



Drivers of moth phenology in England and Wales

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Abstract

Climate change has led to changes in the phenology of Lepidoptera species. While phenological shifts have been previously measured for moth species in England and Wales, the drivers of these shifts are not well known. Here, we use data from the National Moth Recording Scheme and the Garden Moth Scheme to investigate the drivers of phenology in 149 moth species over a 50 year period from 1970 to 2019. We investigate whether there have been phenological shifts in adult emergence using three phenology metrics: First Emergence (FE), Peak Emergence (PE), and Emergence Standard Deviation (ESD) in relation to life history traits and temperature. Overwintering stage had a significant impact on moth phenology, so we analysed species that spend the winter as eggs, larvae or pupae separately. Overall phenological changes were different depending on overwintering stage category and phenological measure, with the rate of phenological shifts increasing with later overwintering life stages in response to both temperature and year. The overwintering stage larva was the only one impacted by diet, with those that feed on woody hostplants emerging ~17 days later than species with herbaceous hostplants. These results indicate that species that either overwinter in earlier life stages or have woody hostplants may be less adaptable to climate change, and thus should be the targets of conservation efforts.

Keywords Phenology · Climate change · Lepidoptera · Life history traits · Linear mixed effects modelling

Introduction

Climate change is impacting many species, especially in relation to their phenology, or timing of their life cycles (Visser and Holleman 2001; Van Asch et al. 2007; Scheffers et al. 2016; Cohen et al. 2018). Lepidoptera are ideal subjects for studying climate change impacts on a large scale, due to their wide distribution and well-understood life-history and taxonomy (Heikkinen et al. 2010; Hill et al. 2021). As poikilothermic insects, Lepidoptera are responsive to temperature (O'Neill et al. 2012), and being such a species-rich group, they contain both economically significant pests and those with a high conservation status (Sparks et al.

2006). Due to their short generation times and considerable phenotypic plasticity, Lepidoptera can respond quickly to climate change, which means we are able to see trends over relatively short time scales (Välimäki et al. 2013; Hill et al. 2021). Further, being charismatic insects, extensive long-term citizen-science data exist in some countries that can be utilised to examine the large-scale impacts of climate change on phenology (O'Neill et al. 2012).

Much research has been done on the phenology of Lepidoptera. Key findings include advanced first emergences (Roy and Sparks 2000; Bonoan et al. 2021; Hällfors et al. 2021), changes in mean flight date (Randle et al. 2019) and flight period length (Altermatt 2010a; Valtonen et al. 2011; O'Neill et al. 2012), and increasing multivoltinism (Altermatt 2010a; Välimäki et al. 2013; Teder 2020), as well as cases of altered body size and fecundity (Honěk 1993; García-Barros 2000; Davidowitz and Nijhout 2004), likely due to temperature altering growth rates. Furthermore, changes in phenology can have implications for population change. Both Macgregor et al. (2019) and Hällfors et al. (2021) found that species that shift their phenology may benefit from the ability to alter their distribution faster than species with a smaller phenological shift. These diverse responses, from

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small-scale changes such as body size up to large-scale population impacts, make predicting the impacts of climate change on Lepidoptera difficult.

The timing of environmental cues can influence the timing of Lepidopteran phenology, as well as that of their larval hostplants. Higher temperatures can cause plants to leaf out earlier (Sherry et al. 2007; Steltzer and Post 2009), and for Lepidoptera to end overwinter diapause earlier (Parmesan 2007; Lindestad et al. 2020). For Lepidoptera species that are dietary specialists, they may lose synchrony with their host plants, leading to mismatched phenology with fitness consequences for the larvae, and impacts on population viability (Visser and Holleman 2001; Van Asch et al. 2007; Pelini et al. 2009; Navarro-Cano et al. 2015). Similarly, species that utilise other environmental cues, such as photoperiod, for diapause induction and termination face a further risk of mismatching if their hostplants are responding to temperature (Sims 2007; Lindestad et al. 2020). A longer favourable season means that Lepidoptera species that have the capacity for multiple generations may build larger populations and/or have more generations due to earlier emergence (Macgregor et al. 2019; Keret et al. 2020; Michielini et al. 2021). Multivoltine species generally have more facultative diapause, for example by lowering the photoperiodic response threshold, but risk being caught out in a developmental trap if they are not ready to enter diapause when winter begins (Tauber et al. 1986; Musolin and Saulich 2012; Van Dyck et al. 2015; Teder 2020). The life stage at which species overwinter appears important for their ability to respond to climatic changes; later life stages are able to reach adulthood faster after winter once the conditions are favourable, providing flexibility in their phenological response to climatic changes (O'Neill et al. 2012; Végvári et al. 2015). Further, the life stage of diapause can influence the way they respond to climate change. Hällfors et al. (2021) found that while overwintering adults were more likely to advance their phenology, species that overwintered as pupa were more likely to undergo range shifts. While it is evident that life history traits play an important part in species' response to climate change, the relative importance of different traits in determining species' responses is still unclear. Many studies have sought to find traits that can predict species response to climate change, but this may not be possible due to the variety of both species and the anthropogenic forces that may impact them (Fox 2013; Wagner et al. 2021; Tordoff et al. 2022). Nevertheless, trait-based studies such as Tordoff et al. (2022) have linked various life history traits to distribution and abundance trends of British moths. Predicting the response of data-deficient species based on their traits is difficult, but it is clear that traits do play a part in species' responses to environmental change. While we have knowledge of which traits impact species' distribution,

the relationship between life history traits and phenological shifts is less clear.

There are many ways to measure changes in species phenology, and species may respond differently to environmental changes at different parts of the season. As well as this, the type of data has to be considered when calculating phenological metrics, and scarcity of standardised, systemic monitoring data has led to an increase in the use of citizen science data for phenological studies (Dickinson et al. 2010; O'Neill et al. 2012; Bishop et al. 2013). Amateur naturalists have been recording the natural world for hundreds of years, with more than 80 recording schemes and societies in the UK alone (Roy et al. 2014). Recorder bias is a significant problem, as there is undoubtedly a period of training as amateur naturalists learn to identify organisms, as well as preference for particular locations and times of recording, a bias which is liable to change over time and between regions (Dickinson et al. 2010; O'Neill et al. 2012). Still, the development of recording schemes to collect datasets with enough information to show long-term spatial and temporal changes is a difficult challenge that requires a large amount of effort on behalf of the volunteer recorders and organisers (Bishop et al. 2013). Such problems are an important consideration in studies that use citizen science data as these can impact results, although methods exist to standardise data to improve reliability of conclusions drawn (Van Strien et al. 2008).

In this article, we utilise long-term citizen science data from 1970 to 2019 on spatial distributions of 149 moth species in England and Wales to investigate drivers of the phenological response of these species to climate change. First, we compare the phenology and phenological shifts across species with different overwintering life stages. We postulate that the way in which species respond to environmental cues, and thus how their phenology responds to global climatic changes, is influenced by their life history traits. We therefore assess the extent to which patterns in species phenological responses of each of three overwintering stage categories (Egg, Larva and Pupa) are dependent on their recorded life history traits and cumulative mean temperature. To achieve these objectives, we used Linear Mixed Effects (LME) modelling to investigate how species differ in their response in space through the random effects of species and Watsonian Vice County.

Methods

Data sources

To analyse changes in moth phenology in Great Britain, data were sourced from two schemes: the National Moth

Recording Scheme (NMRS) (Butterfly Conservation 2022) and the Garden Moth Scheme (GMS) (GMS 2023). The NMRS data comprise presence records of species occurrence from across Britain collected in a non-standardised way by citizen scientists and verified by experienced Lepidopterists (Fox et al. 2011). Spatial and temporal coverage of NMRS records is extensive and has increased dramatically over time (Fox et al. 2011; Randle et al. 2019). We used NMRS data from 1970 to 2019. The GMS data are more standardised than those from the NMRS. As part of the GMS, citizen scientists use light traps in their residential gardens to count widespread moth species once a week from March to November (Bates et al. 2013). However, the trap type, sampling night and weather conditions are not standardised across sites. The scheme started in the West Midlands region of England in 2003 but was expanded across the UK from 2007, with 347 gardens participating in 2019 (Passey 2020). By obtaining data from both NMRS and GMS we aimed to increase the number of records of each species and increase the accuracy of the phenological measures. The final list of 149 species used after standardisation and filtering, their data sources and number of records can be found in Supplementary Table 1. While we recognise the limitations of citizen science data, which can be noisy and error-prone, we propose the advantages far outweigh these negatives (Van Strien et al. 2008; Dickinson et al. 2010). Citizen science provides a large amount of data that allows us to address questions that would otherwise be challenging to answer, and with a larger number of records it is possible to detect patterns at finer scales (Van Strien et al. 2008). Here, we use 3,687,320 records for 149 species from the combined NMRS and GMS data to generate phenological metrics that enable detection of temporal and spatial changes. However, it is worth noting that these are all records of adult moths and thus the data is not temporally structured in terms of life cycle development, hence the need to include life history traits. Life history trait data for each moth species were obtained from Cook et al. (2022), which is an up-to-date source of trait information for macro-moths in Britain and Ireland. Temperature data were obtained from the Met Office (Met Office et al. 2018), and a Cumulative Mean Temperature (CMT) variable was calculated for every 365 day period over the 50 year study period. Thus, for each day of the year, there was an associated CMT value that represented the temperature for the previous year (e.g. a CMT value for 23rd March 2016 to 23rd March 2017, then for the 24th March 2016–2017 and so on). This CMT value was calculated for each 10 km x 10 km grid square (coarse easting and northing) where data was available, and then averaged for each Watsonian Vice County (VC) in England and Wales. The result was a single mean CMT value for each VC for each day of the whole of the study period. The

process of cleaning these data for analysis is illustrated in Supplementary Information Fig. 1.

Phenological metrics, life history traits, and environmental variables

The rate of phenological change for moths may vary throughout the season, depending on the measure used, and spatially, as environmental variables can vary depending on location. We calculated each phenological metric within each Watsonian Vice County (VC) for each year, where there was enough data to do so. The VC system was first developed for plant species distributions and has been used since its conception at the end of the 19th century (Watson 1883). It provides an unchanging set of geographical boundaries within Great Britain. Moreover, by modelling at the VC level we remove zeros due to species absences, instead concentrating only on VCs within the range of each species. Thus, each species was filtered separately in each VC using the methods of Hällfors et al. (2021), whereby we only included species with trait data from Cook et al. (2022) that had at least 30 records a year for at least 10 years in each VC, resulting in 149 species included in the analyses. As a result of calculating at the VC level we had to remove all data from Scotland as there were too few records to meet the criteria of Hällfors et al. (2021), and thus the analysis only included England and Wales. Accordingly, three phenological metrics were derived for each species from the recorded data:

- First Emergence (FE) – the day of the year on which the first 25% of records had been observed for each species each year in each VC (*sensu* Van Strien et al. 2008). Thus, each VC had a separate FE calculated for each year based on the records only in that VC.
- Peak Emergence (PE) – the day with the highest number of records for each species each year in each VC. Where there were several days with the highest number of records, an average day of year was taken for the peak of emergence.
- Emergence Standard Deviation (ESD) – the standard deviation of the average peak emergence. As the standard deviation is the spread of records around the peak emergence it provides an indicator of the duration of the flight period for each species each year in each VC.

We included traits from Cook et al. (2022) that we hypothesised would be phenologically relevant, as they determined the ways in which a species interacts with its environment, and therefore the environmental cues that fine-tune phenology (Table 1). The environmental variables included were:

- Year: a continuous variable we took to both represent change through time, as well as unmeasured environmental variables that have changed linearly, such as precipitation.

Table 1 Seven life history traits used for the included in the analyses, with description from Cook et al. (2022). We hypothesised that these traits would be phenologically relevant and thus have an influence on the way moth species respond to changes in their environment due to global climatic change

Life History Traits	Description
Communal	Larvae that feed or bask communally or inhabit a communal nest.
Daily Activity Period	Listed as either Diurnal, Nocturnal or Both if at least one sex of the species is described as being active during that period.
Hostplant Category	Each species has single or multiple broad hostplant categories assigned depending on hostplants listed in Henwood, Sterling & Lewington (2020).
Number of Hostplants	The number of main and occasional hostplants the species is known to feed on as a larva, according to Henwood, Sterling and Lewington (2020).
Overwinter Stage	The life stage each species adopts as their overwintering strategy.
Pupa location	The location in which species form a pupa (e.g. below ground, externally on the hostplant, in dead wood).
Specificity	The phylogenetic variation in hostplants for each species (e.g. Oligophagous (Family), Oligophagous (Genus))

- Cumulative Mean Temperature - a temperature value that represents the temperature over a 365 day period, averaged for a VC. This was calculated for every rolling 365-day period from 1970 to 2019.

Modelling strategy

We investigated the effects of life history traits and environmental variables hypothesised as being important in determining moth species phenology, utilising three phenological metrics to measure phenological shifts at different points in the flight period of each species (see Sect. 2.2). Due to our concern that voltinism may be changing (Teder 2020), and the complications this would add for peak emergence, we only analysed univoltine moth species. Multivoltine species generally have one smaller and one larger peak, accurate identification of which on a large scale for hundreds of species would have been difficult. Further, due to their ability to have multiple population peaks each year, multivoltine species may respond in different ways to environmental cues, so aggregating univoltine and multivoltine species into one analysis would not be appropriate. Phenological measures can be biased due to recording effort and population changes, and this has to be considered when developing phenological measures from occurrence data (Van Strien et al. 2008; Bonoan et al. 2021). Prior to conducting the analyses, we tested for significant differences in the phenology of species in different categories for each trait, as this would violate the assumptions of Linear Mixed Effects (LME) models. We

found that the species in different overwintering stage categories were significantly different, and as such could not be analysed together (see Table 2). We therefore conducted the analyses on three overwintering stage categories that had at least 20 species in each: Egg, Larva, and Pupa. The distribution of species in each trait category and subfamily for the three overwintering stages can be seen in Figs. 2 and 3 in the Supplementary Information. We carried out a series of LME models with the overwintering stage categories, year and space (VC) for each phenological metric. To determine which of the trait and environmental variables explained the most variation, and therefore were the most important, we developed a series of LME models with environmental variables (see Sect. 2.2) and species' traits, listed in Table 1, as fixed effects. We included VC, Year, Species and Cumulative Mean Temperature as random effects. We then implemented a model selection process whereby the simplest model that explained the most variation was obtained by using stepwise reduction. For each overwintering stage and each phenological metric combination we included all fixed effects hypothesised to be important in determining phenological shifts and then removed non-significant variables stepwise until we obtained the "best" model. We compared each model iteration using AIC and marginal R^2 . Once we had the "best" model in terms of fixed effects, we tested the model with combinations of random effects in terms of AIC and conditional R^2 , until we obtained the final "best" model for each overwintering stage/phenological metrics combination. We used AIC to test for the "best" model as this penalizes overly complex models. All modelling was undertaken in R with R version 4.2.2 (2022-10-31 ucrt) (R Core Team 2022) and the following packages for analyses: tidyverse, nlme, lavaan (Wickham et al. 2019; Pinheiro et al. 2023).

Data structure and model selection

Cumulative mean temperatures for a location were averaged across a VC for each day in each year where data was available. Average cumulative mean temperatures for a VC (hereafter CMT) were matched to the day of year of FE and PE for each VC each year. Thus, for every VC each moth species would have two CMT values associated each year, one matched to FE and one to PE. As ESD is the spread of days around PE there are no CMT values associated with it. Hostplant Categories were simplified into whether the moth species fed on "Woody" or "Herbaceous" plants, or neither. We considered the importance of Pupa Location to be based on whether a species was exposed to the environment during the pupal stage. Accordingly, we also simplified Pupa Location to whether a species pupates in "Exposed" or "Covered" locations, or both. The number of species in each

classification was quite varied as for some traits one or a few categories dominated (Supplementary Information Fig. 2). Subfamily was also very variable in the number of species in each category (Supplementary Information Fig. 3). The “Year” covariable was altered to be a scale of 1–50 as larger numbers can influence model output (Pinheiro and Bates 2000). The overall distribution of each of the phenological metrics and the distribution of overwintering stages can be seen in (Fig. 1).

Results

We determined that we could not analyse all the species at once, as their phenology was highly influenced by their overwintering stage (Fig. 1). Thus, we chose to limit the data to the species that overwinter as either an egg (40 species), larva (65 species) or pupa (44 species) as their main strategy. To confirm we could not include these three overwinter stages in the same model, we ran lme models for each phenological metric, with each overwintering stage category and year as fixed effects, and year and VC as random effects, to see whether the groups were significantly different in their response. For First Emergence and Peak Emergence

the three overwintering stages were significantly different, and Pupa and Egg overwintering stages were significantly different for Emergence SD (Table 2).

Additionally, we tested whether the cumulative mean temperature for each vice county (CMTVC) variable varied with year, as we were including both as fixed effects in the following Linear mixed effects (LME) models that follow. We ran a series of LME models assessing whether the average temperature for each Day Of Year (DOY) in each vice county varied with the fixed effects harmonic variables for seasonality ($\cos(2 \times \pi \times \text{DOY}/365)$ and $\sin(2 \times \pi \times \text{DOY}/365)$) and Year, and the random effects Year and VC. While temperature and year were related in the best model, temperature was also influenced by seasonality and space (Supplementary Information Table 2). The random effects in the best model were Year per VC, which indicates that there is a spatial impact that varies per year independent of temperature. As such, neither the “Year” or “CMTVC” variables could represent the other in a model, as they account for different aspects of the environment a moth encounters, and both could be included without the impact of collinearity. Thus, there was a significant contribution of temperature that varied with VC in addition to the contribution of year. Further, the CMTVC variable, being cumulative, also

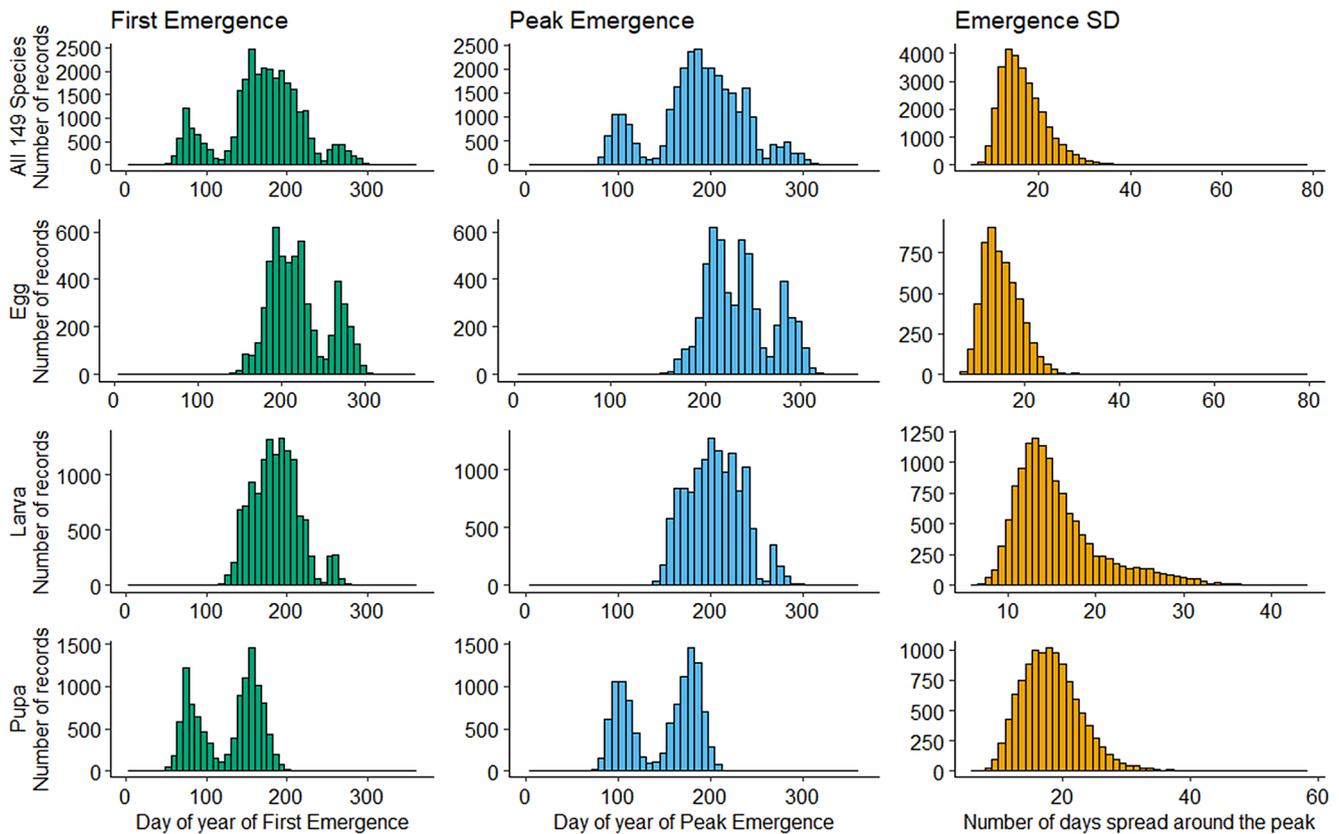


Fig. 1 The number of First Emergence and Peak Emergence records on each day of year, and the number of Emergence SD records of number of days spread, for all 149 species and for each overwintering stage category

Table 2 The results from the best LME model for each of the three phenological metrics when testing for significant difference between each of the overwintering stage categories

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
First Emergence	FE ~ Overwintering Stage + Year, random effect = Year per Watsonian Vice County nested in Species	(Intercept)	231.004	4.342	28,447	53.205	<0.001***
		Larva	-38.742	5.427	146	-7.138	<0.001***
		Pupa	-85.361	5.938	146	-14.375	<0.001***
		Year	-0.213	0.017	28,447	-12.630	<0.001***
Peak Emergence	PE ~ Overwintering Stage + Year, random effect = Year per Watsonian Vice County nested in Species	(Intercept)	243.922	4.335	28,447	56.273	<0.001***
		Larva	-41.920	5.417	146	-7.738	<0.001***
		Pupa	-88.860	5.927	146	-14.993	<0.001***
		Year	-0.035	0.017	28,447	-2.089	0.037*
Emergence SD	ESD ~ Overwintering Stage + Year, random effect = Year per Watsonian Vice County nested in Species	(Intercept)	14.389	0.464	28,447	31.037	<0.001***
		Larva	-0.410	0.577	146	-0.711	0.478 NS
		Pupa	2.382	0.631	146	3.772	<0.001***
		Year	0.018	0.005	28,447	3.663	<0.001***

Table 3 The results from the best LME model for egg overwintering species for each of the three phenological metrics

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
First Emergence	FE ~ Year + Cumulative Mean Temperature, random effect = Watsonian Vice County nested in Species	(Intercept)	275.795	5.839	5,319	47.230	<0.001***
		Year	-0.172	0.009	5,319	-18.484	<0.001***
		Cumulative Mean Temperature	-3.132	0.144	5,319	-21.788	<0.001***
Peak Emergence	PE ~ Year + Cumulative Mean Temperature, random effect = Watsonian Vice County nested in Species	(Intercept)	291.391	5.691	5,319	51.205	<0.001***
		Year	-0.040	0.008	5,319	-5.159	<0.001***
		Cumulative Mean Temperature	-3.438	0.125	5,319	-27.435	<0.001***
Emergence SD	ESD ~ Year, random effect = Watsonian Vice County nested in Species	(Intercept)	14.351	0.475	5,320	30.238	<0.001***
		Year	0.016	0.004	5,320	4.368	<0.001***

represents the metabolic impacts of temperature over the development period.

Egg overwintering species

The best LME models for the 40 species that overwinter as an egg included Year and CMTVC for both FE and PE and Year for ESD, no traits were significant. The slope of change for Year was the largest for FE at -0.172, compared to -0.040 for PE and 0.016 for ESD (Table 3). However, temperature affected PE the most as this had the larger slope of -3.438 compared to -3.132 for FE (Table 3).

Larva overwintering species

The best LME model for each phenological metric was not as consistent for larva overwintering stage as it was for egg. For both FE and PE the best model included Year, CMTVC, and the Hostplant Category trait. There were no traits significant for ESD so only Year was included. The woody hostplant category was significant and had the largest slope for both FE and PE, but the herbaceous hostplant category was not (Table 4). Temperature had a larger slope for FE at -3.276, compared to -3.033 for PE. There was a

large difference in the slope for Year for each phenological metric, with FE advancing much quicker than PE and ESD (Table 4).

Pupa overwintering species

The best LME models for species that overwinter as pupa were the same as for egg overwintering species, with Year and CMTVC included for FE and PE and Year for ESD. In comparison with the other overwintering stages, pupa had a much stronger response to temperature overall, but particularly for FE (Table 5). Further, the year response was also the strongest for all phenological metrics for pupa overwintering species, but particularly for FE as the slope was almost double the equivalent slope for egg and larva overwintering species (Tables 3, 4 and 5).

Discussion

Our results confirmed previous findings that the flight period phenology of univoltine moth species in England and Wales has changed significantly over the last 50 years. Moth flight periods are starting earlier in the year and overall duration

Table 4 The results from the best LME model for larva overwintering species

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
First Emergence	FE ~ Year + Cumulative Mean Temperature + Woody + Herbaceous, random effect = Watsonian Vice County nested in Species	(Intercept)	236.219	8.679	12,452	27.218	< 0.001***
		Year	-0.179	0.006	12,452	-28.137	< 0.001***
		Cumulative Mean Temperature	-3.276	0.084	12,452	-38.896	< 0.001***
		Hostplant Category: Woody	17.165	7.394	62	2.321	0.024*
		Hostplant Category: Herbaceous	-6.230	8.988	62	-0.693	0.491 NS
Peak Emergence	PE ~ Year + Cumulative Mean Temperature + Woody + Herbaceous, random effect = Watsonian Vice County nested in Species	(Intercept)	241.971	8.727	12,452	27.728	< 0.001***
		Year	0.020	0.005	12,452	3.804	< 0.001***
		Cumulative Mean Temperature	-3.033	0.075	12,452	-40.325	< 0.001***
		Hostplant Category: Woody	17.628	7.447	62	2.367	0.021*
		Hostplant Category: Herbaceous	-6.234	9.053	62	-0.689	0.494 NS
Emergence SD	ESD ~ Year, random effect = Watsonian Vice County nested in Species	(Intercept)	13.508	0.415	12,453	32.538	< 0.001***
		Year	0.035	0.003	12,453	13.833	< 0.001***

Table 5 The results from the best LME model for pupa overwintering species

Phenological Metric	Best Model	Variables	Value	Std.Error	DF	t-value	p-value
First Emergence	FE ~ Year + Cumulative Mean Temperature, random effect = Watsonian Vice County nested in Species	(Intercept)	210.645	5.374	10,671	39.198	< 0.001***
		Year	-0.308	0.009	10,671	-35.572	< 0.001***
		Cumulative Mean Temperature	-4.613	0.110	10,671	-42.008	< 0.001***
Peak Emergence	PE ~ Year + Cumulative Mean Temperature, random effect = Watsonian Vice County nested in Species	(Intercept)	213.509	5.330	10,671	40.060	< 0.001***
		Year	-0.049	0.007	10,671	-7.051	< 0.001***
		Cumulative Mean Temperature	-4.126	0.093	10,671	-44.466	< 0.001***
Emergence SD	ESD ~ Year, random effect = Watsonian Vice County nested in Species	(Intercept)	15.291	0.489	10,672	31.285	< 0.001***
		Year	0.053	0.003	10,672	15.254	< 0.001***

is increasing. We extended previous studies by showing that these phenological shifts are different depending on the overwintering stage of the species. Species overwintering as pupa have the earliest First Emergence and Peak Emergence, followed by larva overwintering species and finally egg overwintering species, with approximately 40 days difference between each of these categories. Further, pupa overwintering species had a much longer flight period than egg and larva overwintering species, which further confirms the results in O'Neill et al. (2012), Végvári et al. (2015) and Hällfors et al. (2021). However, this variation in response depending on overwintering stage makes investigating the drivers of species' phenology challenging. The interspecific variation between each of the overwintering stages could not be captured in one model with the proposed error distribution, which would result in inaccurate measures of phenological shifts and their drivers. Thus, by running the model separately for each overwintering stage we could more accurately determine the drivers of emergence phenological shifts. Overall, there is a strong indication from the LME models that temperature is an important driver of phenology, and that phenological shifts vary in space. As well as this, the type of hostplant utilised by species can influence phenology, but the strength of this driver varies depending on the phenological measure and overwintering stage. Here,

we have confirmed and expanded on previous studies on the impact of species' traits on phenology (Altermatt 2010a; Teder 2020; Hällfors et al. 2021).

All of the overwintering stages followed predominantly the same trend of traits not being included in the best model, with the exception of Hostplant Category for the larva overwintering stage. This is likely due to the inclusion of species in the random effects of each model. In essence, a species traits are the parts that make up the sum that is the species itself, so by including both the traits as fixed effects and species as the random effects we were including the "species" explanatory variable twice. However, the models with species included as a random effect were a better fit to the data than the models including the traits as fixed effects. Individual life history traits are not good predictors of phenological change in moths because of interspecific variation. In other words, the individualistic responses of moth species outweigh the predictive value of particular traits. As such, the only variables that were consistently significant across all the models were the environmental variables Year and Cumulative Mean Temperature. Furthermore, the best model for all phenological metrics and overwintering stages included Vice County as a random effect. This demonstrates that averaging phenology to large areas, such as England for example, may be problematic as the variation in

environmental cues over such a large area leads to variation in phenology. Thus, by calculating the phenological metrics and Cumulative Mean Temperature at the Vice County level we included this spatial variation in our models.

It has been shown that phenological measures at the beginning of the season can be highly variable, dependent on recording effort and population changes (Miller-Rushing et al. 2008; Van Strien et al. 2008). Here, we attempted to mitigate this using the First Emergence measure utilised by Van Strien et al. (2008). However, this does not take into account changes in species distribution that may have occurred over the study period. Many moth species have altered their distribution in Britain over the last 50 years (Randle et al. 2019), which could be due to species tracking their ideal climate in response to temperature changes (Lenoir et al. 2020). Furthermore, a change in the timing of phenology for species with an altered distribution could be due to more records where the species previously was not present, but could also represent species responding to environmental variables such as lower temperatures compared climatic conditions in the core part of their distribution. Population changes could also impact measures, as a large increase in abundance could lead to the appearance of earlier emergence due to there being more individuals to record, but could also be a real change in phenology. Similar problems can be seen with increased recording effort. While this study has shown the utility of citizen science data for addressing questions that would be extremely difficult to achieve with a standardized study design over such a long period and spatial area, the are limitations of data quality and recording effort that do need to be acknowledged. We endeavored to reduce some of these problems in the calculation of the phenological metrics. Firstly, by calculating First Emergence as the 25th percentile day of year, we lessened the possibility of erroneous records early in the season impacting the First Emergence metric. Further, by following the methods of Van Strien et al. (2008) we focussed on well-sampled more easily identifiable macro-lepidoptera, along with aggregating to Vice County and thereby integrating over several populations, we attempted to minimise the bias of both recording effort and changes in distribution and abundance.

First Emergence changed the most for pupa overwintering species, which had the largest slope for both year and Cumulative Mean Temperature, followed by species that overwinter as larva, and then egg. This larger slope indicates a faster response of pupa overwintering species, with faster phenological shifts over time and with higher temperatures. For all overwintering stage categories the slopes were negative, indicating an overall phenological shift towards earlier emergence for the species in each category. Additionally, we found that the hostplant category “woody” was significant

for species that overwinter as larva, with these species generally emerging later than those that feed on herbaceous plants, contrary to the finding of Altermatt (2010a) that species that feed on woody plants emerge earlier. This would be intuitive for egg overwintering species, as there is expected to be strong selection pressure on the phenology of moth caterpillars to coincide with the narrow window in which the freshly emerged leaves of woody plants are edible, and indeed such phenological flexibility and significant temporal trends has previously been demonstrated (Visser et al. 2006; Altermatt 2010a; Burgess et al. 2018). However, for larva overwintering species that feed before overwintering, this may instead reflect the conditions of the previous year, such as the extension of the end of the growing season. It is possible that, as Végvári et al. (2015) postulate, the pressure is instead for species to synchronise more closely with herbaceous hostplants which, being shorter-lived than woody hostplants, have a much smaller window within which they can synchronise. In the case of larva overwintering species, those that feed on herbaceous plants may be tracking changes in herbaceous plant phenology, while species that feed on woody plants shift their phenology more slowly, and thus emerge later.

Compared to First Emergence, there was a much more varied response in Peak Emergence phenology across the three overwintering stages. The slope for year for Peak Emergence was positive, indicating delayed phenology, for larva overwintering species. However, for egg and pupa overwintering species the slope was negative, with the strongest response again for pupa overwintering species as with First Emergence, in agreement with previous studies such as Bonoan et al. (2021) and Prior et al. (2009). This disparity may be due to Hostplant Category “woody” being significant for larva overwintering species’ Peak Emergence phenology, with a larger slope than for First Emergence, along with a smaller slope for temperature. However, it is possible that due to only 4 of the 65 larva overwintering species specialising in woody hostplants and 15 of the 65 having both woody and herbaceous, this result of woody being important for larva overwintering species’ phenology is unreliable, and instead represents the different phenological strategies between species that feed on woody and herbaceous plants. This could explain why there was no significance for Hostplant Category for the egg and pupa overwintering species, as the majority have woody hostplants. Evidently, the three overwintering stage categories respond to the same variables differently at different parts of the season. There is an overall larger change across years for Peak Emergence than for First Emergence. However, temperature is more important for early season phenology for both the larva and pupa overwintering species, but not for the egg overwintering species. This may be due to the reliance of

larva and pupa overwintering species on food sources in the early season and thus utilising temperature as a way to fine-tune their phenology, in contrast to egg overwintering species which in spring need to continue to develop before food sources become important, hence the much larger slope for temperature for egg overwintering species' Peak Emergence phenology.

The slope for year for Emergence Standard Deviation was positive for all three overwintering stage categories, indicating they are on the wing for longer, following the trend of lengthening seasons due to a delay in winter onset (Keret et al. 2020). While Bonoan et al. (2021) found that Peak Emergence shifted but overall flight period did not for an endangered butterfly, other studies also found a lengthening of the flight period, which could reflect a move towards multiple generations for some univoltine species (Roy and Sparks 2000; Altermatt 2010b). Species that overwinter as an egg had the smallest change in flight period over time, whereas the slope for year was the largest for larva and pupa overwintering species. However, when compared to the overall response, larva overwintering species were increasing their flight period a lot faster in relation to their change in First and Peak Emergence than the egg and pupa overwintering species. This implies the possibility of a developmental trap; if the flight period does not change at the same rate as the rest of the species' phenology there could be extra generations or species may be present when their hostplant is unavailable (Van Dyck et al. 2015).

The phenology of our three phenological metrics varied considerably between the overwintering stage categories, and responded differently in the models. This illustrates the importance of the choice of phenological measure when investigating impacts of climate change on phenology, as the response of the moths depends on their stage of development through the seasons. While previous studies have grouped Lepidoptera species together in phenological analyses, here we have illustrated this may not be appropriate. Different overwintering life stages had significantly different phenology and thus could not be considered in the same model, and grouping them together could impact the reliability of measured phenological shifts. Indeed, by separately analysing the three overwintering species categories, we were able to determine that they are responding to climate change at different rates. While all three groups were undergoing phenological shifts, with both year and temperature, the *rate* of this change was different. Pupa overwintering species had a much larger slope for year and cumulative mean temperature, indicating a higher rate of phenological change both through time and with higher temperatures. This suggests a higher adaptability to climate change, and thus lower conservation concern for species that overwinter in later life stages (Végvári et al. 2015). Indeed, previous

studies have noted the impact on survivability of egg overwintering species, such as *Operophtera brumata*, if they lose synchrony with their hostplants due to not being able to adapt as quickly (Visser and Holleman 2001). Furthermore, there may be areas where species are at a higher risk, due to the variation in phenological response in space. Thus, these analyses build on previous studies highlighting the conservation concern for species that overwinter in earlier life stages, where there is a risk that they will be unable to adapt fast enough to counteract the impact of climate change on both the species' and its hostplants phenology.

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Author contributions E.J.H conducted the analyses, wrote the main manuscript text, and prepared all figures. S.P.R. and Z.P. provided guidance for the analyses. R.F. provided expert knowledge about the data used and interpretation of the results. All authors reviewed the manuscript.

Declarations

Competing interests The authors declare no competing interests.

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References

- Altermatt F (2010a) Tell me what you eat and I'll tell you when you fly: Diet can predict phenological changes in response to climate change. *Ecol Lett* 13:1475–1484. <https://doi.org/10.1111/j.1461-0248.2010.01534.x>
- Altermatt F (2010b) Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society*

- B-Biological Sciences 277:1281–1287. <https://doi.org/10.1098/rspb.2009.1910>
- Bates AJ, Sadler JP, Everett G et al (2013) Assessing the value of the Garden Moth Scheme citizen science dataset: how does light trap type affect catch? *Entomol Exp Appl* 146:386–397. <https://doi.org/10.1111/eea.12038>
- Bishop TR, Botham MS, Fox R et al (2013) The utility of distribution data in predicting phenology. *Methods Ecol Evol* 4:1024–1032. <https://doi.org/10.1111/2041-210x.12112>
- Bonoan RE, Crone EE, Edwards CB, Schultz CB (2021) Changes in phenology and abundance of an at-risk butterfly. *J Insect Conserv* 25:4995–5010. <https://doi.org/10.1007/s10841-021-00318-7>
- Burgess MD, Smith KW, Evans KL et al (2018) Tritrophic phenological match-mismatch in space and time. *Nat Ecol Evol* 2:970–979. <https://doi.org/10.1038/s41559-018-0543-1>
- Butterfly Conservation (2022) National moth recording scheme
- Cohen JM, Lajeunesse MJ, Rohr JR (2018) A global synthesis of animal phenological responses to climate change. *Nat Clim Change* 8:224–231. <https://doi.org/10.1038/s41558-018-0067-3>
- Cook PM, Tordoff GM, Davis AM et al (2022) Traits data for the butterflies and macro-moths of Great Britain and Ireland, 2022. <https://doi.org/10.5285/33a66d6a-dd9b-4a19-9026-cf1ff969cddb>
- Davidowitz G, Nijhout HF (2004) The physiological basis of reaction norms: the interaction among growth rate, the duration of growth and body size. *Integr Comp Biol* 44:443–449. <https://doi.org/10.1093/icb/44.6.443>
- Dickinson JL, Zuckenberg B, Bontar DN (2010) Citizen science as an ecological research tool: challenges and benefits. *Annu Rev Ecol Syst* 41:149–172. <https://doi.org/10.1146/annurev-ecolsys-102209-144636>
- Fox R (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conserv Divers* 6:5–19. <https://doi.org/10.1111/j.1752-4598.2012.00186.x>
- Fox R, Randle Z, Hill L et al (2011) Moths count: recording moths for conservation in the UK. *J Insect Conserv* 15:55–68. <https://doi.org/10.1007/s10841-010-9309-z>
- García-Barros E (2000) Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biol J Linn Soc* 70:251–284. <https://doi.org/10.1006/bjpl.1999.0374>
- GMS (2023) The garden moth scheme
- Hällfors MH, Pöyry J, Heliölä J et al (2021) Combining range and phenology shifts offers a winning strategy for boreal lepidoptera. *Ecol Lett* 24:1619–1632. <https://doi.org/10.1111/ele.13774>
- Heikkinen RK, Luoto M, Leikola N et al (2010) Assessing the vulnerability of European butterflies to climate change using multiple criteria. *Biodivers Conserv* 19:695–723. <https://doi.org/10.1007/s10531-009-9728-x>
- Hill GM, Kawahara AY, Daniels JC et al (2021) Climate change effects on animal ecology: butterflies and moths as a case study. *Biol Rev* 96:2113–2126. <https://doi.org/10.1111/brv.12746>
- Honěk A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66:483–492. <https://doi.org/10.2307/3544943>
- Keret NM, Mutanen MJ, Orell MI et al (2020) Climate change-driven elevational changes among boreal nocturnal moths. *Oecologia* 192:1085–1098. <https://doi.org/10.1007/s00442-020-04632-w>
- Lenoir J, Bertrand R, Comte L et al (2020) Species better track climate warming in the oceans than on land. *Nat Ecol Evol* 4:1044–1059. <https://doi.org/10.1038/s41559-020-1198-2>
- Lindestad O, von Schmalensee L, Lehmann P, Gotthard K (2020) Variation in butterfly diapause duration in relation to voltinism suggests adaptation to autumn warmth, not winter cold. *Funct Ecol* 34:1029–1040. <https://doi.org/10.1111/1365-2435.13525>
- Macgregor CJ, Thomas CD, Roy DB et al (2019) Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year. *Nat Commun* 10. <https://doi.org/10.1038/s41467-019-12479-w>
- Met Office, Hollis D, McCarthy M et al (2018) HadUK-grid gridded and regional average climate observations for the UK. Centre for environmental data analysis, accessed 2022
- Michielini JP, Dopman EB, Crone EE (2021) Changes in flight period predict trends in abundance of Massachusetts butterflies. *Ecol Lett* 24:249–257. <https://doi.org/10.1111/ele.13637>
- Miller-Rushing AJ, Inouye DW, Primack RB (2008) How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *J Ecol* 96:1289–1296. <https://doi.org/10.1111/j.1365-2745.2008.01436.x>
- Musolin DL, Saulich AK (2012) Responses of insects to the current climate changes: from physiology and behavior to range shifts. *Entomol Rev* 92:715–740. <https://doi.org/10.1134/S0013873812070019>
- Navarro-Cano JA, Karlsson B, Posledovich D et al (2015) Climate change, phenology, and butterfly host plant utilization. *Ambio* 44:S78–S88. <https://doi.org/10.1007/s13280-014-0602-z>
- O'Neill BF, Bond K, Tyner A et al (2012) Climatic change is advancing the phenology of moth species in Ireland. *Entomol Exp Appl* 143:74–88. <https://doi.org/10.1111/j.1570-7458.2012.01234.x>
- Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob Change Biol* 13:1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
- Passy S (2020) Garden moth scheme report 2019
- Pelini SL, Prior KM, Parker DJ et al (2009) In: Letcher TM (ed) Chap. 11 - climate change and temporal and spatial mismatches in insect communities. Elsevier, Amsterdam, pp 215–231
- Pinheiro JC, Bates DM (2000) Mixed-effects models in s and s-PLUS. Springer, New York
- Pinheiro J, Bates D, R Core Team (2023) nlme: Linear and nonlinear mixed effects models. R Package Version 3.1–162
- Prior KM, Dzurisin JDK, Pelini SL, Hellmann JJ (2009) Biology of larvae and adults of *Erynnis propertius* at the northern edge of its range. *Can Entomol* 141:161–171. <https://doi.org/10.4039/n08-019>
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Randle Z, Evans-Hill L, Parsons M et al (2019) Atlas of Britain and Ireland's larger moths
- Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. *Glob Change Biol* 6:407–416. <https://doi.org/10.1046/j.1365-2486.2000.00322.x>
- Roy DB, Harding PT, Preston CD, Roy HE (eds) (2014) Celebrating 50 years of the Biological records Centre. Centre for Ecology & Hydrology
- Scheffers BR, De Meester L, Bridge TCL et al (2016) The broad footprint of climate change from genes to biomes to people. *Science* 354:aaf7671. <https://doi.org/10.1126/science.aaf7671>
- Sherry RA, Zhou X, Gu S et al (2007) Divergence of reproductive phenology under climate warming. *Proc Natl Acad Sci USA* 104:198–202. <https://doi.org/10.1073/pnas.0605642104>
- Sims SR (2007) Diapause dynamics, seasonal phenology, and pupal color dimorphism of papilio polyxenes in southern Florida, USA. *Entomol Exp Appl* 123:239–245. <https://doi.org/10.1111/j.1570-7458.2007.00552.x>
- Sparks TH, Huber K, Dennis RLH (2006) Complex phenological responses to climate warming trends? Lessons from history. *Eur J Entomol* 103:379–386. <https://doi.org/10.14411/eje.2006.051>
- Steltzer H, Post E (2009) Seasons and life cycles. *Science* 324:886–887. <https://doi.org/10.1126/science.1171542>
- Tauber MJ, Tauber CA, Masaki S (1986) Seasonal adaptations of insects. Seasonal adaptations of insects

- Teder T (2020) Phenological responses to climate warming in temperate moths and butterflies: species traits predict future changes in voltinism. *Oikos* 129:1051–1060. <https://doi.org/10.1111/oik.07119>
- Tordoff GM, Dennis EB, Fox R et al (2022) Inconsistent results from trait-based analyses of moth trends point to complex drivers of change. *Biodivers Conserv* 31:2999–3018. <https://doi.org/10.1007/s10531-022-02469-8>
- Välimäki P, Kivelä SM, Mäenpää ML, Tammaru T (2013) Latitudinal clines in alternative life histories in a geometrid moth. *J Evol Biol* 26:118–129. <https://doi.org/10.1111/jeb.12033>
- Valtonen A, Ayres MP, Roininen H et al (2011) Environmental controls on the phenology of moths: Predicting plasticity and constraint under climate change. *Oecologia* 165:237–248. <https://doi.org/10.1007/s00442-010-1789-8>
- Van Asch M, van Tienderen PH, Holleman LJM, Visser ME (2007) Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Glob Change Biol* 13:1596–1604. <https://doi.org/10.1111/j.1365-2486.2007.01400.x>
- Van Dyck H, Bonte D, Puls R et al (2015) The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? *Oikos* 124:54–61. <https://doi.org/10.1111/oik.02066>
- Van Strien AJ, Plantenga WF, Soldaat LL et al (2008) Bias in phenology assessments based on first appearance data of butterflies. *Oecologia* 156:227–235. <https://doi.org/10.1007/s00442-008-0959-4>
- Végvári Z, Juhász E, Tóth JP et al (2015) Life-history traits and climatic responsiveness in noctuid moths. *Oikos* 124:235–242. <https://doi.org/10.1111/oik.01655>
- Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B: Biological Sciences* 268:289–294. <https://doi.org/10.1098/rspb.2000.1363>
- Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147:164–172. <https://doi.org/10.1007/s00442-005-0299-6>
- Wagner DL, Fox R, Salcido DM, Dyer LA (2021) A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous. *Proc Natl Acad Sci* 118(e2002549117). <https://doi.org/10.1073/pnas.2002549117>
- Watson HC (1883) *Topographical botany: being local and personal records towards shewing the distribution of British plants traced through the 112 counties and vice-counties of England, Wales, and Scotland*. B. Quaritch
- Wickham H, Averick M, Bryan J et al (2019) Welcome to the tidyverse. *J Open Source Softw* 4:1686. <https://doi.org/10.21105/joss.01686>

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