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The flight phenological responses of Lepidoptera to climate change in Britain and Germany

(Insecta, Lepidoptera)

by

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Summary: This paper is a revised and updated version of one published in the journal British Wildlife (BURTON & SPARKS, 2002). It incorporates analyses of additional phenological data concerning German Lepidoptera extracted from records of a selection of migrant and partially migrant species published annually in Atalanta. Some comparisons are therefore possible between the influence of recent climate changes on Lepidoptera in southern Britain and Germany.

The British data, much of it encompassing the period 1940-1999, indicates that butterfly species overwintering in Britain in any stage of their life cycle were appearing earlier in the 1990s compared with both the 1940s and the 1970s by an average of 28 days (Table 1). In contrast the German data, encompassing the period 1960-1999, indicate that such overwintering species were appearing earlier by an average of eight days compared with the 1960s and by 12 days compared with the 1970s (Table 3). A comparison between the 1990s and 1970s for four species of butterflies overwintering in both countries in the imago stage (*Gonepteryx rhamni* (L., 1758), *Vanessa atalanta* (L., 1758), *Inachis io* (L., 1758) and *Aglais urticae* (L., 1758)) indicated that they were appearing earlier by an average of 74 days (ca. 10 weeks) in Britain and 27 days (ca. four weeks) in Germany. Thus such day-flying butterflies are now appearing earlier than formerly in both countries, but at least twice as early in southern Britain, presumably because the winters are much milder there on average than those in Germany and central Europe generally.

Likewise, some species of moths in southern Britain are appearing anything up to three weeks to a month earlier than in the 1970s, whereas in Germany the situation is much less clear, with some partial migrant species, like *Macroglossum stellatarum* (L., 1758) and *Phlogophora meticulosa* (L., 1758), appearing anything up to five weeks earlier than in the 1970s and others anything up to five weeks later, though the majority were less than three weeks later.

Introduction

As pointed out by BURTON & SPARKS (2002) and others, the growing concern over global warming has renewed interest in phenology, the study of the timing of recurring natural events. The analysis of recorded phenological data on the way in which animal and plant species have responded to past environmental changes, particularly those of climate and weather, should help the interpretation of how they may respond to such changes in the future (e.g. FITTER et al., 1995; SPARKS, 1999; SPARKS & CAREY, 1995; SPARKS et al., 1997, 2000; SPARKS & MENZEL, 2002).

Britain is fortunate in possessing useful runs of phenological data that have existed from quite early in the 18th century, thanks to such pioneer observers and recorders as the MARSHAM family, who began keeping records in 1736 at the family estates near Norwich, Norfolk, and GILBERT WHITE of Selborne, in north-east Hampshire, who started in 1751. Moreover, numerous local natural history societies have recorded such data in their publications, in some cases well back into the 19th century, and these records, perhaps long undervalued and neglected until quite recently by present-day researchers, are proving to be a valuable resource for those biologists interested in the effects of climate change. Thus, T. H. S. at the Natural Environment Research Council's Centre for Ecology & Hydrology at Monks Wood, Abbots Ripton, Huntingdon, has been analysing a wealth of old and modern data available on a range of animal and plant species. Together with the Woodland Trust, he has organised a national, wide-ranging phenological survey covering certain selected animals and plants, the first report on which, for spring 1998, was published in that year (SPARKS et al., 1998). Currently, in excess of 4000 observers are participating in this scheme. On the European mainland the German Weather Service has been running for many years a phenological recording scheme limited to plants.

Analyses of data on butterflies in Britain

The analysis of the MARSHAM family's phenological records from 1736 onwards (SPARKS & CAREY, 1995), supplemented by national data obtained by the Royal Meteorological Society (R.M.S.) from a network of observers up to 1947, revealed, amongst other things, that most of the phenological variables were significantly related to climatic variables or changed through time. Most of the data collected recorded the first dates of flowering or leafing of plants, the first arrival of migratory birds and the earliest croaking heard of the frog *Rana temporaria* L., 1758. Only one insect was included: "yellow butterfly", the first appearance on the wing of the unmistakable male of *Gonepteryx rhamni* (L., 1758). Analysis of these records showed a relationship with early spring temperatures and SPARKS & CAREY (1995) predicted from it that a 3.5 °C rise in temperature would advance the appearance of this butterfly by nine days.

Using first date of appearance has, of course, its limitations, but it is the event most frequently looked for and recorded by amateur observers. SPARKS & YATES (1997) examined the mean first appearance of butterflies in Britain using data from the phenological reports of the R.M.S. over the period 1883–1947 and from the current Butterfly Monitoring Scheme (B.M.S.) for the years 1976–1993. For the 12 species for which data were available they calculated that, in the absence of evolutionary change, climate warming of the order of 3 °C could advance the annual appearance of these species in Britain by two to three weeks. A later study by ROY & SPARKS (2000), which also used B.M.S. data suggested that warming of 1 °C could advance the first and peak appearances of most butterflies by from two to ten days.

Developments in the 1990s concerning butterflies

J.F.B.'s analysis of data extracted from BOWLES (1990–1999) revealed that, in 1999, the average date of first appearance of 27 of 49 species of butterflies resident in southern Britain was earlier by nine days than the average for the years 1991 to 1998; the other 22 species were later by an average of five days. When the data for 1998 were compared with those for 1991-97, 41 of the 44 species appeared earlier on average by 16 days. Therefore, even in the course of the 1990s, there was up to 1998, an increasing trend to early appearance carrying on from that revealed by a comparison of the 1990s with the 1980s, when the average advancement was 22 days (unpublished results). As regards 1999, although it was the warmest year on record at that time and it was sunnier than 1998, it was rather wet. It was not surprising, therefore, that the average advancement in 1999 over the earlier years in that decade was only nine days and that almost as many species were first seen later.

An analysis made by J.F.B. of the date of first appearance of nine species of butterflies resident on the Isle of Wight, off the south coast of Hampshire, England, as recorded by Knill-Jones (2000) and for which precise dates were available, showed a similar pattern, except that there was an even greater trend to early appearance. Thus, seven of them were earlier in 1999 than the mean for 1991–1998 by an average of 17 days. However, one would expect this from a restricted area in the extreme south of England when compared with records from the far wider area of southern Britain.

The current study

The first dates of appearance of butterflies in southern England during the period 1946–1999 were extracted by J.F.B. from the published records of numerous observers in entomological and other journals. We focused on the 31 species for which at least 20 years of data were available (Table 1). In addition to calculating mean (average) first-observation dates for each decade, we summarised the difference between the 1970s and 1990s and, where data existed, between the 1940s and 1990s.

Have there been changes in Britain?

For all butterfly species, first appearance dates in the 1990s were earlier than in either the 1940s or the 1970s (Table 1). In comparison with the 1940s, species were earlier by between three and 129 days (average 28 days); and in comparison with the 1970s, they were earlier by between eight and 129 days (average 28 days). Five species which overwinter in Britain in the adult state tended to make their appearance much earlier in the year than the others, by an average of 74 days, in the 1990s compared with the 1940s, and by 66 days when compared with the 1970s, usually well in advance of the main flight period. When *Vanessa atalanta* (L., 1758), which seems to have begun hibernating regularly in substantial numbers in Britain only within the last 20 years, is excluded, then the figure drops to 60 days earlier compared with the 1940s, and 50 days earlier compared with the 1970s. If all five that winter as adults are excluded from the 31 species, the average advancement of first appearance for all the other species compared with the 1940s, is reduced to 21 days, and to 22 days compared with the 1970s. When all these decades are compared with each other, it becomes clear that the first dates of appearance for most species were quite constant until the 1990s, when a marked trend to earliness became evident.

Table 1: Mean dates of first appearance (as days from 1st January) of butterflies in southern England overwintering in different stages. Means in italics are based on fewer than five years of data; species with fewer than 20 years of observations excluded.

Species	1940s	1950s	1960s	1970s	1980s	1990s	1990s difference from 40s	1990s difference from 70s
Overwintering in the imago (adult) stage								
Brimstone *Gonepteryx rhamni*	*89 (30 Mar)*	*87 (28 Mar)*	78 (19 Mar)	77 (18 Mar)	55 (24 Feb)	33 (2 Feb)	−56 days	−44 days
Small Tortoiseshell *Aglais urticae*	*83 (24 Mar)*	*86 (27 Mar)*	71 (12 Mar)	67 (8 Mar)	50 (19 Feb)	18 (18 Jan)	−65 days	−49 days
Red Admiral *Vanessa atalanta*	*148 (28 May)*	-	-	*148 (28 May)*	32 (1 Feb)	19 (19Jan)	−129 days	−129 days
Peacock *Inachis io*	*90 (31 Mar)*	*106 (16 Apr)*	84 (25 Mar)	85 (26 Mar)	53 (22 Feb)	13 (13 Jan)	−77 days	−72 days
Comma *Polygonia c-album*	*90 (31 Mar)*	-	84 (25 Mar)	*85 (26 Mar)*	88 (29 Mar)	48 (17 Feb)	−42 days	−37 days
average							**−74 days**	**−66 days**
Overwintering in the egg stage								
Purple Hairstreak *Quercusia quercus*	*188 (7 Jul)*	-	-	195 (14 Jul)	199 (18 Jul)	176 (25 Jun)	−12 days	−19 days
Chalkhill Blue *Lysandra coridon*	*209 (28 Jul)*	-	-	202 (21 Jul)	210 (29 Jul)	185 (4 Jul)	−24 days	−17 days
average							**−18 days**	**−18 days**
Overwintering in the larval stage								
Small Skipper *Thymelicus sylvestris*	*184 (3 Jul)*	*182 (1 Jul)*	*184 (3 Jul)*	*183 (2 Jul)*	182 (1 Jul)	166 (15 Jun)	−18 days	−17 days
Large Skipper *Ochlodes venata*	*165 (14 Jun)*	*168 (17 Jun)*	*151 (31 May)*	*156 (5 Jun)*	160 (9 Jun)	152 (1 Jun)	−13 days	−4 days
Dingy Skipper *Erynnis tages*	*134 (14 May)*	-	*131 (11 May)*	135 (15 May)	135 (15 May)	113 (23 Apr)	−21 days	−22 days
Small Copper *Lycaena phlaeas*	*132 (12 May)*	*146 (26 May)*	*120 (30 Apr)*	*121 (1 May)*	137 (17 May)	100 (10 Apr)	−32 days	−21 days
Brown Argus *Aricia agestis*	*143 (23 May)*	*140 (20 May)*	*145 (25 May)*	149 (29 May)	143 (23 May)	124 (4 May)	−19 days	−25 days
Common Blue *Polyommatus icarus*	*138 (18 May)*	*135 (15 May)*	*128 (8 May)*	*147 (27 May)*	143 (23 May)	123 (3 May)	−15 days	−24 days
White Admiral *Ladoga camilla*	*187 (6 Jul)*	-	-	189 (8 Jul)	188 (7 Jul)	172 (21 Jun)	−15 days	−17 days
Pearl-bordered Fritillary *B. euphrosyne*	*128 (8 May)*	*148 (28 May)*	*161 (9 Jun)*	138 (28 May)	*144 (24 May)*	114 (24 Apr)	−14 days	−24 days
Dark Green Fritillary *Argynnis aglaia*	*180 (29 Jun)*	-	*182 (1 Jul)*	176 (25 Jun)	180 (29 Jun)	162 (11 Jun)	−18 days	−14 days
Silver-washed Fritillary *A. paphia*	*190 (9 Jul)*	-	-	186 (5 Jul)	187 (6 Jul)	170 (19 Jun)	−20 days	−16 days
Wall Brown *Lasiommata megera*	*133 (13 May)*	*138 (18 May)*	*123 (3 May)*	133 (13 May)	137 (17 May)	106 (16 Apr)	−27 days	−27 days
Gatekeeper *Pyronia tithonus*	*188 (7 Jul)*	*188 (7 Jul)*	*169 (18 Jun)*	197 (16 Jul)	180 (29 Jun)	179 (28 Jun)	−9 days	−18 days
Grayling *Hipparchia* semele	*195 (14 Jul)*	*212 (21 Jul)*	*191 (10 Jul)*	195 (14 Jul)	186 (5 Jul)	181 (30 Jun)	−14 days	−14 days
Meadow Brown *Maniola jurtina*	*164 (13 Jun)*	*167 (16 Jun)*	164 (13 Jun)	165 (14 Jun)	164 (13 Jun)	154 (3 Jun)	−10 days	−11 days
Ringlet *Aphantopus hyperantus*	*183 (2 Jul)*	*182 (1 Jul)*	*182 (1 Jul)*	*181 (30 Jun)*	179 (28 Jun)	167 (16 Jun)	−16 days	−14 days
Small Heath *Coenonympha pamphilus*	*132 (12 May)*	*138 (18 May)*	*142 (22 May)*	*135 (15 May)*	146 (26 May)	127 (7 May)	−5 days	−8 days
average							**−17days**	**−17days**
Overwintering in the pupal stage								
Grizzled Skipper *Pyrgus malvae*	*110 (20 Apr)*	-	*121 (1 May)*	134 (14 May)	128 (8 May)	107 (17 Apr)	−3 days	−27 days
Large White *Pieris brassicae*	*98 (8 Apr)*	-	111 (21 Apr)	*106 (16 Apr)*	114 (24 Apr)	85 (26 Mar)	−13 days	−21 days
Small White *Pieris rapae*	*97 (7 Apr)*	*108 (18 Apr)*	98 (8 Apr)	105 (15 Apr)	96 (6 Apr)	69 (10 Mar)	−28 days	−36 days
Green-veined White *Pieris napi*	*105 (15 Apr)*	*150 (30 May)*	110 (20 Apr)	*106 (16 Apr)*	110 (20 Apr)	91 (1 Apr)	−14 days	−15 days
Orange Tip *Anthocharis cardamines*	*115 (25 Apr)*	*139 (19 May)*	114 (24 Apr)	120 (30 Apr)	109 (19 Apr)	79 (20 Mar)	−36 days	−41 days
Green Hairstreak *Callophrys rubi*	*128 (8 May)*	-	*118 (28 Apr)*	132 (12 May)	126 (6 May)	103 (13 Apr)	−25 days	−29 days
Holly Blue *Celastrina argiolus*	*120 (30 Apr)*	*150 (30 May)*	*113 (23 Apr)*	106 (16 Apr)	106 (16 Apr)	79 (20 Mar)	−41 days	−27 days
Speckled Wood *Pararge aegeria*	*115 (25 Apr)*	*148 (28 May)*	114 (24 Apr)	*110 (20 Apr)*	107 (17 Apr)	66 (7 Mar)	−49 days	−44 days
average							**−26 days**	**−30 days**
All species average							**−28 days**	**−28 days**

Does overwintering strategy influence change in phenology?

In a formal analysis, the advancement of appearance since the 1970s of butterflies overwintering in Britain as adults (mean −66 days) is significantly greater ($p < 0.001$ from ANOVA = analysis of variance) than that of species overwintering as eggs (mean −18 days), larvae (mean −17 days) or pupae (mean −30 days). Possibly, those overwintering in the pupal stage were able to develop more rapidly during the winter than formerly. ELLIS et al. (1997) remarked that one of the "many effects of the warming of the global climate that have been predicted is an acceleration of the larval development of insects."

Are there seasonal differences in Britain?

Figure 1 shows the relationship between mean first observation date and difference in mean dates between the 1970s and 1990s. *V. atalanta* and *Inachis io* (L., 1758) have been excluded from this graph because they are highly influential points (March 4, −129 days and March 2, −75 days respectively). The correlation between advancement in date and mean date is highly significant ($p < 0.001$) whether these two species are included or not. It is clear that advancement has been most marked in early emerging species.

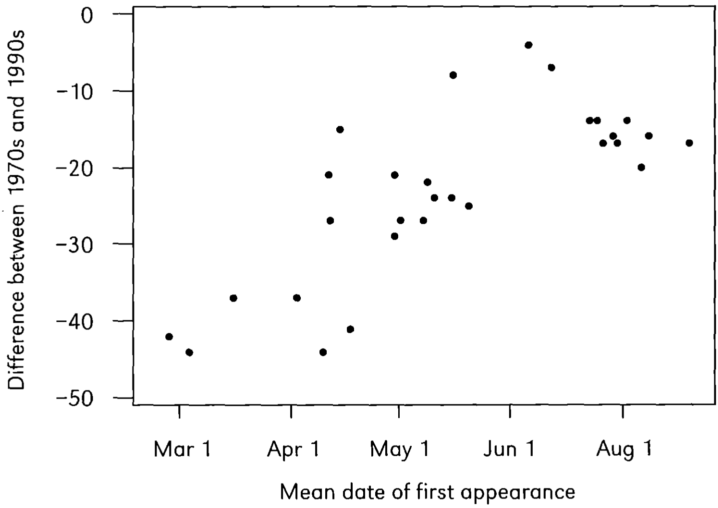

Fig. 1: The relationship between mean first-observation date and difference in mean dates between the 1970s and 1990s. *Vanessa atalanta* and *Inachis io* have been excluded from this graph because they are highly influential points (March 4, −129 days, and March 2, −75 days, respectively).

Does climate influence these changes?

A significant correlation with one or more monthly mean temperatures was evident for 27 of the 31 species in Britain that we examined, and in many cases these correlations were highly significant. The exceptions were *V. atalanta, Maniola jurtina* (L., 1758), *Pyronia tithonus* (L., 1758) and *Pieris napi* (L., 1758). This does not imply that there was no response to tempera-

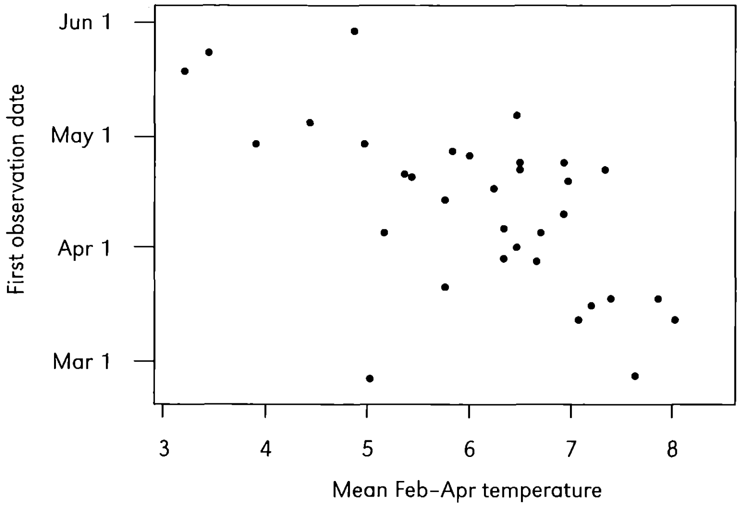

Fig. 2: The relationship between first-appearance date of *Celastrina argiolus* and mean February–April Central England temperature.

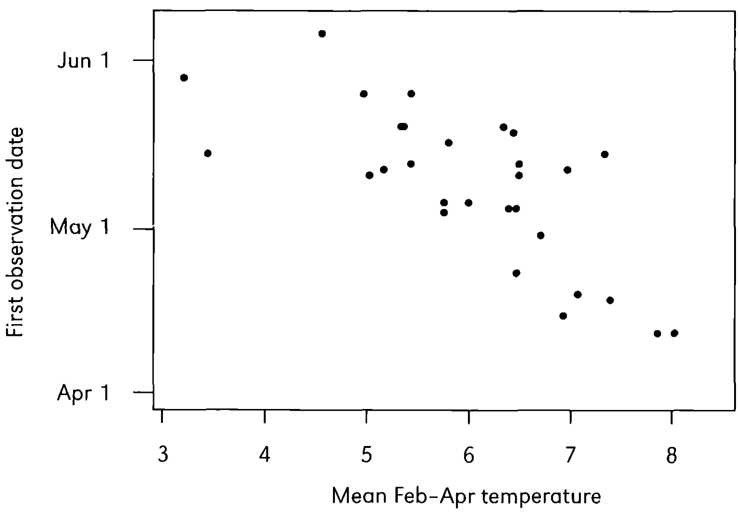

Fig. 3: The relationship between first-appearance date of *Erynnis tages* and mean February–April Central England temperature.

ture by these species; rather, that the observations, at this stage, do not support this hypothesis. Examples of the strength of relationship with temperature are given for *Celastrina argiolus* (L., 1758) (fig. 2) and *Erynnis tages* L., 1758 (fig. 3). Both these relationships are highly significant ($p < 0.001$) and suggest a response of 12 and 9 days respectively for each 1 °C of warming. When viewed in conjunction with other evidence, there can be be very little doubt that climate is a major driver of change in the timing of the appearance of butterflies. Since ROY & SPARKS (2000) found no evidence of a temperature response for the first appearance of *C. argiolus*, our results emphasise that the inclusion of pre-1st April records for early-appearing butterfly species may be very important.

Results of analyses of data on butterflies in Germany

Since 1964 the Deutschen Forschungszentrale für Schmetterlingswanderungen has published in the journal Atalanta detailed records of those species of Lepidoptera which are known to be either fully or partially migratory. These have usually included the first and last dates of appearance of each species, thus providing much useful phenological data covering a span of 37 years up to 2001 which in itself fully justifies the publication by the editors of the records supplied over these years by many contributors. An analysis J.F.B. made of the first emergence dates of seven species of butterflies in southern Germany for the years 1960–1999, where summer temperatures have risen by up to 1.5 °C over the 30 years up to 1995 (OTT, 1996), suggest that the average advancement in the 1990s compared with the 1960s of 14 days for six of them (*Aporia crataegi* (L., 1758), *Pieris rapae* (L., 1758), *P. napi*, *G. rhamni* and *I. io*), and 16 days compared with the 1970s, is indeed rather less than in southern Britain, presumably because average early spring temperatures are still not as high as they are in Britain. For some, so far unexplained, reason, the seventh, *Pieris brassicae* (L., 1758), appeared 16 days later in the 1990s than in the 1960s, and 15 days later than in the 1970s. Judging by available data for the years 2000 and 2001, the situation has not changed. *P. brassicae* had also been appearing later in southern Britain than previously. With the exception of *P. napi*, all species appeared later in southern Germany than in southern England. The trend to earliness of *G. rhamni* was similar in both countries.

Since analysing the data for the seven species mentioned above, J.F.B. has analysed data extracted from Atalanta for 11 additional species, which, added to the original seven, are shown in Table 2. It will be seen that in a similar way to the data in Table 1, the data has been subdivided into those species overwintering in the imago stage (including those V. atalanta which are thought to have overwintered), those in the egg stage, those overwintering either as eggs or larvae, and those only as larvae. The last subdivision contains species considered to be immigrants to Germany from farther south, including those records of V. atalanta which are thought to refer to immigrants rather than individuals which have successfully survived the winter. All species have been included where 19 or more years of observations are available, unlike Table 1 where the minimum requirement was 20 years. Nevertheless, more than 20 years data were available for all but two species.

Analysis of the mean date of first appearance for each decade during the period 1960–1999 for the 18 species listed in Table 2, 14 of which are mainly resident in Germany and four mainly

Table 2: Dates from 1st January of first appearance of butterflies in the imaginal stage in southern Germany.

Species overwintering as an imago	Years of data	1960s	1970s	1980s	1990s	1990s difference from 60s	1990s difference from 70s	1990s difference from 80s
Gonepteryx rhamni (L.)	29	55 (24 Feb)	80 (21 Mar)	53 (22 Feb)	40 (9 Feb)	−15 days	−40 days	−13 days
Aglais urticae (L.)	28	59 (28 Feb)	47 (16 Feb)	54 (23 Feb)	39 (8 Feb)	−20 days	−8 days	−15 days
**Vanessa atalanta* (L.)	35	94 (4 Apr)	99 (9 Apr)	84 (25 Mar)	57 (26 Feb)	−37 days	−42 days	−27 days
Inachis io (L.)	26	46 (15 Feb)	*57 (26 Feb)*	61 (2 Mar)	41 (10 Feb)	−5 days	−16 days	−20 days
Nymphalis polychloros (L.)	22	-	*94 (4 Apr)*	76 (17 Mar)	68 (9 Mar)	-	−26 days	−8 days
N. antiopa (L.)	22	*62 (3 Mar)*	-	90 (31 Mar)	84 (25 Mar)	+22 days	-	−6 days
Average						−11 days	−26 days	−15 days
Species overwintering as a pupa								
Papilio machaon L.	31	*118 (28 Apr)*	103 (13 Apr)	111 (21 Apr)	114 (24 Apr)	−4 days	+11 days	+3 days
Iphiclides podalirius (L.)	30	*121 (1 May)*	123 (3 May)	137 (17 May)	123 (3 May)	+2 days	0 days	−14 days
Pieris brassicae (L.)	32	93 (3 Apr)	94 (4 Apr)	108 (18 Apr)	109 (19 Apr)	+16 days	+15 days	+1 day
P. rapae (L.)	29	99 (9 Apr)	92 (2 Apr)	86 (27 Mar)	80 (21 Mar)	−19 days	−12 days	−6 days
P. napi (L.)	28	*101 (11 Apr)*	97 (7 Apr)	90 (31 Mar)	81 (22 Mar)	−20 days	−16 days	−9 days
Average						−5 days	0 days	−5 days
Species overwintering either as a pupa or larva								
Pontia daplidice (L.)	19	*124 (4 May)*	*156 (5 Jun)*	146 (26 May)	132 (12 May)	+8 days	−24 days	−14 days
Issoria lathonia (L.)	19	*134 (14 May)*	*112 (2 Apr)*	137 (17 May)	119 (29 Apr)	−15 days	+7 days	−18 days
Average						+12 days	−9 days	−16 days
Species overwintering as a larva								
Aporia crataegi (L.)	34	150 (30 May)	146 (26 May)	144 (24 May)	142 (22 May)	−8 days	−4 days	−2 days
Colias alfacariensis Ribbe	21	*136 (16 May)*	*125 (5 May)*	130 (10 May)	115 (25 Apr)	−21 days	−10 days	−15 days
Average						−15 days	−7 days	−4 days
Average for species overwintering						−8 days	−12 days	−11 days
Immigrant species from the south								
**V. atalanta* (L.)	35	112 (22 Apr)	118 (28 Apr)	122 (2 May)	114 (24 Apr)	+2 days	−4 days	−8 days
Cynthia cardui (L.)	33	100 (10 Apr)	117 (27 Apr)	119 (29 Apr)	121 (1 May)	+21 days	+4 days	+2 days
Colias crocea (Geoff.)	26	*150 (30 May)*	180 (29 Jun)	183 (2 Jul)	181 (30 Jun)	+31 days	+1 day	−2 days
C. hyale (L.)	22	*129 (9 May)*	-	129 (9 May)	133 (13 May)	+4 days	-	+4 days
Average						+15 days	0 days	−1 day
Average for all species						**−3 days**	**−10 days**	**−9 days**

Notes: 1. Averages in italics are based upon fewer than five years of data. 2. Species with fewer than 19 years of records are excluded; all but *P. daplidice* and *I. lathonia* have, however, more than 20. 3. *This asterisk indicates that an attempt has been made to separate apparently hibernating *V. atalanta* from those that immigrated in the spring. 4. Averages working out at .5 or above are rounded upwards (e. g., 4.5 is counted as 5), whereas less than .5 are rounded downwards (e. g., 4.4 is counted as 4).

immigrants, revealed that 10 species were earlier in the 1990s than in the 1960s and eight were later; 11 were earlier than in the 1970s, five later and for one there was no change; while 15 were earlier in the 1980s and four later.

All those species which overwinter in the imaginal (adult) stage were notably earlier in the 1990s, apart from *Nymphalis antiopa* (L., 1758), which was much later than in the 1960s. However, it should be noted that less than five years data were available for this species in the 1960s and none in the 1970s. Excluding *N. antiopa*, the mean first appearance date for for this group of species was 19 days earlier in the 1990s than in the 1960s. *V. atalanta* has been added to this group by attempting to separate those records that apparently refer to hibernating individuals from those that seemed to have been genuine immigrants.

When a comparison is made between the 1990s and the 1970s for the four species of butterflies in the first group of Table 2, which overwinter in the imago stage (*G. rhamni, V. atalanta,* *I. io* and *A. urticae* (L.,1758)) in both Britain and Germany, it will be seen that they were appearing earlier in Britain by an average of 74 days (ca. 10 weeks) and in Germany by an average of 27 days (ca. four weeks). Thus, such day-flying species are now appearing earlier than formerly in both countries, but at least twice as early in southern Britain, presumably because the winters are much milder there on average than those in Germany and central Europe as a whole.

Of those species overwintering in the pupal stage, *Papilio machaon* L., 1758, *P. rapae* and *P. napi* were earlier in the 1990s than in the 1970s, the two latter by 12–16 days, while *P. machaon* was 11 days later. In the 1990s *Iphiclides podalirius* (L., 1758) seemed to be appearing at about the same time as it did in the 1960s and 1970s, but, on average, two weeks earlier than it did in the 1980s.

Pontia daplidice (L., 1758) and *Issoria lathonia* (L., 1758) are species that may overwinter in Germany either as pupae or as larvae. The former was apparently more than three weeks earlier in the 1990s than in the 1970s and the latter a week later, but it should be borne in mind that less than five years data were available for the latter decade, so comparisons between the dates in Table 2 may not be valid. However, both species appeared two weeks or more earlier in the 1990s than in the 1980s.

Both the species in Table 2 which overwinter as larvae were earlier in the 1990s: *A. crataegi* by approximately a week compared with the 1960s, four days compared with the 1970s and two with the 1980s. *Colias alfacariensis* Ribbe, 1905 appeared in the 1990s up to three weeks earlier than in the 1960s and 10 days earlier than in the 1970s. Overall, those species overwintering in any stage of their life cycle in Germany were appearing earlier in the 1990s compared with the 1960s by an average of eight days and by 12 days compared with the 1970s.

Regarding the small group of species in Table 2 that are primarily immigrants to Germany from farther south, J.F.B. has included *V. atalanta* by attempting, as already explained, to separate genuine immigrants from those that by their very early appearance dates would seem to have passed the winter in hibernation in Germany. In this case, *V. atalanta* appeared, on average, two days later in the 1990s than in the 1960s, but four to eight days earlier compared to the 1970s and 1980s. Of the other immigrant species in this group, *Cynthia cardui* (L., 1758) and *Colias crocea* (Geoffroy, 1758) were markedly later (three to four weeks) compared with the 1960s, but very much less so when compared with the two subsequent decades. The data for *Colias hyale* (L., 1758) indicate that it is arriving in Germany a few days later than was formerly the case, but the difference is small.

With the possible exception of *N. antiopa*, those species overwintering in the imaginal stage or, in some instances, in the pupal or larval stages, were appearing on the wing notably earlier in the 1990s than 30 years previously. Immigrant butterfly species tended to be later than in the 1960s. This contrasts with the day-flying moth *Macroglossum stellatarum* (L., 1758) which was appearing six weeks earlier in the 1990s, on average, than in the 1960s. If, as with *V. atalanta*, records of obvious hibernators are separated from presumed immigrants then the average dates of first appearance for the latter for each decade are as follows: 1960s: day 143

(23 May); 1970s: day 134 (14 May); 1980s day 120 (30 April); 1990s: day 92 (2 April). Thus, as an immigrant, it would seem to have been arriving consistently earlier with each successive decade and some seven weeks earlier in the 1990s than in the 1960s.

In conclusion, the advancement of appearance since the 1970s of butterflies overwintering in Germany as imagines (mean −26 days) was significantly greater ($p < 0.05$ from ANOVA = analysis of variance) than that of immigrants or species overwintering in other stages. However, of those overwintering as pupae, the advancement of the 1990s over the 1970s was substantial in only two species, *P. rapae* and *P. napi*, (mean −14 days). Two other species, *P. machaon* and *P. brassicae*, were substantially later (mean +13 days) and there was no apparent difference in the case of a fifth species, *I. podalirius*.

Results of analyses of data on moths in the Netherlands, Germany and Britain

Survey by Ellis et al., (1997) and Kuchlein & Ellis (1997) of the average peak-flight dates of 104 common species of Microlepidoptera in the Netherlands during the period of 1975–94 produced an advancement of 12 days over this period. This shift, which was relatively small compared with some reported phenological trends, could be predicted.

In Germany, J.F.B. (Table 3) has extracted from Atalanta and analysed published first dates of appearance of 18 species of larger moths (Macrolepidoptera), all of which are migratory, though most are resident and only partial migrants). This gives a mixed picture: of these 18 species, compared with the 1970s, seven were appearing on the wing earlier in the 1990s, by about a week in the cases of three of them, almost two weeks in the case of *Macdunnoughia confusa* (Stephens, 1850) and by around five weeks in the cases of *M. stellatarum* and *Phlogophora meticulosa* (L., 1758). One species, *Acherontia atropos* (L., 1758), showed no change. *M. confusa* appeared 13 days earlier compared with the 1970s. The 10 species which appeared later in the 1990s than in the 1970s did so by up to about three weeks, except for *Agrius convolvuli* (L., 1758), which was more than five weeks later. So, as far as the influence of climate change is concerned, the results of this analysis seem inconclusive. If that is the chief causal factor then some are responding favourably to it and others unfavourably, depending presumably on differences in their ecological requirements. Only *M. stellatarum, N. pronuba, Mythimna albipuncta* (D. & S., 1775), *P. meticulosa* and *M. confusa* seem to be significantly earlier than in the 1970s. The others may perhaps have been adversely affected more by the frequent unsettled and rather cold springs of the past 30 years.

Once again, as pointed out by Burton & Sparks (2002), the timing of the flight period of the species seems to have an influence on the results. It is clear that most change has occurred in early-appearing species, whilst those appearing later in the year have become later still. This is true for both butterflies ($r = 0.48$, $p < 0.05$) and moths ($r = 0.60$, $p < 0.01$). Figure 4 shows a general pattern for advance (earliness) in early species and a delay in later ones. In Figure 5 (moths only), the pattern is confused by the extreme point of *Omphaloscelis lunosa* (Haworth, 1809) (mean 10th September, change six days). When this species is excluded, the relationship is significant ($p < 0.05$).

Table 3: Dates in days from 1st January of first appearance of imagines of moths in southern Germany.

Species	Years of data	1960s	1970s	1980s	1990s	1990s difference from 60s	1990s difference from 70s	1990s difference from 80s
Acherontia atropos (L.)	26	145 (25 May)	174 (23 Jun)	191 (10 Jul)	174 (23 Jun)	+29 days	0 days	−17 days
Agrius convolvuli (L.)	34	162 (11 Jun)	174 (23 Jun)	200 (19 Jul)	212 (31 Jul)	+50 days	+38 days	+12 days
Macroglossum stellatarum (L.)	34	124 (4 May)	120 (30 Apr)	116 (26 Apr)	81 (22 Mar)	−43 days	−39 days	−35 days
**Hyles galii* (ROTT.)	17	-	153 (2 Jun)	189 (8 Jul)	168 (17 Jun)	-	+15 days	−21 days
H. euphorbiae (L.)	23	-	*148 (28 May)*	155 (4 Jun)	164 (13 Jun)	-	+16 days	+9 days
Agrotis ipsilon HUFN.	25	*114 (24 Apr)*	*141 (21 May)*	155 (4 Jun)	163 (12 Jun)	+49 days	+22 days	+8 days
**A. segetum* D. & S.	19	-	137 (17 May)	144 (24 May)	139 (19 May)	-	+2 days	−5 days
**A. exclamationis* (L.)	20	-	134 (14 May)	138 (18 May)	131 (11 May)	-	−3 days	−7 days
**Noctua pronuba* (L.)	20	-	146 (26 May)	151 (31 May)	140 (20 May)	-	−6 days	−11 days
**N. fimbriata* SCHREBER	19	-	170 (19 Jun)	182 (1 Jul)	183 (2 Jul)	-	+13 days	+1 day
**Xestia c-nigrum* L.	25	*147 (27 May)*	128 (8 May)	129 (9 May)	137 (17 May)	−10 days	+9 days	+8 days
**Mythimna albipuncta* D. & S.	23	-	142 (22 May)	139 (19 May)	135 (15 May)	-	−7 days	−4 days
**M. l-album* L.	21	-	164 (13 Jun)	164 (13 Jun)	166 (15 Jun)	-	+2 days	+2 days
**Omphaloscelis lunosa* HAW.	21	*281 (29 Sep)*	256 (4 Sep)	264 (12 Sep)	262 (10 Sep)	−19 days	+6 days	−2 days
Phlogophora meticulosa L.	23	-	95 (5 Apr)	110 (20 Apr)	61 (2 Mar)	-	−34 days	−49 days
**Macdunnoughia confusa* STEPH.	24	*142 (22 May)*	129 (9 May)	143 (23 May)	116 (25 Apr)	−26 days	−13 days	−27 days
Autographa gamma (L.)	28	107 (17 Apr)	128 (8 May)	126 (6 May)	*125 (5 May)*	+18 days	−3 days	−1 day
**A. bractea* D. & S.	20	-	174 (23 Jun)	188 (7 Jul)	*186 (5 Jul)*	-	+12 days	−2 days
Average						+6 days	+2 days	−8 days

Notes: 1. Averages in italics are based upon fewer than five years of data. 2. species with fewer than 17 years of records are excluded; all but *H. gallii*, *A. segetum* and *N. fimbriata* have, however, more than 20. 3. Species marked with an asterisk * are mainly resident in Germany, but also migrate within their range; the others are entirely or almost entirely immigrants. 4. Averages working out at .5 or above are rounded upwards (e. g., 4.5 is counted as 5), whereas less than .5 are rounded downwards (e. g., 4.4 is counted as 4).

At Selborne in north-east Hampshire, England, ASTON (2001) has kept a careful record since 1992 of the dates of his first capture of non-hibernating moths in his mercury vapour light trap. So far, he has found that, of 381 species emerging in the months January to July inclusive, 246 (64.6%) arrived earlier in the period 1995–97 than in 1992–94. Twenty other species (5.2%) had the same earliest date in both periods, whilst 115 (30.2%) arrived later in the period 1995–97. Over the course of both periods, 119 (31.2%) of them appeared up to a month earlier than normally expected. Preliminary results from the long-term light trapping undertaken since 1976 by the Rothamsted Insect Survey (RIS) at six widely spaced sites in Britain also demonstrated an increasing tendency, consistent with climate change, for some species of moths to emerge anything up to three weeks or more earlier (WOIWOD, 1997). Moreover, many species of Lepidoptera, previously univoltine as a rule in Britain, are now regularly producing second generations as they normally do on the European mainland.

Other insect groups

Similar situations are already being identified in other insect groups, such as the Odonata (OTT, 1996), Orthoptera and Diptera. For example, recent analysis by MORRIS (2000) of 15 years of data (1985–1999) collected for some of the commoner spring-flying hoverflies in Surrey, England, has produced clear evidence of a shift to earlier appearance than formerly in apparent response to changing weather conditions.

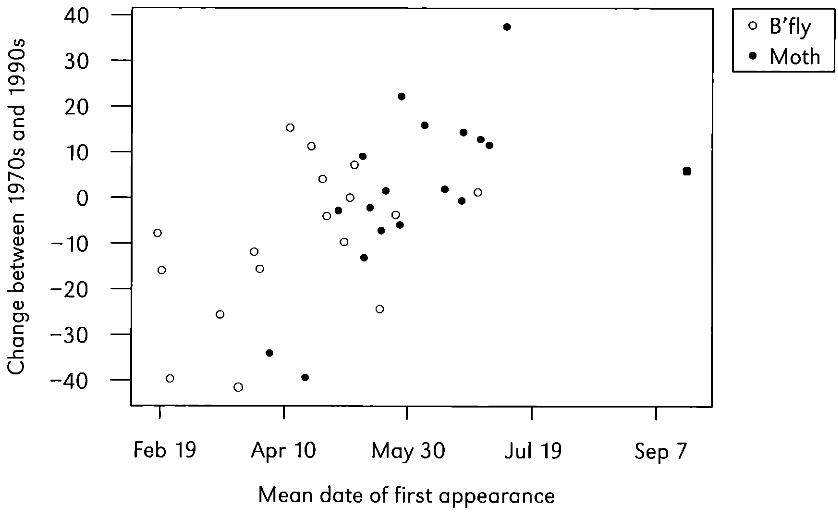

Fig. 4: The relationship between first-appearance date and advancement of appearance of Lepidoptera (butterflies and moths) in southern Germany.

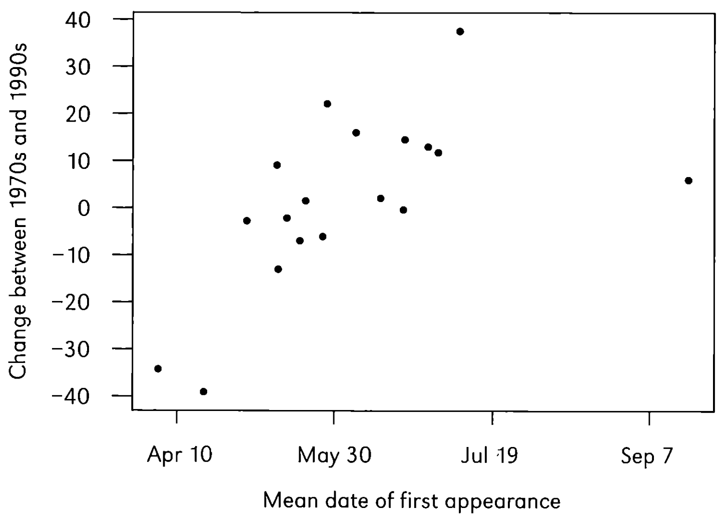

Fig. 5: The relationship between first-appearance date and advancement of appearance of Heterocera (moths) in southern Germany.

Conclusions

Whichever set of data one examines, they all indicate that many species of Lepidoptera are appearing on the wing significantly earlier than a decade or more ago, early enough for some normally univoltine species in Britain to complete their life cycle in time to produce a second generation (or even more) before the onset of winter.
With this information, we are, perhaps, on surer ground in providing evidence of the reality of the effects of recent climate change. Convincing evidence of a link between changes in temperature over the course of recent decades and the timing of such natural events as the appearance of Lepidoptera on the wing each year is growing, as we hope this paper has made clear.

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