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Complex phenological responses to climate warming trends? Lessons from history

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Abstract. Responsiveness of Lepidoptera phenology to climate has been detected in a number of species during the current trend in global warming. There is still a question of whether climate signals would be evident in historical data. In this paper we examine the climatic response of 155 species of moths and butterflies collected during the period 1866–1884 in Wiltshire, southern England. In general, species responded to increased temperature in the previous October by delayed appearance and to increased temperature in the current spring by advanced appearance. Thus, differential changes in temperatures of the autumn and spring could well affect changes in the relative pattern of the phenology of species. Attributes influencing the species' ecology were examined to see if they influenced temperature responsiveness. In general, few consistent effects emerged, though responsiveness to climate was found to be greater for species eclosing later in the year, specifically to the previous autumn temperatures, and to hibernal environment, increasingly for species less exposed to air temperatures. These findings warn against expecting simple responses to climate warming.

INTRODUCTION

Historical data can provide valuable evidence on the effects of temperature and other climate variables on the phenology of species, both plant and animal. For some species that have no current phenological monitoring, examination of past data is the only way we can understand the likely effects of climate change on the timing of their life cycles. Furthermore, historic data were collected at an enormous cost in time and money and it is highly desirable that these data are fully exploited.

Data on the phenology of Lepidoptera is largely restricted to butterflies (e.g. Roy & Sparks, 2000; Forister & Shapiro, 2003; Stefanescu et al., 2003; Dell et al., 2005) whilst that for moths is sparser (e.g. Kuchlein & Ellis, 1997; Burton & Sparks, 2003). These papers broadly suggest a recent advance in the appearance of adult Lepidoptera in conjunction with increased temperatures, and typically a greater advance in species appearing early in the year (e.g. Burton & Sparks, 2003). Kuchlein & Ellis (1997) reported on the changing phenology of 104 micromoths in the Netherlands and Burton & Sparks (2003) on 18 macromoths in southern Germany. Other studies have focussed on the phenology of single pest species such as gypsy moth *Lymantria dispar* (e.g. Regniere & Nealis, 2002) or codling moth *Cydia pomonella* (e.g. Boivin et al., 2005). Only one study has examined the phenological response of a large number of macromoths to temperature and other climatic variables. Woiwod (1997) studied 94 flight periods covering 58 moth species recorded by Rothamsted Insect Survey light traps having more than 20 individuals per year. Phenology was measured by calculating the date for five percentiles of individuals caught (5^{th}, 25^{th}, 50^{th}, 75^{th}, 95^{th}); 93 were significant, 88 negative (earlier) and 5 positive (later). All percentiles showed a significant tendency, based on the sign test, for advanced emergences. This result confirmed earlier work by Zhou et al. (1996) on aphid phenology using a similar technique. These data relate to the systematic current worldwide period of warming temperatures (Dennis, 1993; IPCC, 2001), experienced regionally in Britain as at Rothamsted (Woiwod, 1997); there are no observations, as far as we are aware, of climate signals in Lepidoptera phenology from large numbers of historic moth and butterfly data.

In this paper, we focus on the susceptibility of British moths and butterflies to climate change in an historical dataset preceding currently recognised warming trends. It is expected that conditions prior to emergence of adults will affect their timing of emergence. For instance, it is expected that higher temperatures and increased sunshine will advance emergence dates but that increased rainfall and cloud may retard emergence dates. An important issue is how far in advance of emergence dates are significant influences recorded; do climate influences impact on the period immediately prior to emergence, a month beforehand when Lepidoptera are passing through the final (pupal) stage, or are influences recorded for earlier periods, and therefore stages, as is the case with population numbers (Pollard & Yates, 1993)? Any responsiveness of phenology to climate is expected to be complicated by Lepidoptera biology: by the typical period of emergence (i.e. spring to autumn), voltinism or brood number each year, body size, hibernation stage and micro-environment, larval feeding environment (i.e. whether on low growing herbs or higher up on shrubs and trees) internally or externally on substrates. Susceptibility may also be related to edge of range, conservation status, migration capacity and ease of recording or recording

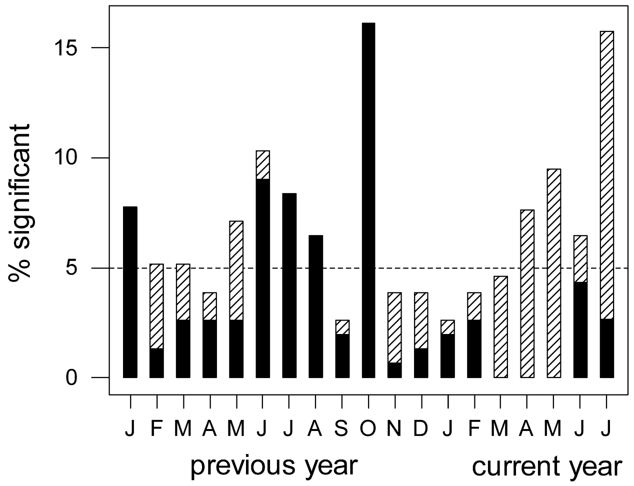

Fig. 1. Percentage of significant positive (solid bars) and negative (hatched bars) correlations between first appearance date of lepidopteran species and calendar monthly mean temperatures. The dotted line represents the 5% level of significant results expected by chance.

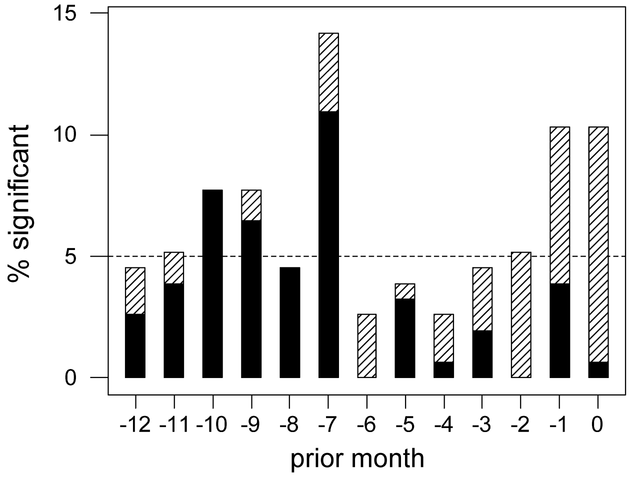

Fig. 2. As Fig. 1 except summarised by month prior to the mean date of each species.

methodology, i.e. whether day flying or night flying. In addition, indirect effects via host plant phenology may be important, such as plant development following previous year's rainfall, although beyond the scope of the current work.

Work on competitive, stress-tolerant and ruderal (CSR) strategies of larval host plants among British butterflies would suggest that responsiveness to climate changes is not unexpected (Dennis et al., 2004). As such, it is clearly of value to determine whether susceptibility to climate change links to biological attributes in moths and butterflies. The present dataset allows some links to be directly tested.

In this paper we examine the phenology of a large number of Lepidoptera species recorded in the second half of the nineteenth century, examine their responsiveness to temperature, and seek to answer the following questions:

– How far in advance of emergence do climate influences affect emergence dates?

– What aspects of a species' ecology influences its responsiveness to temperature [for example, later flying species may actually emerge later with increasing temperatures (Buse & Good, 1996; Woiwod, 1997)]?

MATERIAL AND METHODS

The Marlborough College Natural History Society (MCNHS) (51°25´N, 1°44´W) collected a vast amount of phenological data in the mid-nineteenth century and in 1885 privately published the first 19 years of its results. In this paper we focus on the first observations of appearance in 1866–1884 of Lepidoptera (moths and butterflies) because the phenology of moths, in particular, is rarely studied. Over 500 species of Lepidoptera are included in the MCNHS report. However, we have focussed on the 155 species (121 moths and 34 butterflies; Table 1) for which at least 10 years of data were present. We do not know exactly how these records were obtained but assume they were collected by members of the MCNHS with verification by TA Preston, founder of the MCNHS.

In the same report are summarised weather measurements taken at Marlborough. From these records we have abstracted monthly averages of mean air temperature and total rainfall and have converted these to metric scales.

In determining the impact of climate, we examined which months' temperatures and rainfall totals were most influential on first appearance patterns. We had anticipated that conditions during the latter stages of larval growth and pupal development would most likely affect development rates and timing of adult stages (Dell et al., 2005). For each species, we examined the correlation with the weather in the month in which its mean first appearance date occurred, and in the preceding months back to January of the previous year. Correlations were summarised in two ways, by calendar month and by month prior to the mean date of each species. The pattern of significant correlations with calendar monthly temperatures (Fig. 1) was similar to that of mean correlation coefficients. Significant correlations in the current year were predominantly negative (warmer = earlier) while those of the previous year, particularly October, were predominantly positive. The pattern of correlations with prior months was much clearer (Fig. 2); those with recent months were negative but were positive further back in time. Significant correlations with monthly rainfalls (Fig. 3) were rarely above the level expected by chance alone, but tended to be positive (higher rainfall = later). The pattern with prior months' rainfall was broadly similar (not shown). Because significant rainfall correlations were rarely more than the expected background levels, rainfall was subsequently disregarded in favour of temperature. Figs 1, 2 and 4 show that two periods of temperature appear to be important in determining first appearance date: October of the previous year and the three prior months to mean date. Subsequently a multiple regression for each species of first appearance date on October temperature and on the mean of the previous three monthly mean air temperatures was undertaken to predict the likely effect of a 1°C increase in temperature in these two periods. The regression coefficients from these two variables (temperature responses) for the 155 species were examined in relation to different aspects of species ecology using either weighted regression, weighted ANOVA or weighted ANCOVA as appropriate with weights equal to the numbers of years of records for each species. Thus, greater emphasis was given to species whose temperature response was

TABLE 1. Summary information on the 34 butterfly and 121 moth species for which at least ten years of data are available. Species are arranged in increasing date of mean first appearance in each group.

Scientific name	English name	mean day	mean date	sd	n
BUTTERFLIES					
Aglais urticae	Small Tortoiseshell	58.3	27 Feb	18.7	16
Gonepteryx rhamni	Brimstone	62.0	03 Mar	13.8	17
Inachis io	Peacock	84.9	26 Mar	37.8	16
Nymphalis polychloros	Large Tortoiseshell	98.7	09 Apr	17.1	12
Pieris rapae	Small White	99.9	10 Apr	17.5	18
Pieris napi	Green-veined White	111.9	22 Apr	19.0	18
Pieris brassicae	Large White	116.2	26 Apr	23.9	18
Vanessa atalanta	Red Admiral	120.4	30 Apr	35.9	12
Anthocharis cardamines	Orange Tip	127.6	08 May	11.6	18
Pyrgus malvae	Grizzled Skipper	134.6	15 May	8.7	18
Lycaena phlaeas	Small Copper	136.2	16 May	11.5	17
Erynnis tages	Dingy Skipper	136.4	16 May	8.0	18
Pararge aegeria	Speckled Wood	138.8	19 May	22.9	17
Lasiommata megera	Wall Brown	139.1	19 May	10.5	17
Coenonympha pamphilus	Small Heath	140.2	20 May	9.4	18
Boloria euphrosyne	Pearl-bordered Fritillary	140.9	21 May	10.4	18
Callophrys rubi	Green Hairstreak	145.1	25 May	13.0	14
Vanessa cardui	Painted Lady	146.0	26 May	23.5	16
Polyommatus icarus	Common Blue	149.5	30 May	20.9	19
Hamearis lucina	Duke of Burgundy Fritillary	150.0	30 May	9.3	17
Boloria selene	Small Pearl-bordered Fritillary	154.3	03 Jun	12.9	17
Aricia agestis	Brown Argus	154.8	04 Jun	13.5	13
Ochlodes venata	Large Skipper	157.0	06 Jun	11.5	17
Cupido minimus	Small Blue	163.1	12 Jun	19.3	16
Maniola jurtina	Meadow Brown	168.1	17 Jun	19.4	17
Aphantopus hyperantus	Ringlet	182.5	01 Jul	6.1	13
Argynnis aglaja	Dark Green Fritillary	184.2	03 Jul	19.6	15
Pyronia tithonus	Gatekeeper	187.7	07 Jul	20.9	10
Thymelicus sylvestris	Small Skipper	191.4	10 Jul	10.4	15
Argynnis adippe	High Brown Fritillary	192.1	11 Jul	16.7	14
Melanargia galathea	Marbled White	194.7	14 Jul	13.7	14
Argynnis paphia	Silver-washed Fritillary	198.3	17 Jul	14.1	14
Polyommatus coridon	Chalkhill Blue	203.2	22 Jul	16.0	10
Neozephyrus quercus	Purple Hairstreak	209.3	28 Jul	18.0	12
MOTHS					
Theria rupicapraria	Early Moth	48.1	17 Feb	15.6	15
Agriopis marginaria	Dotted Border	65.6	07 Mar	14.4	15
Alsophila aescularia	March Moth	75.0	16 Mar	12.9	10
Scoliopteryx libatrix	The Herald	78.1	19 Mar	41.5	11
Orthosia cerasi	Common Quaker	80.6	22 Mar	13.9	12
Orthosia incerta	Clouded Drab	86.9	28 Mar	11.7	10
Orthosia gothica	Hebrew Character	87.8	29 Mar	23.7	14
Archiearis parthenias	Orange Underwing	90.2	31 Mar	6.9	10
Selenia lunularia	Lunar Thorn	96.8	07 Apr	18.7	12
Xanthorhoe fluctuata	Garden Carpet	116.4	26 Apr	13.9	17
Anticlea derivata	The Streamer	125.1	05 May	11.3	10
Eupithecia vulgata	Common Pug	130.0	10 May	29.1	12
Menophra abruptaria	Waved Umber	130.2	10 May	10.9	13
Xanthorhoe spadicearia	Red Twin-spot Carpet	130.3	10 May	6.8	14
Opisthograptis luteolata	Brimstone Moth	133.2	13 May	11.2	17
Xanthorhoe biriviata	Balsam Carpet	133.7	14 May	18.8	15
Watsonella cultraria	Barred Hook-tip	138.4	18 May	26.7	11
Mimas tiliae	Lime Hawk-moth	138.6	19 May	27.3	12
Spilosoma lubricipeda	White Ermine	140.1	20 May	10.2	17
Phragmatobia fuliginosa	Ruby Tiger	140.5	20 May	30.1	10
Petrophora chlorosata	Brown Silver-line	141.1	21 May	13.3	16
Asthena albulata	Small White Wave	141.4	21 May	9.7	14
Lomographa bimaculata	White-pinion Spotted	142.3	22 May	16.8	11
Jodis lactearia	Little Emerald	142.4	22 May	7.7	17
Xanthorhoe montanata	Silver-ground Carpet	142.5	23 May	8.7	15
Cabera pusaria	Common White Wave	142.7	23 May	8.9	16
Lomographa temerata	Clouded Silver	143.7	24 May	18.1	11
Eupithecia subfuscata	Grey Pug	144.9	25 May	16.2	11
Anthophila fabriciana	Nettle-tap Moth	145.8	26 May	37.0	12
Diaphora mendica	Muslin Moth	145.8	26 May	14.8	13
Chiasmia clathrata	Latticed Heath	146.9	27 May	31.6	17
Callistege mi	Mother Shipton	149.0	29 May	13.1	15
Spilosoma lutea	Buff Ermine	149.1	29 May	9.8	17
Odontopera bidentata	Scalloped Hazel	149.2	29 May	12.7	10
Electrophaes corylata	Broken-barred Carpet	149.7	30 May	12.2	15
Lomaspilis marginata	Clouded Border	149.7	30 May	13.1	18
Phytometra viridaria	Small Purple-barred	149.8	30 May	16.2	13
Tyria jacobaeae	The Cinnabar	150.1	30 May	13.9	16
Phlogophora meticulosa	Angle Shades	150.2	30 May	20.5	13
Scopula floslactata	Cream Wave	150.7	31 May	13.4	12
Korscheltellus lupulina	Common Swift	151.7	01 Jun	12.6	15

Chloroclysta siterata	Red-green Carpet	151.8	01 Jun	15.4	17
Cyclophora linearia	Clay Triple-lines	152.1	01 Jun	21.3	10
Macroglossum stellatarum	Humming-bird Hawk-moth	152.9	02 Jun	50.4	17
Drepana falcataria	Pebble Hook-tip	154.1	03 Jun	20.1	12
Pechipogo strigilata	Common Fan-foot	154.2	03 Jun	11.1	11
Mamestra brassicae	Cabbage Moth	154.8	04 Jun	15.5	18
Crambus pratella	NONE	155.0	04 Jun	17.1	11
Ligdia adustata	Scorched Carpet	155.1	04 Jun	17.7	15
Autographa gamma	Silver Y	155.8	05 Jun	24.0	17
Calliteara pudibunda	Pale Tussock	156.2	05 Jun	13.0	10
Parasemia plantaginis	Wood Tiger	156.7	06 Jun	9.2	13
Minoa murinata	Drab Looper	157.2	06 Jun	11.2	13
Cosmorhoe ocellata	Purple Bar	157.9	07 Jun	24.8	12
Odezia atrata	Chimney Sweeper	158.3	07 Jun	15.7	16
Cilix glaucata	Chinese Character	159.0	08 Jun	23.4	11
Cyclophora punctaria	Maiden's Blush	159.1	08 Jun	22.9	10
Acronicta psi	Grey Dagger	160.3	09 Jun	16.8	14
Cabera exanthemata	Common Wave	160.4	09 Jun	25.5	12
Ptilodon capucina	Coxcomb Prominent	160.9	10 Jun	33.9	10
Adscita geryon	Cistus Forester	161.4	10 Jun	15.7	16
Opsibotys fuscalis	NONE	162.4	11 Jun	11.8	12
Charanyca trigrammica	Treble Lines	163.0	12 Jun	10.4	14
Ematurga atomaria	Common Heath	163.3	12 Jun	10.5	12
Atolmis rubricollis	Red-necked Footman	163.9	13 Jun	9.6	13
Smerinthus ocellata	Eyed Hawk-moth	164.5	13 Jun	19.8	11
Camptogramma bilineata	Yellow Shell	164.6	14 Jun	10.2	17
Noctua pronuba	Large Yellow Underwing	165.6	15 Jun	18.8	17
Sphinx ligustri	Privet Hawk-moth	165.8	15 Jun	17.0	12
Deilephila porcellus	Small Elephant Hawk-moth	165.9	15 Jun	14.4	10
Apamea sordens	Rustic Shoulder-knot	166.2	15 Jun	13.8	13
Laothoe populi	Poplar Hawk-moth	166.5	16 Jun	25.4	15
Eurrhypara hortulata	Small Magpie	166.8	16 Jun	18.6	13
Udea olivalis	NONE	168.4	17 Jun	12.5	14
Epirrhoe rivata	Wood Carpet	169.2	18 Jun	23.0	10
Agrotis exclamationis	Heart and Dart	169.6	19 Jun	12.2	16
Hada plebeja	The Shears	170.0	19 Jun	10.8	12
Chloroclysta truncata	Common Marbled Carpet	170.0	19 Jun	33.1	17
Lacanobia oleracea	Bright-line Brown-eye	170.2	19 Jun	25.7	12
Hydrelia flammeolaria	Small Yellow Wave	172.5	21 Jun	12.9	11
Oligia strigilis	Marbled Minor	174.1	23 Jun	9.4	13
Idaea aversata	Riband Wave	175.1	24 Jun	11.8	12
Deilephila elpenor	Elephant Hawk-moth	175.9	25 Jun	26.0	12
Hepialus humuli	Ghost Moth	176.2	25 Jun	16.4	14
Scotopteryx luridata	July Belle	176.7	26 Jun	21.7	10
Hypena proboscidalis	The Snout	176.7	26 Jun	14.3	15
Idaea seriata	Small Dusty Wave	176.8	26 Jun	16.5	10
Rusina ferruginea	Brown Rustic	177.4	26 Jun	26.3	10
Zygaena filipendulae	Six-spot Burnet	179.3	28 Jun	19.1	16
Apamea monoglypha	Dark Arches	179.7	29 Jun	11.7	14
Euphyia unangulata	Sharp-angled Carpet	179.8	29 Jun	18.8	10
Diarsia mendica	Ingrailed Clay	180.8	30 Jun	20.4	10
Udea prunalis	NONE	183.4	02 Jul	19.5	10
Perizoma alchemillata	Small Rivulet	183.9	03 Jul	19.1	11
Rhinoprora rectangulata	Green Pug	184.5	03 Jul	20.7	10
Euthrix potatoria	The Drinker	184.6	04 Jul	12.7	14
Campaea margaritata	Light Emerald	186.6	06 Jul	8.1	11
Cidaria fulvata	Barred Yellow	187.5	06 Jul	8.9	13
Perizoma didymata	Twin-spot Carpet	188.3	07 Jul	14.5	13
Diachrysia chrysitis	Burnished Brass	189.2	08 Jul	26.9	14
Aphomia sociella	Bee Moth	190.0	09 Jul	24.8	11
Amphipoea oculea	Ear Moth	191.1	10 Jul	22.9	12
Abraxas grossulariata	The Magpie	191.4	10 Jul	10.1	11
Mythimna pallens	Common Wainscot	192.2	11 Jul	20.7	10
Chloroclysta citrata	Dark Marbled Carpet	192.2	11 Jul	20.2	13
Philereme vetulata	Brown Scallop	193.8	13 Jul	12.3	10
Eulithis pyraliata	Barred Straw	193.8	13 Jul	10.3	12
Xestia c-nigrum	Setaceous Hebrew Character	194.0	13 Jul	29.6	10
Arctia caja	Garden Tiger	194.4	13 Jul	16.6	14
Triodia sylvina	Orange Swift	194.5	13 Jul	35.6	10
Peribatodes rhomboidaria	Willow Beauty	196.1	15 Jul	6.6	10
Cryphia domestica	Marbled Beauty	196.7	16 Jul	24.3	14
Macaria wauaria	The V-Moth	198.7	18 Jul	33.5	12
Paradrina clavipalpis	Pale Mottled Willow	199.0	18 Jul	24.8	12
Ourapteryx sambucaria	Swallow-tailed Moth	200.0	19 Jul	28.6	14
Scotopteryx chenopodiata	Shaded Broad-bar	200.1	19 Jul	7.8	12
Hydriomena furcata	July Highflyer	210.4	29 Jul	17.0	13
Tholera decimalis	Feathered Gothic	225.3	13 Aug	27.2	10
Ennomos alniaria	Canary-shouldered Thorn	236.5	25 Aug	20.0	11
Orgyia antiqua	The Vapourer	237.3	25 Aug	22.2	13
Diloba caeruleocephala	Figure of Eight	251.4	08 Sep	38.5	11

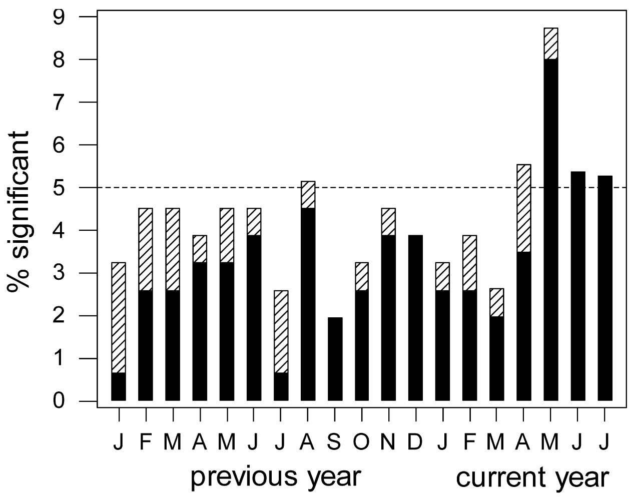

Fig. 3. Percentage of significant positive (solid bars) and negative (hatched bars) correlations between first appearance date and calendar monthly rainfall. The dotted line represents the 5% level of significant results expected by chance.

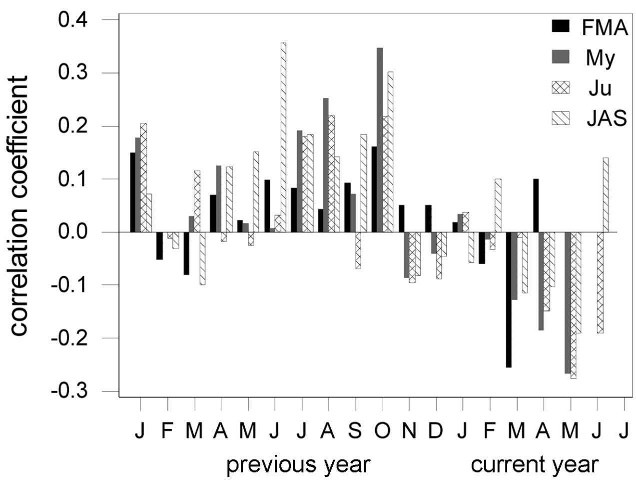

Fig. 4. Mean correlation coefficients with monthly mean temperatures grouped by four first appearance periods (February–April, May, June, July–September).

derived from more years of data. Mean values are presented ± se, regression, ANOVA and ANCOVA results are summarised by F ratio and probability value.

Information on the different aspects of the species ecology were abstracted and converted to scales and categories as shown in Table 2.

RESULTS

Table 1 lists the species, the mean and standard deviation of first appearance date and the numbers of years of data available. Two species had mean first appearance date in February, nine in March, seven in April, 42 in May, 57 in June, 34 in July, three in August and one in September. Butterfly species were significantly earlier, on average, than moth species (May 26 and June 10 respectively, $F_{1,153}$ = 6.62 P = 0.011) and significantly better recorded, respectively an average of 15.6 years of data compared to 12.9 years ($F_{1,153}$ = 37.75 P < 0.001). The standard deviation of butterflies was slightly but not significantly smaller than that of moths (16.3 days and 18.1 days respectively, $F_{1,153}$ = 1.43 P = 0.23). Neither the slightly negative relationship ($F_{1,32}$ = 2.32, P = 0.14) between standard deviation and mean date for butterflies or the slightly positive relationship ($F_{1,119}$ = 2.45, P = 0.089) for moths was significant.

There were no significant trends in temperature during the study period (each month, P > 0.10). The response to October temperature averaged 3.63 ± 0.38 days/ºC i.e. warmer Octobers tended to delay first appearance date in the following year. The response to three prior months' temperature, in contrast, averaged –3.05 ± 0.54 days/°C indicating earlier first appearance with warmer temperatures preceding first appearance. Fig. 5 presents histograms of the two responses clearly indicating the contrasting effects. An attempt has been made to ascertain whether the response to climate of the species falls into any natural or logical groupings.

Conservation status

The responsiveness of species to October and three prior months temperatures did not differ significantly between species of conservation interest (n = 126) and other species (n = 29; Table 3). Whilst species of conservation status did not differ significantly from other species in mean date of appearance, they were significantly larger (40.0±1.3 mm and 33.0 ± 1.9 mm respectively, $F_{1,153}$ = 5.45 P = 0.021).

TABLE 2. A summary of the investigated variables.

Variable	Source	Reduced to
Conservation status	Waring et al. (2003)	Binary: conservation interest or not
Distributional range	Emmet & Heath (1991)	Binary: England & Wales or including Scotland
Voltinism	Emmet & Heath (1991)	Binary: mainly univoltine or more generations
Day or night flying	Emmet & Heath (1991)	Binary: predominantly day or night flying
Wing expanse	Emmet & Heath (1991), Waring et al. (2003)	Average of extremes.
Feeding preferences	Emmet & Heath (1991)	Binary: Grasses/herbs or shrubs/trees
Migratory status	Emmet & Heath (1991)	Binary: partly/wholly migratory or resident
Hibernation environment	Emmet & Heath (1991), Waring et al. (2003)	5 point ordinal scale 1 = exposed, 5 = underground
Larval exposure	Emmet & Heath (1991)	3 point ordinal scale: not, moderately or fully exposed
Pupal exposure	Emmet & Heath (1991)	3 point ordinal scale: not, moderately or fully exposed

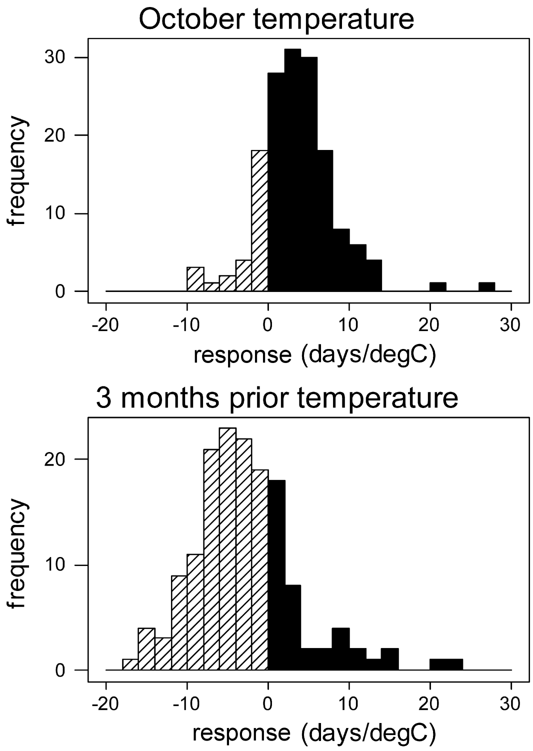

Fig. 5. Histograms of responses to a 1°C increase in October and three prior months temperature. Hatched bars negative response, solid bars positive response.

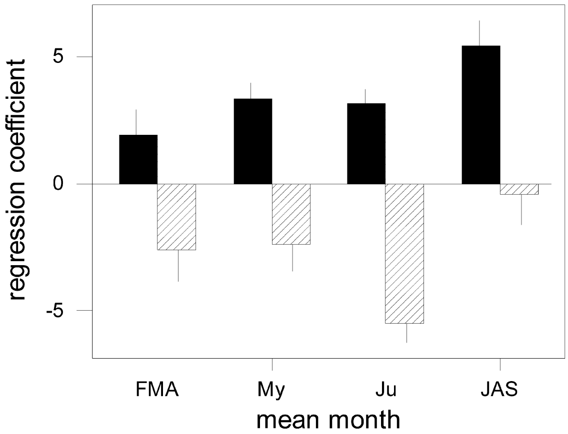

Fig. 6. Mean regression coefficients of first appearance date on October temperature (solid bars) and three prior months temperatures (hatched bars), grouped by four first appearance periods (February–April, May, June, July–September). Vertical lines represent one standard error of the mean.

Distributional range

The responsiveness of species with ranges including Scotland was not significantly different from those restricted to England and Wales (Table 3).

Voltinism

The responsiveness of univoltine species for three prior months (–3.74 ± 0.58 days/°C, n = 116) was greater, but not significantly greater (Table 3) than multivoltine species (–1.22 ± 1.23 days/°C, n = 36).

Mean date of appearance

A significant linear relationship existed between October response and mean first appearance date but not for the three prior months (Table 3). For October temperatures, the delayed first appearance with warmer temperatures was more pronounced for species first observed later in the year. When examined between four month groups (February–April, May, June, July–September) significant differences between month groups were apparent for both temperature responses (Table 3, Fig. 6). In Fig. 6 the clear trend for a greater positive response to October temperatures and lower response to three prior months' temperature is apparent.

Butterfly or moth

No significant differences were found in responsiveness of butterflies and moths (Table 3).

Day or night flying

Day flying Lepidoptera (mean 2.57 ± 0.56 days/°C, n = 44) were almost significantly less responsive to October temperature than night flying Lepidoptera (4.06 ± 0.48 days/°C, n = 111, Table 3). Day flying Lepidoptera were on average earlier (May 29 ± 6 and June 10 ± 3, respectively, $F_{1,153}$ = 4.36 P = 0.038) and larger than night flying Lepidoptera (43.2 ± 2.3 mm and 36.9 ± 1.3 mm respectively, $F_{1,153}$ = 7.01 P = 0.009). However, after elimination of mean date and size in an ANCOVA, the difference in October response was further from significance ($F_{1,151}$ = 1.59, P = 0.21).

Wing size

There was no significant relationship between wing expanse and responsiveness (Table 3).

Family

Table 4 summarises the mean responses of the eight families for which at least five members were represented. Despite the large differences, there was no significant difference in responsiveness between families (Table 3) as a consequence of the large variability within families.

Feeding preferences

Species feeding on grasses and herbs had a mean temperature response to three prior months temperature of –3.62 ± 0.71 days/°C (n = 89) compared to shrub and tree feeders whose mean response was –1.56 ± 0.90 days/°C (n = 53). The difference was not quite significant (Table 3).

Migrants

The few migrant or partially migrant species were significantly less temperature responsive to October temperatures (1.17 ± 1.19 days/°C, n = 14) than residents (3.88 ± 0.40 days/°C, n = 141) (Table 3). However migrants were significantly earlier (May 8 ± 10 cf. June 9 ± 3, $F_{1,153}$ = 13.59 P < 0.001) and larger (53.4 ± 3.4 mm cf. 37.2 ± 1.2, $F_{1,153}$ = 21.33 P < 0.001). After eliminating the effects of mean date and size in ANCOVA, there was

TABLE 3. Statistical tests of differential responses to October and mean of three prior month temperatures on a range of Lepidoptera attributes. Reg = regression, significant ($P < 0.05$) results in bold.

Variable	Test	Oct coefficient		Three prior months coefficient	
		Test statistic	P	Test statistics	P
Conservation status	ANOVA	$F_{1,153} = 0.46$	0.50	$F_{1,153} = 0.15$	0.70
Distributional range	ANOVA	$F_{1,153} = 0.26$	0.61	$F_{1,153} = 0.10$	0.75
Voltinism	ANOVA	$F_{1,150} = 1.51$	0.22	$F_{1,150} = 2.94$	0.089
Mean appearance date	Reg	**$F_{1,153} = 8.30$**	**0.005**	$F_{1,153} = 0.42$	0.52
Appearance month group	ANOVA	**$F_{3,151} = 3.25$**	**0.024**	**$F_{3,151} = 4.83$**	**0.003**
Butterfly vs Moth	ANOVA	$F_{1,153} = 2.41$	0.12	$F_{1,153} = 0.75$	0.39
Day vs night flying	ANOVA	$F_{1,153} = 3.76$	0.054	$F_{1,153} = 0.59$	0.44
Wing expanse	Reg	$F_{1,153} = 2.37$	0.13	$F_{1,153} = 0.43$	0.51
Family	ANOVA	$F_{7,131} = 0.91$	0.50	$F_{7,131} = 0.84$	0.55
Feeding preferences	ANOVA	$F_{1,140} = 0.97$	0.33	$F_{1,140} = 3.20$	0.076
Migratory status	ANOVA	**$F_{1,153} = 5.82$**	**0.017**	$F_{1,153} = 2.35$	0.13
Hibernation environment	Reg	$F_{1,153} = 1.22$	0.27	**$F_{1,153} = 4.95$**	**0.028**
Larval exposure	Reg	$F_{1,136} = 0.76$	0.38	$F_{1,136} = 0.58$	0.45
Pupal exposure	Reg	$F_{1,136} = 0.66$	0.42	$F_{1,136} = 0.01$	0.91

still a difference in temperature responsiveness ($F_{1,151} = 5.40$ $P = 0.021$).

Hibernation environment

Nine species that overwinter as adults were eliminated from this test. A significant relationship existed between three prior month temperature response and hibernation environment (Table 3). Species whose hibernation stages were less exposed had a greater negative response to temperature.

Larval and pupal exposure

No significant differences in responsiveness were detected (Table 3).

DISCUSSION

Since the phenology of moths has been rarely reported, and then only for the period affected by systematic changes in temperatures over the past half century (Woiwod, 1997), this use of historical data is valuable in increasing our understanding of the effects of climate on life cycle timings. During the period of study, annual mean temperatures were c. 0.9°C cooler than currently. The Lepidoptera include species of high conservation status and high pest status, and species of both low and high (migratory) mobility. As such they are an interesting group with which to further the study of climate impacts. What is very obvious is that, taken as a whole, these species are generally responsive to a warming environment. In general, species appeared much more responsive to temperature than rainfall, although this may not be true in other countries where water is deficient or in Britain during periods with a wider range of rainfall conditions. Other factors, such as host abundance or population dynamics may play a role in first detection date (for an example with birds see Tryjanowski et al., 2005) but we do not have contemporary data on these for our Lepidoptera. Temperatures of three months prior to appearance seemed to affect appearance in a negative way; higher temperatures advancing appearance dates. It was somewhat of a surprise that temperatures of the previous autumn, and in particular October, were having such a positive effect on appearance date. There was no significant correlation between temperature in the previous October and those in the current year (each month, $P > 0.13$) to explain this result. Since the magnitude of change arising from October and three prior months temperatures approximately cancel one another out the relative changes in temperature in these two periods will have a major influence on the changing pattern of phenology.

Some of the responses in individual species may be aberrant because of small sample size, but we used weighted regression to give greater emphasis to results based on more years.

In the examination of a large number of species attributes, we were surprised that we did not detect more patterns in the temperature responses of these Lepidoptera. Migratory species did not appear very responsive to pre-

TABLE 4. Mean ± se for response of Lepidoptera families represented by at least five species.

	n	Oct coefficient		Three prior months coefficient	
		Mean	SE	Mean	SE
Arctiidae	8	4.60	1.60	1.65	2.86
Geometridae	57	3.45	0.64	–3.27	0.80
Lycaenidae	8	2.95	1.00	–4.26	2.06
Noctuidae	30	4.58	1.00	–3.26	1.38
Nymphalidae	17	3.09	1.07	–4.89	1.67
Pieridae	5	0.50	1.63	–1.08	1.57
Pyralidae	7	5.63	1.05	–4.28	1.33
Sphingidae	7	2.16	2.61	–2.79	2.44

vious October temperature; an intuitive result since they are not in Britain at that time to experience that weather. Climate effects on migrants are likely to be very complex as they experience a range of climates at different parts of their life cycle (Sparks et al., 2005). Overall, however, migrants are likely to be more flexible in response to a changing climate than their sedentary cousins (Dennis, 1993).

The greatest difference appeared to result from the timing of the species; late flying species are particularly sensitive to previous October temperature and much less so to three prior months' temperature whilst the response of June species to the latter was particularly strong. If climate warming happens evenly through the year, these results suggest that late flying species will get progressively later whilst June species will get earlier. If change does not occur in synchrony with host or predator phenology then serious consequences may become apparent (for discussion, see Root et al., 2003).

Do recent advances in spring phenology of moths and butterflies point to a differential warming, with greater temperature increase at the beginning of the year and less in autumn? Could recent advances in phenology be retarded as autumn temperatures start to increase? An obvious caveat is that our data are from a relatively small number of years from a single location. Our inability to detect many patterns in examining temperature response to species attributes may be because they are difficult to detect statistically in our relatively short data set or that we did not have available other appropriate species attributes. A more worrying alternative is that temperature responses in Lepidoptera species appear random or chaotic. If so, our ability to predict the consequences of a changing climate on Lepidoptera communities may be seriously challenged.

We hope that the findings in the Marlborough data will encourage other holders of long term data sets to examine them for features of species' ecology that may influence temperature response, in order that the consequences of a changing climate on Lepidoptera can be more fully understood. Influences that emerge in the current dataset (i.e. related to hibernal environment and mean emergence date) suggest complicated scenarios with climate change and this, together with the absence of definitive explanations for these relationships, points to fruitful areas for future research.

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REFERENCES

BOIVIN T., CHADOEUF J., BOUVIER J.C., BESLAY D. & SAUPHANOR B. 2005: Modelling the interactions between phenology and insecticide resistance genes in the codling moth Cydia pomonella. *Pest Manag. Sci.* **61**: 53–67.

BURTON J.F. & SPARKS T.H. 2003: The flight phenological responses of Lepidoptera to climate change in Britain and Germany. *Atalanta* **34**: 3–16.

BUSE A. & GOOD J.E.G. 1996: Synchronization of larval emergence in winter moth (Operophtera brumata L.) and budburst in pedunculate oak (Quercus robur L.) under simulated climate change. *Ecol. Entomol.* **21**: 335–343.

DELL D., SPARKS T.H. & DENNIS R.L.H. 2005: Climate change and the effect of increasing spring temperatures on emergence dates of the flagship butterfly Apatura iris (Lepidoptera: Nymphalidae). *Eur. J. Entomol.* **102**: 161–167.

DENNIS R.L.H. 1993: *Butterflies and Climate Change*. Manchester University Press, Manchester, 302 pp.

DENNIS R.L.H., HODGSON J.G., GRENYER R., SHREEVE T.G. & ROY D.B. 2004: Host plants and butterfly biology. Do host plant strategies drive butterfly status? *Ecol. Entomol.* **29**: 12–26.

EMMET A.M. & HEATH J. (eds) 1991: *The Moths and Butterflies of Great Britain and Ireland. Vol. 7, Part 2*. Harley Books, Colchester, 400 pp.

FORISTER M.L. & SHAPIRO A.M. 2003: Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biol.* **9**: 1130–1135.

IPCC 2001: *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

KUCHLEIN J.H. & ELLIS W.N. 1997: Climate-induced changes in the Microlepidoptera fauna of the Netherlands and the implications for nature conservation. *J. Insect Conserv.* **1**: 73–80.

POLLARD E. & YATES T.J. 1993: *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London, 274 pp.

REGNIERE J. & NEALIS V. 2002: Modelling seasonality of gypsy moth, Lymantria dispar (Lepidoptera: Lymantriidae), to evaluate probability of its persistence in novel environments. *Can. Entomol.* **134**: 805–824.

ROOT T.L., PRICE J.T., HALL K.R., SCHNEIDER S.H., ROSENZWEIG C. & POUNDS J.A. 2003: Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.

ROY D.B. & SPARKS T.H. 2000: Phenology of British butterflies and climate change. *Global Change Biol.* **6**: 407–416.

SPARKS T.H., ROY D.B. & DENNIS R.L.H. 2005: The influence of temperature on migration of Lepidoptera into Britain. *Global Change Biol.* **11**: 507–514.

STEFANESCU C., PEÑUELAS J. & FILELLA I. 2003: Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology* **9**: 1494–1506.

TRYJANOWSKI P., KUŹNIAK S. & SPARKS T.H. 2005: What affects the magnitude of change in first arrival dates of migrant birds? *J. Ornithol.* **146**: 200–205.

WARING P., TOWNSEND M. & LEWINGTON R. 2003: *Field Guide to the Moths of Great Britain and Ireland*. British Wildlife Publishing, Dorset, 432 pp.

WOIWOD I.P. 1997: Detecting the effects of climate change on Lepidoptera. *J. Insect Conserv.* **1**: 149–158.

ZHOU X., HARRINGTON R., WOIWOD I.P., PERRY J.N., CLARK S.J. & BALE J.S. 1996: Impact of climate change on aphid flight phenology. *Aspects Appl. Biol.* **45**: 299–305.

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