Recent shifts in phenology of Microlepidoptera, related to climatic change (Lepidoptera)

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Abstract: 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. Insect populations living in temperate climates generally have one or more generations per year, punctuated by the winter resting period. We hypothesised that a gradual shift in the timing of these generations towards an earlier date will take place. For this purpose we analysed the phenology of a large sample of the most common Microlepidoptera in The Netherlands. Our results show that during the period 1975 - 1994 the flight peak has shifted to a date 11.6 days on average earlier. This shift is primarily associated with a rise in spring temperatures. The phenological data are based on a large body of observations brought together at little cost by amateur recorders, and the results suggest a relatively inexpensive method of monitoring future climatic change.

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Introduction

A global change of our climate is becoming more and more apparent, and the discussion about its reality is taken over now by predictions about its multifarious effects (e.g., Dennis, 1993; Harrington & Woiwod, 1995; Kennedy, 1995; Sparks & Carey, 1995; Woiwod, in press; Woiwod & Harrington, 1994). Organisms respond to a rise in ambient temperature by an acceleration of their development, as long as temperatures remain below lethal values. This means that organisms in temperate regions living shorter than one year, reach maturity at an earlier calendar date. Insects in particular, and many other cryptobionts, would pass through their larval stages faster, and become adult earlier, under the regime of a global rise in temperature.

Material and methods

We tested this hypothesis on 104 of the most common species of Microlepidoptera in The Netherlands. Since about 1955 nocturnal moths (to which most Microlopidoptera belong) are mostly collected with light-traps. The automated versions of these traps in particular capture large numbers aselectively, ena-

bling a fairly unbiased estimate of their occurrence and phenology. Records before about 1955 are much more scanty, and the numbers are lower. The Tinea foundation maintains a database containing faunistical and phenological data of Heterocera in The Netherlands. The database includes almost 1400 species of Microlepidoptera (approximately 340 000 records). Each record refers to one or more specimens of a single species, date, and locality. The 104 species were selected as being well represented in the database, and covering a wide range of families (table 1). The relatively few species known to hibernate as adults were excluded. For the present study records were selected of specimens collected or observed as adults in the field; records with dubious or imprecise data or identifications were omitted. Many of the smallest species are usually collected as larvae, and these species are therefore underrepresented in our sample. For each species, the information about a particular year was used only if the number of observed specimens was at least 30. This limit is fairly low, possibly introducing some additional noise in the data. We did not set a higher limit because that might lead to a skip of species-years simply because the species had a "bad year", which might introduce a bias. One species

Table 1. List of the species used in the study. Provided are: species name (nomenclature following Kuchlein & Donner, 1993), voltinism (either 1 or 2 peaks/ year), number of usable years (with number of individuals recorded ≥ 30) from the start of the observations on, average peak and distributional preference for the northern, central or southern sector (indicated only when O_{sz}/E_{sz} -1 ≥ 0.3 and $P \leq 0.01$, where O_{sz} is the number of records of species s in sector z, and E_{sz} is the expected value, based on the marginal total for all species included in the study; the probability was calculated using a G-test, cf. Sokal & Rohlf, 1995).

| species	peaks	n	av. peak	dist
Adelidae				
Adela reaumurella	1	17	11-May	N
Nemophora degeerella	1	15	10-Jun	N
Bucculatricidae				
Bucculatrix ulmella	2	7	12-May	C
Choreutidae				
Anthophila fabriciana	2	12	16-Jun	N
Coleophoridae				
Coleophora laricella	1	13	05-Jun	C
Coleophora serratella	1	14	30-Jun	
Elachistidae				
Elachista apicipunctella	1	3	06-May	N
Elachista cerusella	2	13	02-Jun	
Gelechiidae				
Aristotelia ericinella	1	7	18-Jul	
Exoteleia dodecella	1	10	02-Jul	C
Neofaculta ericetella	1	10	23-May	N
Teleiodes proximella	1	8	10-Jun	N
Teleiodes vulgella	1	1	03-Jul	C
Gracillariidae				
Caloptilia alchimiella	2	18	24-May	
Phyllonorycter harrisella	2	10	22-May	C
Phyllonorycter quercifoliella	2	9	12-May	N
Incurvariidae				
Incurvaria masculella	1	10	14-May	N
Nepticulidae				
Ectoedemia albifasciella	1	8	05-Jun	S
Oecophoridae				
Batia lunaris	1	6	23-Jun	
Batia unitella	1	6	16-Jul	C
Carcina quercana	1	21	01-Aug	
Denisia stipella	1	1	25-May	
Diurnea fagella	1	19	09-Apr	
Diurnea phryganella	1	3	02-Nov	
Ethmia funerella	1	6	22-Jun	C
Pleurota bicostella	1	8	12-Jun	
Stathmopoda pedella	1	5	11-Jul	N
Plutellidae				
Plutella xylostella	1	31	23-May	N
Pterophoridae				
Platyptilia gonodactyla	2	0	-	
Pterophorus pentadactyla	1	9	30-Jun	N
Pyralidae				
Agriphila inquinatella	1	25	06-Aug	NS
Agriphila straminella	1	44	22-Jul	
Agriphila tristella	1	36	05-Aug	
Anerastia lotella	1	11	01-Jul	
Aphomia sociella	1	14	08-Jun	C
Cataclysta lemnata	1	16	21-Jun	N
Catoptria margaritella	1	12	10-Jul	N
Chilo phragmitella	1	24	27-Jun	
Chrysoteuchia culmella	1	44	27-Jun	
Crambus ericella	2	7	19-Jul	
Crambus lathoniellus	1	35	14-Jun	N
Crambus pascuella	1	21	29-Jun	S
Crambus perlella	1	36	05-Jul	S
Elophila nymphaeata	1	21	25-Jun	N
Endotricha flammealis	1	19	22-Jul	N
Eurrhypara hortulata	1	25	01-Jun	
Evergestis forficalis	1	23	03-Jun	
Hypsopygia costalis	1	21	24-Jun	S
Metriostola betulae	1	10	23-Jun	S
Numonia advenella	1	16	03-Aug	S
Ostrinia nubilalis	1	14	06-Jul	S
Phycita roborella	1	22	29-Jul	S
Pleuroptya ruralis	1	28	28-Jul	S
Pyrausta aurata	2	16	25-May	
Schoenobius forficella	1	19	09-Jul	C
Scoparia ambigualis	1	24	20-Jun	N
Synaphe punctalis	1	17	19-Jul	N
Tischeriidae				
Tischeria ekebladella	1	9	10-Jun	
Tortricidae				
Agapeta hamana	1	8	08-Jul	
Aleimma loeflingiana	1	17	29-Jun	
Ancylis achatana	1	8	26-Jun	C
Ancylis mitterbacheriana	1	10	02-Jun	C
Apotomis betuletana	1	20	06-Aug	
Archips podana	1	27	04-Jul	S
Archips xylosteana	1	26	09-Jul	S
Bactra lancealana	2	12	09-Jun	N
Capua vulgana	1	14	25-May	C
Celypha striana	1	15	06-Jul	C
Choristoneura hebenstreitella	1	5	12-Jun	N
Clepsis consimilana	1	12	03-Jul	
Clepsis spectrana	1	19	14-Jun	
Cydia pomonella	1	23	19-Jun	S
Cydia splendana	1	18	18-Jul	
Epiblema cynosbatella	1	3	23-Jun	N
Epiblema rosaecolana	1	11	27-Jun	C
Epiblema uddmanniana	1	13	29-Jun	N
Epinotia bilunana	1	4	17-Jun	
Epinotia immundana	2	11	14-May	N
Epinotia nisella	1	1	23-Aug	
Epinotia solandriana	1	6	24-Jul	
Epinotia tedella	2	6	31-May	N
Epinotia tetraquetrana	1	5	18-May	S
Eucosma cana	1	13	06-Jul	
Eupoecilia angustana	1	5	28-Jun	
Gypsonoma dealbana	1	14	08-Jul	
Hedya dimidioalba	1	25	26-Jun	S
Lathronympha strigana	1	11	19-Jun	S
Olethreutes arcuella	1	3	10-Jun	
Olethreutes bifasciana	1	8	05-Jul	N
Olethreutes lacunana	1	24	21-Jun	
Olethreutes schulziana	2	12	05-Jun	N
Pandemis cerasana	1	26	27-Jun	
Rhopobota naevana	1	13	25-Jul	C
Tortricodes alternella	1	14	22-Mar	
Tortrix viridana	1	30	24-Jun	
Zeiraphera isertana	1	17	13-Jul	
Yponomeutidae				
Argyresthia bonnetella	1	4	14-Jul	C
Argyresthia brockeella	1	11	28-Jun	N
Argyresthia conjugella	1	10	08-Jun	N
Argyresthia goedartella	1	19	29-Jul	
Argyresthia pruniella	1	7	07-Jul	
Argyresthia retinella	1	13	28-Jun	
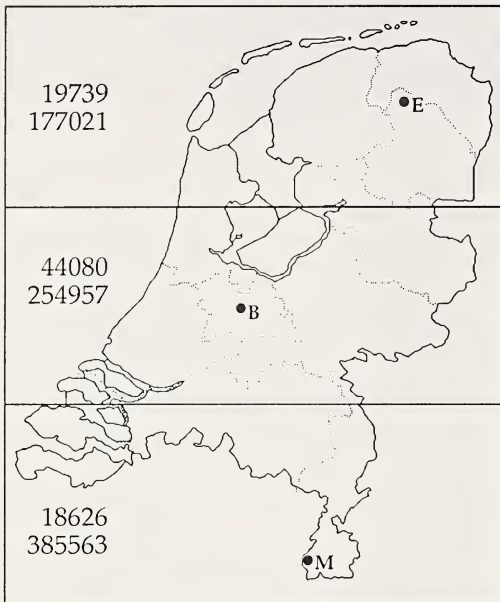
Fig. 1. Sketch map of The Netherlands, indicating the three sectors into which we divided the country and the location of the three weather stations (Eelde, de Bilt and Maastricht). The values give the number of records (top) and the number of individuals that have been sampled over all years and all 104 species of the study. The striking discrepancy between the two values in the southern sector is caused by mass flights of *Plutella xylostella* (Linnaeus) in 1962 and 1986.

failed this criterium for all years and was not used further. Because the number of usable species-year observations before 1955 are relatively small (25 datapoints), we limited our analysis to the period 1955-1994 (1485 datapoints); introduction of the pre-1955 data into the regressions did not change the results to a notable extent.

Because temperatures in the northern part of the country are appreciably lower than in the south, and many insect species have either a preponderantly northern or southern distribu-

tion, it was deemed useful to study the phenology on a narrower geographic scale. To this end, we divided the country into a northern, central and southern sector (fig. 1). Many of the species were recorded preponderantly in one of the sectors (table 1). If the number of specimens per species, year and sector were at least 30, calculations were done not only for the country as a whole, but also per sector.

As a benchmark of the phenology of a species we chose the peak of occurrence, which obviously is more reliable than the date of its first observation. A small computer programme selected for each species, for each acceptable year, the first date of observation (all dates are expressed as Julian dates, i.e. 1..365). A running average of the number of individuals over 21 days was then calculated for each of the 50 days following the first day of occurrence of the species. The day with the highest running average value was taken as its peak date. A limited number of species are bivoltine, having two annual peaks, each consisting of one or more overlapping generations (table 1); in these cases only the first peak was taken into account. To make the peak dates of the species comparable, we standardised them to a value D (Deviation): D_{sy} = observed peak date of species s in year y minus the average peak date of species s over all acceptable years.

We compared our results with monthly temperature data, obtained by the Royal Netherlands' Meteorological Institute ("KNMI") for representative locations in the three sectors (Eelde, de Bilt, and Maastricht, respectively; fig. 1). These monthly temperature values are averages of 24 hourly readings per day. A country-wide average was calculated over these three values. We tested for a relation between the value of D_{sy} (both regional

Table 2. Results of a simultaneous linear regression of D' on the calendar year and average temperatures in previous winter, spring, and summer. (β Is the standardized form of the regression coefficient (b); its value enables comparison of the relative contribution of the independent variables in the prediction of D'.)

variable	β	st. error (β)	b	std. error (b)	t(df=1399)	P
year	0.0180	0.0247	0.0020	0.0021	0.7300	0.4653
winter	-0.0570	0.0261	-0.0480	0.0220	-2.1800	0.0294
spring	-0.4960	0.0244	-0.5010	0.0247	-20.3100	0.0000
summer	-0.1070	0.0247	-0.1100	0.0255	-4.3200	0.0000

Fig. 2. Trend lines of the values of *D* of all species (heavy line, left axis; the 1490 individual data points not shown), and of the yearly average temperatures in The Netherlands (°C, thin line, right axis) in the period 1950 - 1994. (Trends are calculated using the locally weighted least square error method; smoothing factor 66%).
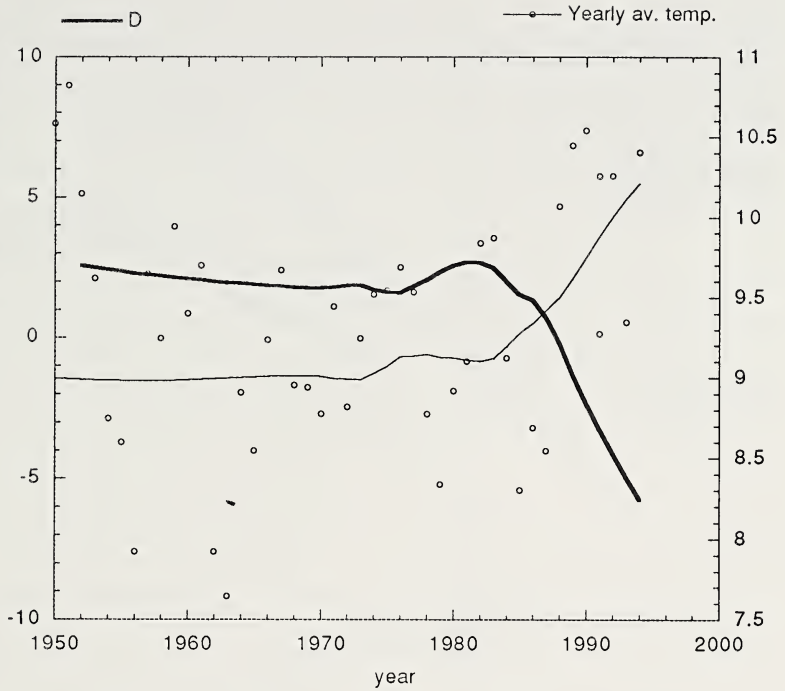
and country-wide) by simultaneous linear regression with the following three temperature values: winter (average of the months October-December of year y-1, January-March of year y), spring (April-June of year y), and summer temperature (July-September of year y). Moreover, the calendar year was entered to allow for the possibility that an additional trend might be present that was not explained by the three temperature values. To improve the normality of the residues after regression, *D* was transformed as $D' = 0$ if $D = 0$, $(D/(abs(D))*log(abs(D)))$ if $D \neq 0$. Missing data were handled by casewise deletion.

Results

The peak date in the northern sector occurs on average 5.1 days later than in the southern sector (Paired *t*-test; *t*=3.558, df=185; *P*<0.001); the median peak date over the whole country is on day 180 (June, 29). The yearly average temperature (1950-1994) is 8.8°, 9.5° and 9.7° C in the northern, central and southern sector, respectively.

As predicted by our hypothesis, *D* de-

creased with the calendar year. This decrease is visible in all sectors and country-wide; it is expressed most strongly in the last two decades (fig. 2). Figure 3 shows this for the two species that produced most datapoints. The linear regression coefficient *(b)* for the central sector was -0.39 *(N=228; P=0.034)* in the period 1955-1975, and -0.58 (*N*=821; *P* < 0.000) in 1976-1994. Analyses of the other sectors and the country as a whole gave similar results. This implies a negative shift in average peak date of 11.6 days during the last twenty years. In that period the yearly average temperature rose from 9.0° to 9.9° C (linear regression).

As fig. 2 indicates, there is a negative correlation between annual mean temperature and *D*. Figure 4 shows the regression lines for the country as a whole, and the three sectors separately. To analyse this in more detail, a simultaneous linear regression was done of *D'* on yearly temperatures; table 2 shows the results for all observations (country-wide) since 1955 (*N*=1404, *P*=0.000). The regression is clearly dominated by the spring temperature; the effect of the summer temperature is much

Fig. 3. Trend lines of the values of D for the two species that offfered the highest number of usable data-points, viz. *Chrysoteuchia culmella* (Linnaeus) and *Agriphila straminella* (Denis & Schiffermüller).
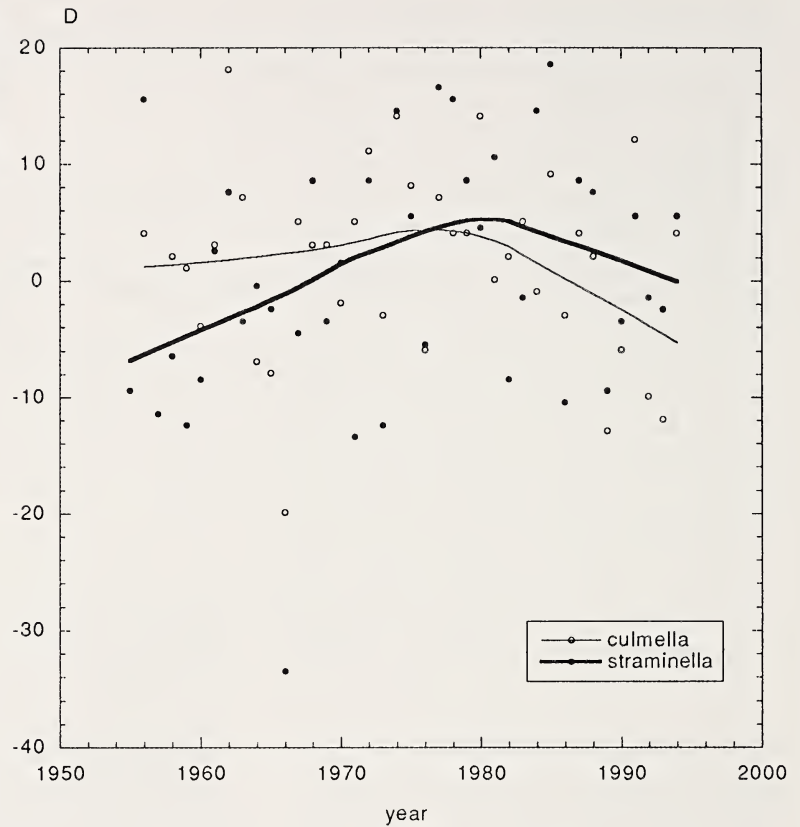
more limited. The contribution by the winter temperature is significant but very low; and the factor 'year' has nothing to contribute.

Similar multiple regressions, calculated separately for uni- and multivoltine species, or for the species with a mainly northern, central, or southern distribution in The Netherlands, did not show appreciable differences. In particular, the pervasive effect of spring temperature was apparent. Not surprisingly, when species were segregated by their average peak date, the species with an average flight peak before June 29 showed no effect of summer temperature (β for spring and summer -0.353 and -0.000, respectively) while those peaking on average after that date were significantly influenced by the summer temperature as well (β -0.478 and -0.156).

Discussion

The difference in yearly average temperature between the southern and northern sector is 1.1 °C; this accounts for a difference in flight peak date of 5.1 days. The countrywide temperature rose since 1975 with approximately 0.9 °C, which has resulted in a phenological shift of 11.6 days. These two data pairs, although not fully congruous, may serve as an indication of the phenological effects of temperature changes.

The current trend of warming up of the planet may have started as early as 1900. Even so, between about 1935 and 1975 there is an interruption in the trend with more or less normal, albeit fluctuating, temperatures (Graves & Reavy, 1996). Our data span the end of this relatively cool period, and the current warm period. The break in temperature trend around 1975, and its effect, is well illustrated in our results (fig. 2 and 3).

A comparable shift in flight date was found for aphids in Great Britain by Fleming & Tatchell (1994, 1995) who observed an advan-

Fig. 4. Linear regression of all species' values of D on yearly average temperature, both countrywide and for the three sectors separately (period 1955 - 1994; individual datapoints not shown).
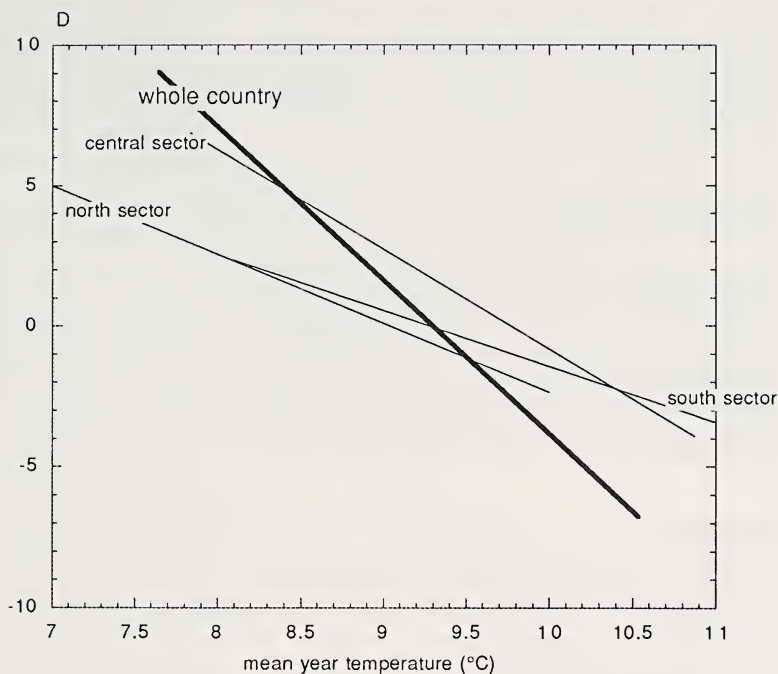
ce of 3-6 days over the last 25 years. In the case of aphids, however, the effects of climate may be more complicated; the flight phenology was most strongly dominated by winter temperatures (Harrington et al., 1995; Zhou et al., 1995). Our results indicate a strong general shift in flight peak primarily induced by rising spring temperatures. Our data are not sufficient to analyse this at the specific level in more than a few cases. Yet it is clear at least that there is no fundamental difference between early flying species (before the end of June) and late species. This contrasts with the results obtained for plants by Fitter et al. (1995), who found that in the south of England, late species come into flower earlier when temperatures are up, but early plants species are retarded. Probably this is connected with the fact that the flowering season starts at a moment when most insect species are still dormant, and the perennial habit of most plant species. Such a situation may lead to a mismatch in phenology of flowers and their pollinators.

It has been assumed that the rising global CO_2 level would only have limited effects on plant-herbivore interaction (Bazzaz, 1990).

Our results suggest that the associated rising temperatures sufficiently alter the phenology of herbivorous insects to have profound effects on their interactions with host plants. These effects will probably be even stronger in short-lived phytophages such as spider mites, that can have many generations per season. There are also many, albeit anecdotal suggestions that insect species are extending their distributional area northward (e.g., De Vos & Zumkehr, 1995). That insects indeed are capable of extensive shifts of distribution is amply documented in the late Pleistocene record (Coope, 1973, 1990, 1995). This mobility is matched by a 500-1000 km northward shift that has been predicted from North American plants (Overpeck et al., 1991). The implication is that plant populations may become exposed not only to herbivores that develop faster, but also to novel herbivore species (Bond, 1995; Graves & Reavey, 1996).

For this, and many other reasons it is imperative that the global change in temperature, and its multifarious effects on ecosystems, is thoroughly monitored. An example of such an approach, based on data from the British Butterfly Monitoring Scheme, is given by

Pollard (1988). Monitoring projects like the one reported on here, offer an inexpensive, yet powerful tool, once more stressing the role amateur entomologists play in the management of nature and environment.

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