyzed for phenological trends (Peñuelas

et al., 2002). Peñuelas *et al.* focus primarily on plants (the vast majority of which have responded to warming conditions), but discuss one butterfly (*P. rapae*), which has appeared 11.4 days earlier over the course of 48 years. *Pieris rapae* in our study sites in California has changed its DFF by 19.53 days. The results from our analyses are also consistent with studies that have focused on higher latitudes. Roy & Sparks (2000) found that 26 out of 35 species (74%) of butterflies in England show a trend towards earlier flight over the past 23 years (with 13 of those being significant). Like the fauna we examined, the phenology of the English butterflies is changing in varied ways, with some extreme changes. The largest advance in flight period of the English fauna was made by the same species that has shown the most change in California (*V. atalanta*), although the butterfly has different habits in the two places; in England it is a migrant that may occasionally overwinter (Asher *et al.*, 2001), while in California it primarily overwinters as an adult though may be considered an occasional migrant. In terms of the proportion of the fauna showing altered phenology, our results are also similar to those in a study of 385 English plant species, in which 76% showed a trend toward earlier flowering (Fitter & Fitter, 2002). Bradley *et al.* (1999) showed that 73% of spring events (including the first bloom of herbaceous plants and the arrival of migrating birds) in Wisconsin were happening earlier (in both the Wisconsin study and the English plant survey, not all the trends are significant).

Mediterranean climates are highly variable, with large fluctuations around means of temperature and precipitation. One might expect the fauna from such areas to be adapted to a variable climate, and hence unlikely to respond to relatively subtle annual trends in temperature and precipitation. Butterflies from higher latitudes, on the other hand, are often at the limits of their ranges (Heath *et al.*, 1984), and it is not surprising that even minor climatic changes at those range margins can have large impacts on the phenology and distribution of the fauna (Dennis, 1993; Roy *et al.*, 2001; Warren *et al.*, 2001). However, not only are the Central Valley butterflies responding to changing conditions, they are doing so in a way that is similar to butterflies from the more northern climate of England (Roy & Sparks, 2000). It is becoming increasingly clear that plants from disparate parts of the globe are responding in similar ways to warmer temperatures (Peñuelas & Filella, 2001), and the results presented here suggest that insects may be responding in a similarly universal manner.

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