phenModel: A temperature-dependent phenology/voltinism model for a herbivorous insect incorporating facultative diapause and budburst

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ABSTRACT

A comprehensive phenology/voltinism model was developed for *Phratora vulgatissima,* an important pest of bioenergy crops. The model, phenModel, was developed based on development times of different life cycle stages (eggs, larvae, pupae, pre-oviposition, oviposition, sexual maturation) obtained from constant temperature laboratory experiments. As part of this study, a number of linear and non-linear models which describe the temperature-dependent development rate (inverse of development time) for each of the different life cycle stages were fitted. Based on the criteria of model parsimony and model fit, the non-linear Lactin-2 model was chosen as the optimum model to describe temperature-driven development in *P. vulgatissima*. To account for the variation in development times between individuals, an important but often ignored aspect in phenology models, a number of stochastic models (2- and 3- parameter Weibull and logistic models) were evaluated, based on the assumption that normalised development times conform to a similar shaped ('same shape') distribution. Novel aspects of the phenology model include the incorporation of a biologically relevant biofix, based on a budburst model for *Salix viminalis,* and a photoperiod threshold to induce facultative diapause. The model, which is written in R for accessibility, requires inputs of daily minimum and maximum temperature and site latitude and produces outputs describing the timing of completion of developmental stages for specified proportions of the population. It was evaluated against available field data and found to largely reproduce the observations providing a measure of its potential utility. A key component of the model allows for a sensitivity analysis of the model parameters. The model is structured so that it can easily be adapted for other leaf-feeding beetles which display a facultative reproductive diapause cued by photoperiod, and where the onset of oviposition is dependent on budburst, assuming relevant life cycle stage parameters are available.

1. Introduction

The blue willow beetle *Phratora vulgatissima* is the most serious pest feeding in short rotation crop (SRC) willow in Europe (Stenberg et al., 2010). Outbreaks in willow plantations are common (Sage and Tucker, 1998), with reported damage extremes varying from 40% reduction in stem growth (Björkman et al., 2000) to death of new shoots throughout the crop (Kendall et al., 1996; Mitchell, 1995). SRC willow (*Salix* spp.) is widely cultivated in northern Europe and in North America as a perennial biomass crop (Keoleian and Volk, 2005; Volk et al., 2006). While the area under SRC has largely plateaued in western Europe, countries in Eastern Europe are increasing their production (Lindegaard et al., 2016). It is a high volume, low value crop, and the prophylactic use of pesticide treatments is not currently economically viable or environmentally acceptable, while also being technically problematic (though targeted spraying of pesticides may be considered at times when the crop is seriously threatened (Dawson, 2010)). Measures such as inclusion of resistant varieties (Peacock and Herrick, 2000) and conservation of natural enemies within the crop (Stephan et al., 2016) are part of an integrated approach to manage and reduce the potential impact of herbivory on SRC willow. However, such an approach requires a sufficient knowledge of the pest biology and phenology.

Adult *P. vulgatissima* emerge from overwintering during the spring and colonise newly emerged *Salix* foliage (Sage et al., 1999). Adults

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require a period of feeding to reach reproductive maturity (Karp and Peacock, 2004), with oviposition in May and June. Late third instar larvae leave the foliage and pupate in the soil near the base of the tree (Karp and Peacock, 2004; Kendall et al., 1996; Sadeghi et al., 2004; Sage and Tucker, 1998). Upon eclosion in mid to late summer (late July to early August), this new generation of beetles returns to the willow stems to start feeding before leaving the plantations in autumn to seek suitable refugia or overwintering sites (Dalin, 2011). Feeding damage occurs from late spring to early autumn with three phases of attack, beginning with overwintering adults returning to the willow plantations, followed by larvae and finally newly developed adults.

In northern Europe *P. vulgatissima* is usually univoltine. A partial second generation has been observed in some years, though the relatively low number of larvae suggests reproduction by a small fraction of the population only (Dalin, 2011). Since damage caused by this beetle can be substantial, particularly by the larvae due to their greater density and restricted movement (SLU, 2014), attack by a second generation of willow beetle larvae and adults could have significant consequences for SRC willow. Hence, it is important to understand the conditions under which this may occur. Dalin (2011) demonstrated that the winter diapause is facultative, in response to declining day length, and suggested that warmer spring and summer temperatures, due to ongoing climate change, could increase the proportion of *P. vulgatissima* that initiate a second generation prior to entering diapause. However, only limited research has been conducted on the effects of temperature on *P. vulgatissima*, mostly reporting development times based on field observations (e.g. Kelly and Curry, 1991; Kendall and Wiltshire, 1998) or experimentally, at a limited number of constant temperatures (e.g. Dalin, 2011 (10, 15 and 20 °C); Puentes et al., 2015 (16, 20 and 24 °C)).

The objective of this research was to integrate available laboratory data on the development times of *P. vulgatissima* eggs, larvae and pupae and on the post-diapause pre-oviposition developmental period of adult insects at a range of multiple constant temperatures (10, 12, 15, 20, 25, 27, 28, 29 °C) into a phenology model representing the entire insect life cycle, driven by daily temperatures. The developed model, phenModel, includes a variable temperature dependent biofix used to initiate insect development within the model, based on the simulated date of budburst; a critical day length threshold (photoperiod) to initiate diapause (facultative), and a stochastic component to represent variability in insect development times within each life cycle stage. The stochastic component was incorporated to account for inherent variation observed in insect development times which have been identified as the next critical step in the development of phenological models (Rebaudo and Rabhi, 2018). The advantage of incorporating a stochastic component within the developed model means that model outputs for each life cycle stage can be represented as different emergence proportions.

2. Justification for developing the model

A variety of modelling approaches (e.g. Sharpe and DeMichele, 1977; Curry et al., 1978; Schoolfield et al., 1981; Wermelinger and Seifert, 1999) and model development tools (e.g. Wagner et al., 1984; Sporleder and Chavez, 2009; Shi et al., 2011) have been established that relate temperature to insect development rates or times. Linear models have been recognised as efficient modelling functions within a restrictive temperature range (Campbell et al., 1974; Gilbert and Raworth, 1996; Honek, 1999). More realistic approaches take account of the nonlinear, unimodal nature of physiological responses to temperature using the rate summation paradigm which can account for the intrinsic variation of development rates within populations (Sharpe and DeMichele, 1977; Lactin et al., 1995; Briere et al., 1999). Based on such techniques, temperature-dependent development for the life-cycles of various pest species have been developed, including a range of coleopteran species (e.g. Bentz et al., 1991; Wermelinger and Seifert, 1998). Previous studies on coleopterans have focused attention on the effects of temperature on specific life cycle stages, for example, egg-

adult development (e.g. Kontodimas et al., 2004; Walgama & Zalucki, 2006; Arbab et al., 2008; Jalali et al., 2010), including survival (e.g. Son and Lewis, 2005a) or reproduction (e.g. Son and Lewis, 2005b). The effects of temperature and photoperiod on voltinism and diapause have also received attention (e.g. Dalin et al., 2010; Dalin, 2011; Jönsson et al., 2011; Wainhouse et al., 2014; Lehmann et al., 2015). More comprehensive approaches, which include the influence of temperature and photoperiod on insect life cycle, have been developed for other insect groups. Examples of such models for lepidopteran and hemipteran species include Chen et al. (2011) (*Paralobesia viteana*) and Nielsen et al. (2016) (*Halyomorpha halys*). The current work contributes to this growing body of literature but for coleopteran species (e.g. Akşit et al., 2007; Jönsson et al., 2011; Wang et al., 2013; Wainhouse et al., 2014; Schubert and Berger, 2015; Fernanda et al., 2017). The model simulates emergence proportions for various life cycle stages, rather than just the mean or median development time. This allows for an improved representation of inherent insect variability and provides an improved means to evaluate the model against available field observations. The model also includes a likelihood function to allocate observed life cycle stages to different development phases; for example, adult beetles observed in the field might either be those that had overwintered (post-diapause) or 1st generation adults.

Ultimately, the model provides a basis to assess how temperature influences the life cycle of *P. vulgatissima*, and therefore could provide an important basis for developing a decision support system for use in the management of SRC willow. Where experimental data is available for other similar species, estimated parameters can be readily incorporated into the phenology model. The model can also provide a basis for developing an understanding of how this species may respond to past or future simulated changes in temperature due to climate change.

3. Materials

3.1. Insect development time data

Laboratory data used to estimate the development rate and development time models was obtained from Pollard (2014) and are summarised in Tables 1 and 2. For background, information on the laboratory experiments is outlined in the Supplementary Material. Observational data for *P. vulgatissima* used to evaluate the model was obtained from two sources: 1) field observation records and a field observation log at Long Ashton, Bristol, UK (51°26′N, 2°38′W) obtained during 1995 by Kendall and Wiltshire (1998); and, 2) field observation records on the presence of different life-cycle stages for *P. vulgatissima* at Donard, Co. Wicklow, IE (53°01′, N 6°37′W) during site visits in 2013 from Pollard (2014).

The development data for *P. vulgatissima* sexual maturation life-cycle stage was limited (e.g. small N at the available constant temperatures) in comparison to the data available for the other life-cycle stages (Table 1). On the basis of the experimental data available, sexual maturation of *P. vulgatissima* was found to require approximately twice the time to complete the stage at each constant temperature as the post-diapause pre-oviposition stage. Consequently, post-diapause development-time data at each constant temperature was increased by a factor of two to provide an estimated value for sexual maturation at the equivalent temperature.

3.2. Meteorological data

Daily minimum and maximum temperature observations were obtained from two sources. For the model evaluation at Long Ashton (UK), daily temperature data from Westonbirt, Gloucestershire, UK, approximately 35 km from the site, was obtained from the British Atmospheric Data Centre (BADC); for the model evaluation at Donard (IE), daily temperatures were obtained from Casement Aerodrome,

Table 1

Post-diapause pre-oviposition period and oviposition period (defined as the number of days from first to last oviposition) at different constant temperatures of *P. vulgatissima* that had emerged from diapause. The available mean development times for the sexual maturity stage (SE not included due to low numbers) and total fecundity (total number of eggs laid per post-diapause female) are also shown. N is the number of samples (Data source: Pollard, 2014).

Temp		Pre-oviposition (days)		Oviposition period (days)		Sexual Maturity (days)			Total fecundity
(°C)	N	Mean (± SE)	N	Mean (± SE)	N	Mean (± SE)	N		Mean (± SE)
10	23	34.26 ± 1.44	14	78.86 ± 7.96				14	127.07 ± 12.38
12	21	28.10 ± 1.39	14	61.36 ± 8.35				14	164.21 ± 16.15
15	36	12.47 ± 0.29	12	48.58 ± 3.75	3	27.00		12	204.92 ± 13.46
20	33	7.79 ± 0.36	14	31.07 ± 2.41	11	14.18		14	218.93 ± 22.01
25	40	5.78 ± 0.11	15	23.00 ± 1.69	6	15.17		15	146.07 ± 20.91
27	39	5.95 ± 0.24	15	22.53 ± 1.41	7	12.71		15	151.33 ± 17.69
28	0	–	0	–	2	14.0		0	–

approximately 33 km from the site, from the Irish meteorological service, Met Éireann. Comparison of temperatures recorded using data loggers located within, and on the perimeter of, the field site at Donard with mean temperatures recorded at Casement Aerodrome indicated only small differences over a sample measurement period, June to September 2013, which coincided with the insect development season (Pollard, 2014). Additional minimum and maximum temperature data employed in the budburst model was also obtained from Met Éireann, for sites in close proximity to, or co-located with, the budburst observations.

Both the UK and IE field sites lie in subdivisions of the Atlantic Central (ATC) classification, an environmental classification developed by Metzger et al. (2005) for Europe based on range of parameters including climate (temperature, precipitation and sunshine, oceanicity) and landscape topographical measures (altitude, slope). ATC2 incorporates South Eastern England (UK), South western Dutch lowlands (Netherlands) and North Rhine-Westphalia (Germany); ATC3 incorporates Western Ireland (IE) which extends across the southern and part of the eastern half of the island. The Atlantic Central zone is characterised by relatively mild winters and cool summers. Average temperatures over the period 1981–2010 from Lyneham, a station in close proximity to Westonbirt, display an annual average maximum temperature of 13.6 °C, annual average minimum temperature of 6.2 °C and annual average rainfall of 745.2 mm, relatively evenly distributed throughout the year (UK Met Office, 2019). Annual average maximum and minimum temperatures from Casement Aerodrome over the same period are very similar (annual average maximum temperature of 13.4 °C and annual average minimum temperature of 6.1 °C) to Lyneham, as is the annual average precipitation receipt of 754.2 mm (Met Éireann, 2019).

3.3. Budburst data

Observed budburst data for *Salix viminalis* was obtained from an Irish network of phenological garden sites participating in the International Phenological Network (IPN) (Chmielewski et al., 2013). Fragmented budburst data series were available from a number of locations, including Valentia Observatory, Co. Kerry, John F. Kennedy Arboretum, Co. Wexford, and the National Botanic Gardens, Co. Dublin, over the period from the mid-1980s to 2010 (n = 37) (Fig. 1). Additional observations from Carton House, Co. Kildare, Armagh Observatory, Co. Armagh, Millstreet County Park, Co. Cork and Markree Castle, Co. Sligo were also included from the period 2010–2012 (n = 10).

3.4. Climate change simulations

Data from two representative concentration pathways (RCPs) were obtained from Fealy et al. (2018), based on the Weather Research and Forecasting (WRF) regional climate model simulations for Europe for the period 1951–2100. These regional climate simulations which were dynamically downscaled from the ICHEC EC-Earth earth system model contributed to the EURO-CORDEX experiment, a pan-European initiative to develop high resolution multi-model climate simulations for a domain over Europe. Bias corrected daily maximum and minimum temperature data for two RCPs, namely 2.6 and 8.5, were obtained for a model grid location approximating the location of Casement Aerodrome. RCP2.6 represents a future world where emissions peak around mid-century and decline thereafter; RCP8.5 represents a future where emissions continue to increase over the present century.

4. Phenology/voltinism model development

4.1. Model description/Overview

The phenology/voltinism simulation model was originally written in MATLAB™ (Mathworks, Massachusetts, USA), but has been updated and rewritten in R (R Core Team, 2019) and implemented as the phenModel Package (Moral and Fealy, 2019) to facilitate use. A schematic of the phenology model is shown in Fig. 2. As inputs, the model
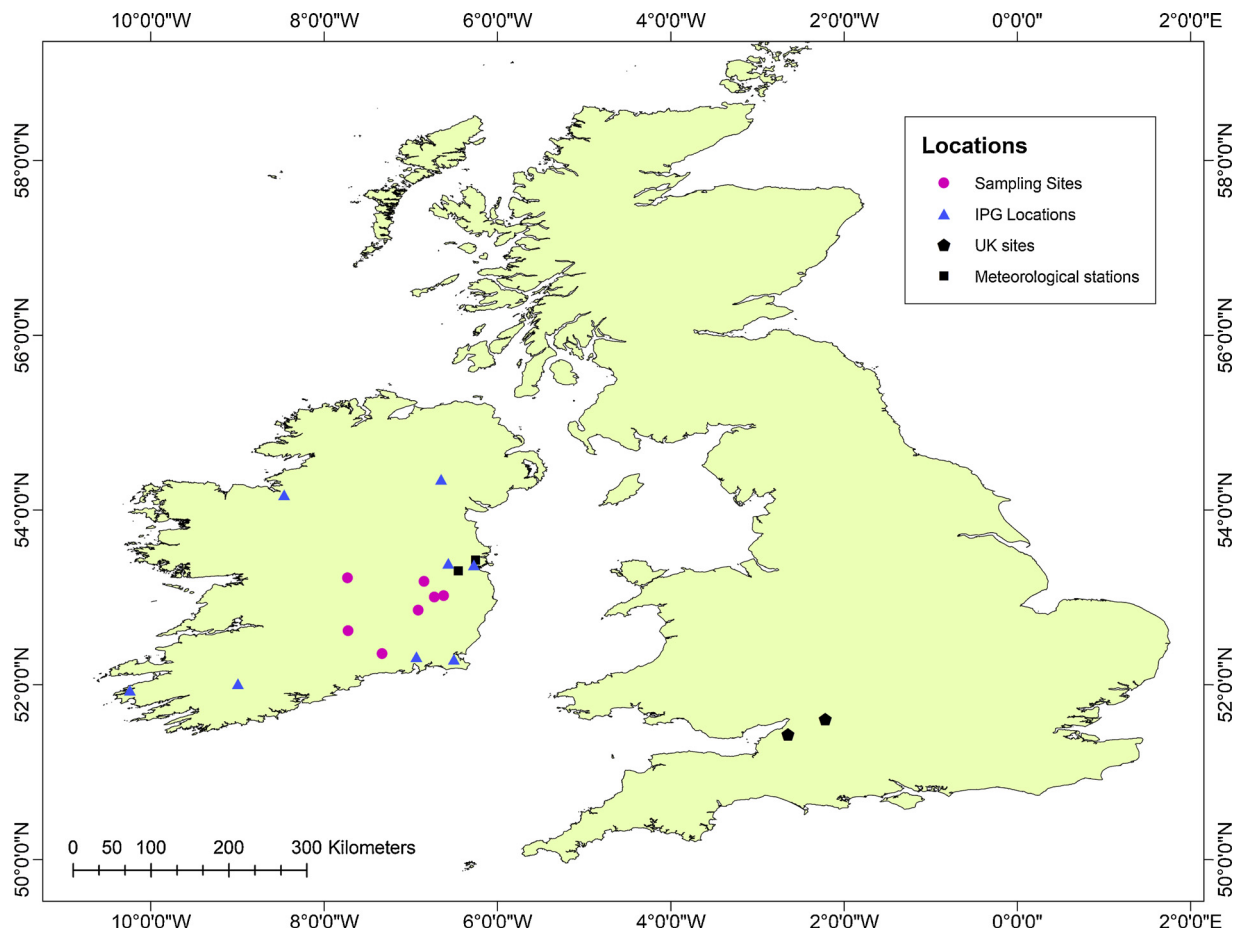
Table 2

Mean (± standard error) development times (in days) and survival proportion (%) for *P. vulgatissima* life stages at eight constant temperatures (no development denoted by -). N represents the number of individuals in each treatment. Eggs and larvae did not develop at 29 °C, while no pupae developed at 28 °C (Data source: Pollard, 2014).

Temp.		Eggs (days)			Larvae (days)			Pupae (days)		
(°C)	N	Mean (± SE)	Survival %	N	Mean (± SE)	Survival %	N	Mean (± SE)	Survival %
10	131	28.20 ± 0.14	71.6	38	61.03 ± 0.35	41.8	24	20.64 ± 0.22	60.0
12	471	18.00 ± 0.14	70.4	237	48.42 ± 0.22	44.7	49	17.82 ± 0.08	79.0
15	293	13.18 ± 0.09	82.5	430	30.52 ± 0.21	71.4	225	11.36 ± 0.08	90.7
20	337	7.40 ± 0.03	86.0	420	21.34 ± 0.18	74.5	136	7.38 ± 0.06	88.3
25	375	6.06 ± 0.03	73.1	376	17.02 ± 0.14	65.7	127	5.69 ± 0.05	89.4
27	226	5.56 ± 0.04	74.1	383	14.19 ± 0.17	46.3	29	5.83 ± 0.12	56.9
28	75	5.81 ± 0.06	62.5	15	14.47 ± 0.19	12.5	0	–	0
29	0	–		0	–				

Fig. 1. Sites from which the laboratory based population of beetles were obtained are indicated by the circles. Locations of the International Phenological Garden (IPG) sites are indicated by a triangle symbol; and meteorological station locations with a box symbol. The UK sites employed for evaluating the phenology model (Westonbirt and Long Ashton) are also shown.

requires site latitude and daily minimum and maximum temperatures from the 1st November of the preceding year. Development, quantified by a temperature dependent development rate model defined for each life cycle stage, is initialised in the model following the simulated date of budburst, a biofix dependent on the accumulation of required thermal and chilling days from the 1st November of the preceding year, described below. Once budburst is simulated to have occurred, post-diapause pre-oviposition development commences. Following completion of the post-diapause pre-oviposition stage, the first day of egg-lay is returned for adult females emerging from overwintering. Oviposition period stage advancement occurs when the required development for this life cycle stage has been completed. Egg, larval and pupal development stages are then initiated sequentially. Following completion of the pupal development stage, the emerging adults enter a sexual maturation or post-eclosion pre-oviposition period. This life-cycle stage is hypothesised to be sensitive to a diapause-inducing stimulus – photoperiod (Tauber et al., 1986; Danks, 1987; Dalin, 2011; Hodek, 2012; Pollard, 2014) – defined in the model as a critical day length (CDL) threshold. New generation adults that finish sexual maturation after the critical day length (CDL) enter into a state of reproductive diapause. *P. vulgatissima* adults that complete development prior to the CDL threshold can begin ovipositing to initiate subsequent generations.

To account for the distribution in the development times of individual cohorts of insects within each life-cycle stage, a stochastic approach has been incorporated into the model (e.g. Régnière, 1984; Stinner et al., 1975; Wagner et al., 1984). The stochastic component runs in parallel to each of the respective life cycle stages; this allows for different cohorts or proportions of insects to progress to subsequent

development stages at different times. The stochastic component was included in order to replicate natural insect variability within the model (Ma and Bechinski, 2009; Wagner et al., 1991), due to either persistent or random variations (e.g. Yurk and Powell, 2010). It also facilitates an examination of emergence proportions in the model simulated output.

4.2. Budburst biofix model

To calculate budburst, we employed the Alternating model which classifies each day as either a forcing or chilling day, depending on whether a particular day's temperature is above or below a critical threshold (e.g. Cannell and Smith, 1983; Murray et al., 1989). On forcing days, the temperature sum above the threshold is accumulated (thermal time units). On a chilling day, the chill day count increases by one. Thermal time (forcing) units accumulate in the model once temperatures exceed the threshold of 7 °C from the 1st November in the preceding year. The threshold and start date were selected based on an evaluation of different thermal thresholds and start dates relative to the observed date of budburst. Chill day counts are accumulated from the same start date at temperatures less than or equal to 7 °C.

The accumulated thermal time units and count of chill days at the date of observed budburst, derived from all available locations (Fig. 1), provided the basis for establishing the empirical budburst model which takes the form of an exponential equation, as follows:

$$\hat{y} = \hat{b} exp^{\hat{m}x} \tag{1}$$

where, $\hat{y}$ is the estimated accumulated thermal units at the date of budburst, $\hat{b}$ and $\hat{m}$ are model estimated parameters with values of
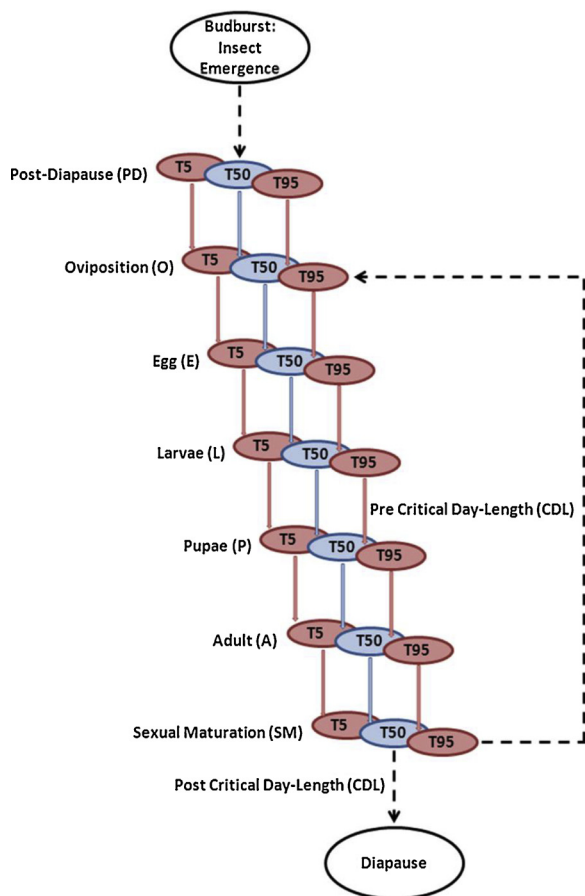
Fig. 2. Schematic diagram of the life-cycle of *P. vulgatissima* as condensed for use in the phenological model. T5, T50 and T95 represent selected emergence proportions at 5%, 50% and 95% of the population.

540.19602 and −0.01599, respectively, and x is the number of chill days at the date of budburst (Fig. 3). The predicted budburst date in the model is the first day when the observed accumulated thermal units is greater than the predicted thermal units, $\hat{y}$.
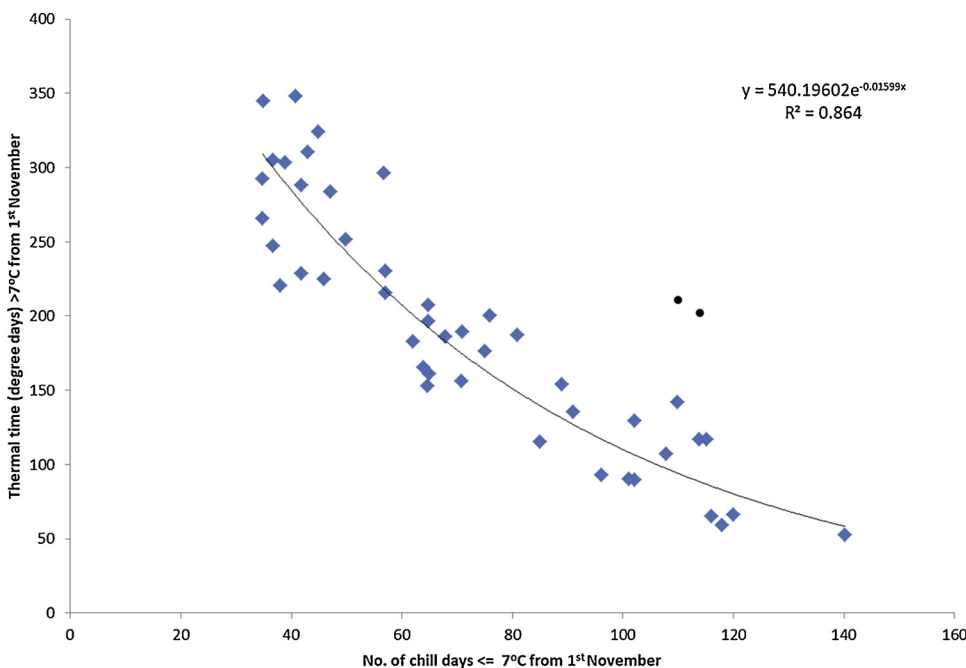
4.3. Temperature-dependent development rate models

The relationship between temperature and development rate (expressed as the reciprocal of the mean development time of each life stage), was initially evaluated using a number of linear and non-linear models. We consider that the development rate $d \sim N(r(T),\sigma^2)$, with $r(T)$ a linear or non-linear predictor that models the rate of development as a function of the temperature, T (°C).

The linear model was based on the linear relationship between the rate of development (linear portion) and temperature, and is described as follows:

$$r(T) = a + bT \qquad (2)$$

where a is the intercept and b is the slope of the line (Campbell et al., 1974). The lower temperature threshold (T_L) and thermal constant (K) can be derived from the intercept and slope terms. T_L is calculated as:

$$T_L = \frac{-a}{b}$$

and K is the reciprocal of the slope b:

$$K = \frac{1}{b}$$

The linear model was fitted to the linear portion of the data for post-diapause, egg, larval and pupal development and oviposition period.

Three non-linear methods were also evaluated, namely the Brière-2 (hereafter Brière) and Lactin-2 (hereafter Lactin) models (which have been widely employed in the literature) and a more complex biophysical model. We initially sought to fit the Sharpe-Schoolfield-Ikemoto (SSI) model (Ikemoto, 2005), a thermodynamic model based on enzymatic reactions, which is a modified function of the Schoolfield et al. (1981) and Sharpe and DeMichele (1977) models. However, due to complexities in deriving parameters, requiring a grid-search to minimise a weighted residual sum of squares statistic, profiled over a three-dimensional parameter space (namely the parameters $T\phi$, ΔH_L and ΔH_H) and the number of model parameters required to be estimated relative to data points, the 6-parameter Schoolfield model (Schoolfield et al., 1981) was ultimately selected for use in the evaluation.

The Brière-2 (Briere et al., 1999) is a three coefficient model described as,

Fig. 3. Exponential inverse relationship for 47 records of the dates of budburst of *S. viminalis* from three IPG sites (Valentia, Johnstown Castle and National Botanic Gardens) and an additional 10 records from four other IPG sites (Carton House, Armagh Observatory, Millstreet County Park and Markee Castle (two outliers - Armagh 2011 and Millstreet 2011 - indicated by black solid circles were excluded from the model fitting) with thermal time units > 7 °C from 1 st November and chill days ≤ 7 °C from 1 st November. The derived budburst model resulted in an R^2 (adjusted) value of 0.86 (RMSE 13.08) when fitted to the observed budburst data from all sites.

$$r(T) = aT(T - T_L)(T_U - T)^{\frac{1}{b}} \tag{3}$$

where a, b and T_U are parameters to be estimated. T_U is an upper temperature threshold, T_L is as previously defined.

The Lactin-2 model is,

$$r(T) = exp^{\rho T} - exp^{\left(\rho Tm - \frac{(Tm - T)}{\Delta T}\right)} + \lambda \tag{4}$$

where $r(T)$ is the rate of development at temperature T, and ρ, T_m, ΔT, and λ are parameters to be estimated.

The Schoolfield model (Schoolfield et al., 1981) is described by,

$$r(T) = \frac{p(25^oC)(\frac{T}{298})exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right]}{1 + exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_{1/2L}} - \frac{1}{T}\right)\right] + exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_{1/2H}} - \frac{1}{T}\right)\right]} \tag{5}$$

where T is the absolute temperature in Kelvin, $p\phi$ is the mean development time at the intrinsic optimum temperature, $T\phi$ is the intrinsic optimum temperature at which no enzyme inactivation is hypothesized, ΔH_A, ΔH_L, and ΔH_H represent enthalpy changes, R is the universal gas constant, and $T_{1/2L}$ and $T_{1/2H}$ represent temperatures below (L) and above (H) an optimum temperature, at which an enzyme is 50% active.

The three non-linear functions were fitted over the entirety of the data for each life cycle stage, including where no recorded development took place at the upper temperatures. Coefficients for the non-linear functions were estimated using the Levenberg-Marquardt algorithm (Marquardt, 1963; Elzhov et al., 2016), with a convergence criterion set to 0.00001 and the confidence level for all intervals set at 95.0. The method requires the provision of initial starting values to initiate parameter estimation. These initial values were based on published coefficients from other coleopteran species (e.g. Jalali et al., 2010; Wermelinger and Seifert, 1998).

To assess the goodness-of-fit of the models, two criteria were employed: (1) model parsimony and fit of the model to the experimental data, assessed by four statistics: the residual sum of squares (RSS), the root-mean-square error (RMSE), the Akaike information criterion (AIC) and the Bayesian information criterion (BIC); and (2) whether the estimates of lower (T_L), optimum (T_{OPT}) and upper (T_U) threshold parameters were biologically realistic (applicable for the Brière and Lactin models).

4.4. Distribution model of development time

A key limitation associated with the use of development rate models for use in phenological applications is that they are deterministic; they model insect development based on the mean or median times of all individuals or cohorts per temperature treatment. Consequently, they do not account for intrinsic differences among individuals or proportions within a population in spite of the fact that insects reared under similar environmental conditions develop at different times (e.g. Yurk and Powell, 2010). The integration of deterministic development rate models with stochastic development time models is therefore considered a fundamental requirement for inclusion in phenology models (Wagner et al., 1985; Ma and Bechinski, 2009; Rebaudo and Rabhi, 2018).

Two types of models were initially considered, logistic and Weibull (two- and three- parameter), to describe the development times of proportions of individuals in the population (Stinner et al., 1975; Wagner et al., 1984; Régnière, 1984).

The logistic model is described by:

$$f(x) = \{1 + exp^{[-k(x-1)]}(0.5^{-q} - 1)\}^{-1/q} \tag{6}$$

where f(x) is cumulative frequency distribution of development rate relative to the normalised time x, k is a shape parameter that determines the steepness of the curve and Q is a skew parameter that identifies a symmetric curve when equal to zero (a negative curve when greater than 0 and a positive curve when less than zero) (Régnière

et al., 1984).

The two and three parameter Weibull are described as follows,

$$f(x) = 1 - exp^{[-(x/\alpha)]^\beta} \tag{7a}$$

$$f(x) = 1 - exp^{-[(x-\gamma)/\alpha]^\beta} \tag{7b}$$

where $f(x)$ is the cumulative probability of completing development by the normalized time x, α is a scale parameter, β is a shape parameter and γ is the lag in the onset of emergence.

The logistic model (Régnière, 1984) differs from the Weibull, in that the equation describes the cumulative frequency distributions of development rates (instead of development time) relative to the median rate (instead of median time). Prior to fitting these functions, development times (or rates) were derived as cumulative frequency distributions at each temperature; development times for each percentile were then divided by the respective median value of the distribution to produce a normalised ('same shape') distribution of development times at each temperature (Wagner et al., 1984, 1991). Based on the 'same shape' assumption, a single cumulative distribution representing the normalised distributions for all temperature treatments was produced by averaging all the distributions, weighted by the total frequency of each distribution (Wagner et al., 1984, 1991). While the median distribution may under or over represent particular proportions of development times, it offers a pragmatic way to incorporate variability in cohort development times into the phenology model.

4.5. Diapause induction

Critical day length (CDL), defined as the day length threshold inducing diapause in 50% of a population, was estimated to be 14.92 h (95% CI: 14.46–15.41 hrs) on the basis of laboratory experiments (Pollard, 2014). Thus, assuming that the adult phase is the photoperiod sensitive stage, *P. vulgatissima* will enter reproductive diapause within the first half of August in Ireland.

4.6. Classification of observations for adults in model evaluation

When validating the model's predictions using observed data for different *P. vulgatissima* life stages, it is possible to compare days when the insect was found at different life stages with the ones predicted by the model, and hence conclude whether projections are realistic. The model simulates emergence of post-diapause adults from the previous year, as well as adults from the first generation that will emerge later, but the field observations do not discriminate between these two categories. A simple solution was proposed, based on approximating the distributions of adult and post-diapause emergence times to a normal distribution, and consists of the following steps: (1) fit a normal model to the emergence times predicted by the phenology model for each of the two categories; (2) for each observation (real data point) calculate the probability that a value equal to that or more extreme is generated from each of the two fitted normal distributions; and (3) assign that observation to the category that yielded the highest probability, i.e. either post-diapause or not. The same procedure is then repeated for those observations who were not classified as post-diapause to discriminate the first generation adults that have emerged later in the year and the post-diapause ones that were ovipositing. While this approach ultimately represents a simplification, it provides a statistical solution to facilitate a comparison between the model output and the field data.

4.7. Sensitivity analysis

A sensitivity analysis was conducted on the various parameter estimates within the model, including base temperature threshold, budburst/date of budburst, both Lactin and Weibull parameters and the specified critical day length (CDL). Model parameters were sampled

1000 times, within a specified range of their estimated values, to assess the impact on the proportion of the population completing a particular life cycle stage (i.e. days from the 1st November). In addition, a climate change experiment is also performed, to evaluate the performance of the model over a multi-year period where temperatures are increasing. Results are presented for the 0.5 quantile, representing 50% of the insects completing a particular stage.

5. Results

5.1. Development time and development rate model selection

The linear model provided a good fit to the data for all life-cycle stages with high R^2 values ranging from 0.97 to 0.99. T_L was estimated for each stage by extrapolation of the line to the x-axis. Estimations for T_L decreased through the successive stages of development: 7.5 °C for post-diapause development, 5.7 °C for egg development, 5.1 °C for larval development and 4.2 °C for pupal development. K values estimated by the linear model were considerably lower for the post-diapause (100), egg (116.3) and pupal (123.5) stages when compared to the estimated value for larval stage (321.5) due to the greater time requirement for larval development. While the linear model could have been utilised to estimate development time in the phenology model based on the typical temperatures experienced in Ireland (i.e. temperatures lie within the linear portion), it would have potentially restricted the use of the model in other locations and its use in climate change applications, where daily temperature may exceed the range of the linear model.

Based on the statistical evaluation of the non-linear models, the Lactin and Schoolfield models resulted in better fits, based on the goodness-of-fit metrics employed, relative to the Brière model (Table 3). The Schoolfield model generally produced the best fit, across most metrics, followed closely by the Lactin model. Due to the relative similarity in goodness-of-fit scores and considering the higher required number of estimated parameters relative to the number of observations for the Schoolfield model, the Lactin model (Lactin et al., 1995) was ultimately selected to simulate the temperature dependent development times for each life cycle stage (Fig. 4). Model estimated parameters for the Lactin model are outlined in Table 4.

For development time, the Weibull three parameter (3 P) model was

Table 3
Statistical results for non-linear models fitted to *P. vulgatissima* post-diapause pre-oviposition, oviposition period, egg, larval, pupal development rates.

Stage	Model	RSS	RMSE	AIC	BIC
Pre-oviposition	Brière	3.27E-04	1.04E-02	−39.935	−40.20547
	Lactin	1.62E-04	7.34E-03	−44.861	−45.1315
	Schoolfield	8.22E-05	9.07E-03	−45.6021	−45.98074
Oviposition period	Brière	1.29E-04	6.57E-03	−46.4192	−46.68966
	Lactin	3.52E-06	1.08E-03	−71.6501	−71.92052
	Schoolfield	4.55E-07	6.75E-04	−81.9711	−82.34972
Sexual Maturation	Brière	2.738E-04	9.55E-03	−41.1778	−41.4482
	Lactin	3.829E-05	3.57E-03	−54.9471	−55.2175
	Schoolfield	2.054E-05	4.53E-03	−55.3061	−55.6848
Egg	Brière	1.05E-03	1.62E-02	−38.7969	−38.39967
	Lactin	1.90E-04	6.90E-03	−52.4612	−52.06395
	Schoolfield	6.36E-05	5.64E-03	−57.2340	−56.67793
Larva	Brière	2.09E-04	7.23E-03	−51.7160	−51.31884
	Lactin	2.04E-05	2.26E-03	−70.3418	−69.94459
	Schoolfield	1.60E-05	2.83E-03	−68.2940	−67.73789
Pupa	Brière	7.90E-04	1.62E-02	−33.7594	−34.02989
	Lactin	6.11E-05	4.51E-03	−51.6749	−51.94535
	Schoolfield	2.56E-05	5.06E-03	−53.7610	−54.13961

selected on the basis of the statistical evaluation criteria (Table 5); it also represented the most pragmatic choice to simulate variation in development rate for the pre-oviposition, egg, larva and pupae life cycle stages (Table 6; Fig. 5). The use of a single model for each life cycle stage also minimises the complexity of the overall phenology model. The Weibull 3 P equation with the same parameters as those used to describe post-diapause pre-oviposition development time variability was employed to define sexual maturation development time variability. This was a necessary assumption in order to include a stochastic component of development times for this stage for *P. vulgatissima*.

Oviposition period was described using an adapted version of the method proposed by Wermelinger and Seifert (1999). The relative cumulative oviposition data (number of eggs per female per day divided by oviposition period for each temperature treatment and adjusted for surviving females during each observation) was plotted against relative oviposition time (time divided by maximum oviposition period for each temperature treatment). While the selection of a single model to represent the relative cumulative oviposition represents an over-simplification (Fig. 6), future development of the model will incorporate alternative approaches (e.g. Weibull for different temperature thresholds). Overall, the Weibull (3 P) function gave the best fit (Table 5) and consequently, was also selected to describe development rates for this stage (Table 6).

5.2. Model evaluation

While the phenology model calculates the emergence for all proportions (e.g. 0.01, 0.1,…,0.90, 0.99), we largely focus our discussion on the evaluation of the model on the emergence proportions (EP) at 5%, 50% and 95% life cycle stage completion as they account for the proportion of early, median and late emerging insects along the respective cumulative distribution curves (Wagner et al., 1984; Knight et al., 1991; Schaafsma and Whitfield, 1991; Logan and Thomson, 2002). Evaluation of the phenology model was undertaken using observed data on the presence of different life-cycle stages of *P. vulgatissima* in the field. Observational data for *P. vulgatissima* obtained from Long Ashton, Bristol, UK (1995) (Kendall and Wiltshire, 1998) and Donard, Co. Wicklow, IE (2013) (Pollard, 2014) provided the primary data used to evaluate the model. As the ecology and physiology of Irish *P. vulgatissima* populations, upon which the phenology model components are developed, are assumed to be similar to UK populations (Sage and Tucker, 1998; Karp and Peacock, 2004), the phenology/voltinism model should be capable of broadly simulating the life cycle of *P. vulgatissima* in the UK, in a similar environmental zone (ATC). It is also assumed that *P. vulgatissima* populations in the UK adhered to the same critical thresholds for temperature and day length as the population employed here. These were necessary assumptions to facilitate a broader evaluation of the model. The model simulations run from the 1st November of the preceding year, therefore days from the 1st November are reported here, with dates provided in brackets.

The model simulated estimates of *P. vulgatissima* development stages were found to broadly correspond with observed field data from SRC at Long Ashton during 1995 (Fig. 7), with model simulated stage/emergence proportions largely spanning dates of recorded observations in the field. Kendall and Wiltshire (1998) first record adults in the field on day 164 (13 April) and adults were observed almost continuously until day 332 (28 September); however, no adults were sighted on visits to the site on day 248 (7 July) or the subsequent site visit on day 262 (20 July). Eggs were recorded between days 182 and 242 (1 May – 30 June); larvae were observed between days 204 and 249 (23 May – 7 July).

Based on temperature data from Westonbirt, UK, the model simulated budburst to occur on day 127 (7 March). The 5% emergence proportion (EP) was simulated to occur on day 186 (5 May), 22 days later than adults were first observed in the field, with 50% adult post-diapause development simulated to occur on day 188 (7 May) and the
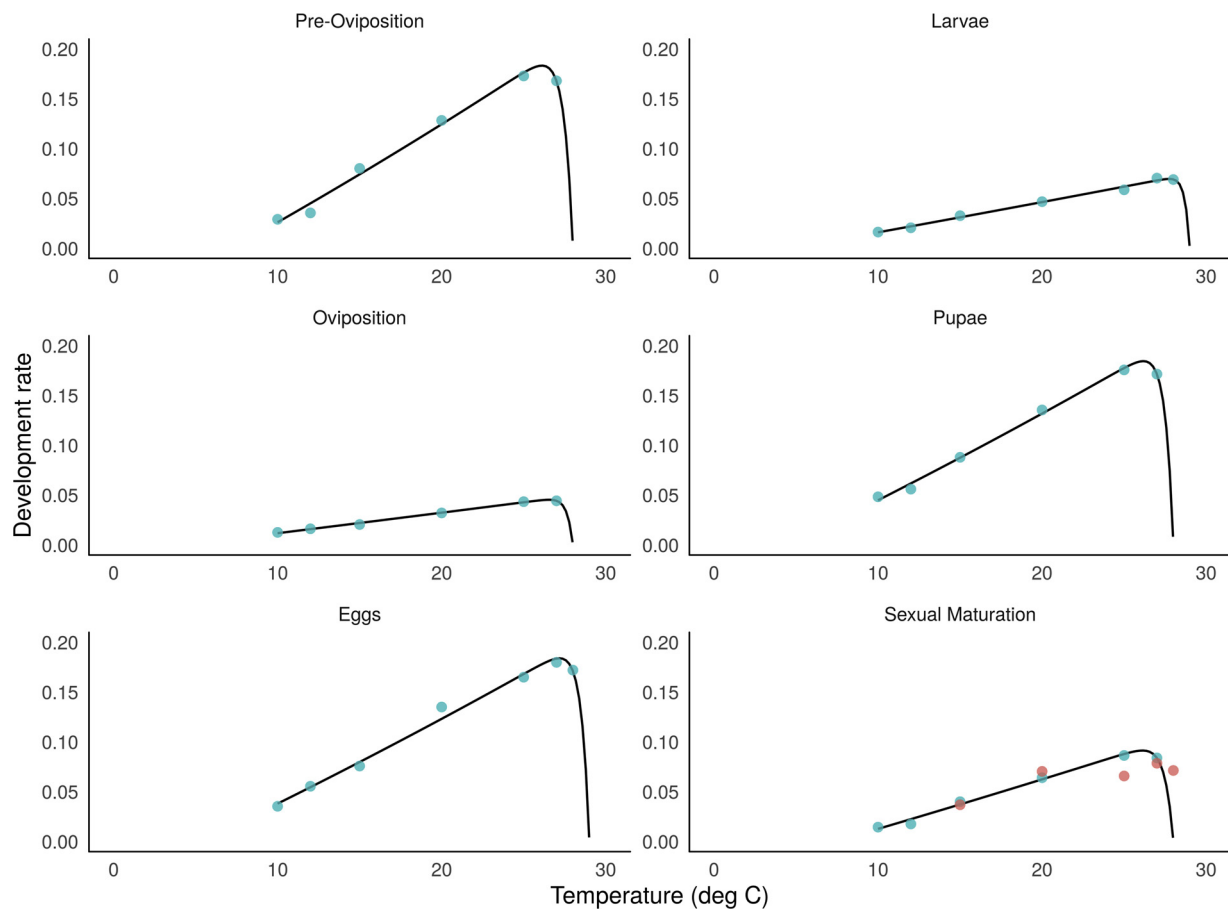
Fig. 4. Lactin model fitted to *Phratora vulgatissima* development rates for post-diapause pre-oviposition, oviposition, eggs, larvae, pupae and sexual maturation. The orange dots in the sexual maturation graph represent the laboratory observations of post-eclosion pre-oviposition development times converted to development rate and are included for comparison purposes.

95% EP on day 205 (24 May). The model simulated 5–95% proportion for oviposition period development from day 187–250 (6 May – 8 July) corresponds with the recorded observations of eggs between days 182 and 242 (1 st May – June 30th). The 5–95% model estimated larvae emergence was simulated to occur between days 208 and 261 (27 May – 19 July), corresponding with observed larvae emergence. Based on

the probability of adult emergence (see Section 4.6), observed adult emergence occurred between day 269 (27 July) and day 332 (28 Sep), while the model simulated 5–95% proportions occurred between days 251–296 (9 July – 23 Aug). The simulated date for 50% adult emergence on day 269 (27 July) corresponds with the first recorded adult beetles attributed to this stage (Section 4.6). 50% of the newly

Table 4
Parameter estimates for the Lactin model fitted to *P. vulgatissima* developmental rates of post-diapause pre-oviposition, oviposition, sexual maturation, eggs, larvae and pupae. Sexual maturation was derived based on the pre-oviposition development times, as outlined in text. The critical thresholds for T_L, T_U and T_{OPT} were derived by assessing where the modelled line crossed the x-axis (T_L and T_U) and the temperature at the maximum value of the line (T_{OPT}).

Parameters	Development stage		
	Pre-oviposition	**Oviposition**	**Sexual Maturation**
p	0.008637 ± 0.0005	0.001996 ± 0.00008	0.0046 ± 0.0002
T_m	28.9444 ± 0.1569	29.06 ± 0.197	29.23 ± 0.2019
ΔT	0.521031 ± 0.0898	0.3438 ± 0.0655	0.5127 ± 0.0873
Λ	−1.06401 ± 0.0094	−1.008 ± 0.00149	−1.0346 ± 0.0048
T_L	7.19	4.13	7.35
T_U	28.0	27.99	28.0
T_{OPT}	26.12	26.55	26.12
	Eggs	**Larvae**	**Pupae**
p	0.007589 ± 0.0003	0.00290 ± 0.0001	0.0077382 ± 0.0003
T_m	29.85 ± 0.1466	29.75 ± 0.2843	28.86 ± 0.097
ΔT	0.4741 ± 0.0833	0.2812 ± 0.1072	0.4777 ± 0.0558
Λ	−1.040674 ± 0.008	−1.0133 ± 0.0027	−1.0354 ± 0.0058
T_L	5.26	4.57	4.51
T_U	29.0	28.99	28.0
T_{OPT}	27.18	27.75	26.18

Table 5

Statistical results for non-linear models fitted to *P. vulgatissima* post-diapause development time distribution and oviposition period and egg, larval, pupal stages.

Stage	Model	RSS	RMSE	AIC	BIC
Pre-oviposition	Weibull (2 P)	6.0659	0.121	−569.51	−561.46
	Weibull (3 P)	6.1012	0.1214	−565.12	−553.04
	Logistic	0.5021	0.0797	−171.42	−166.68
Oviposition period	Weibull (2 P)	0.0322	0.0383	−77.146	−74.964
	Weibull (3 P)	0.0058	0.0162	−112.99	−109.71
Egg	Weibull (2 P)	0.006	0.0165	−114.29	−112.11
	Weibull (3 P)	0.0017	0.0087	−140.37	−137.1
	Logistic	0.3364	0.0829	−101.02	−97.239
Larva	Weibull (2 P)	0.0367	0.0408	−74.292	−72.11
	Weibull (3 P)	0.0006	0.0053	−162.3	−159.02
	Logistic	0.2775	0.0578	−233.61	−228.77
Pupa	Weibull (2 P)	0.0041	0.0136	−122.66	−120.48
	Weibull (3 P)	0.0027	0.0112	−129.32	−126.04
	Logistic	0.176	0.0753	−68.334	−65.466

developed adults were simulated to have reached sexual maturation on day 285 (12 Aug), a proportion of which were simulated to initiate a partial (0.05) second generation as they completed sexual maturation prior to the CDL threshold. This partial second generation reaches adult emergence, within the day ranges of adults observed in the field (days 269–332), however, Kendall and Wiltshire (1998) indicate that only one generation occurred during the year.

Periodic observations of *P. vulgatissima* from SRC located at Donard, Co. Wicklow, IE, were available for the period from May to September during a field campaign in 2013 from Pollard (2014). For an evaluation of the phenology model at this site, daily maximum and minimum temperature data from the nearest synoptic station, located at Casement Aerodrome, was utilised as input to the model (Fig. 8). Based on the available observations, adults were recorded in the field on days 185, 228, 287 and 333 (4 May, 16 Jun, 14 Aug, 29 Sept). Eggs were observed on days 199 and 242 (18 May, 30 Jun) and larvae on days 228 and 264 (16 Jun and 22 Jul). Model estimates of *P. vulgatissima* stage development were again found to be reasonably consistent with the field observations of *P. vulgatissima* at Donard (Fig. 8). Budburst was estimated to occur on day 144 (24 Mar), with the 5–95% proportion of adult post-diapause development simulated to have occurred between days 201–217 (20 May – 5 Jun). Adult beetles were observed on day 185 (4 May) and 228 (16 Jun); based on the model derived probability of life cycle stage, the observation of adult beetles in the field on day 228 is an adult beetle present during oviposition period (Section 4.6). The model simulated 5–95% proportion for oviposition period development occurs between 203 and 258 (22 May – 16 Jul) corresponds with the period during which eggs were observed (18 May – 30 Jun) in the field. The model simulated 5–95% proportion of larvae emergence occurs between days 219–269 (7 Jun – 27 Jul), again encompassing the observations for this life cycle stage. The first generation of adults emerging is simulated between days 257–323 (15 Jul – 19 Sep), a period which encompasses the latter two observations of adult beetles at Donard. 50% of first generation adults are simulated to have completed

sexual maturation by day 303 (30 Aug). A partial second generation is simulated to have reached adult emergence stage at Donard, within the day range of adults observed in field (days 288–333), however, the field observations do not discriminate if the latter observed adult is first or second generation.

In spite of a number of pragmatic choices made here to simplify development and coding of the phenology model and the fact that the temperature data employed was obtained from meteorological stations located approximately 30 km from both sites, the model was found to broadly replicate the limited available observations from the two available sites based on the model simulated proportions reported here. A key advantage to incorporating the stochastic element in the model, to replicate inherent variability in insect development times, is the ability to examine proportions of a population completing a particular life cycle stage. The use of proportions is also likely to better represent actual insect development compared to the use of just the mean or median development time.

5.3. Sensitivity analysis

The sensitivity of the model to changes in parameter values was evaluated by sampling specified model constants (e.g. base temperature threshold for defining forcing and chill days), CDL and parameter values (e.g. Lactin; Weibull parameter estimates) within a specified range of their estimated values. The ranges specified are not biologically determined, but purely to evaluate the sensitivity of the model to changes in parameter values. Once a range is specified within the model, the range of values is sampled 1000 times and the model is run for each sample, with simulated outputs reported for the 0.5 proportion of the population completing a particular life cycle stage. Boxplots are employed to represent the spread in days across the 1000 samples; the discussion here focuses on the 2.5%, 50% and 97.5% values. The sensitivity analysis is performed for one year, 2013, with temperature data from Casement Aerodrome employed in all runs. For each sensitivity experiment, the respective constant or model specific parameters are changed on a one by one, or block by block (i.e. all parameters for that equation or component), basis for both the Lactin and Weibull parameters, with remaining inputs held the same.

Changes in the base temperature threshold have a direct impact on the model simulated date of budburst, requiring more or fewer days to meet the thermal and chilling requirements. Based on the specified sampling range around the original estimated parameter values (i.e. 30% equivalent to ~ ± 2 °C around the base temperature of 7 °C), the simulated date of budburst varies between day 125 (2.5%) and day 170 (97.5%) compared to the base temperature (7 °C) day of budburst of 143 (Fig. 9). The estimated parameters for the budburst equation were also varied by ± 30% to assess the influence on date of budburst and subsequent life cycle stages. Based on this analysis, the date of budburst varied from day 111 (2.5%) to day 179 (97.5%). Consistent with the sensitivity analysis on the base threshold temperature, the date of budburst was found to have little impact on the timing of the subsequent life cycle stages (Fig. 10). On further investigation, the date of the subsequent post diapause stage was found to be relatively insensitive to a budburst day range between days 80 and 160 (20 Jan; 8/9 April), after the 1st November in the preceding year. This is likely attributable to the maritime climate experienced in Ireland, temperatures

Table 6

Parameter estimates for the 3 parameter Weibull model fitted to *P. vulgatissima* pre-oviposition, relative oviposition, egg, larval, pupal development time. Model parameters from the pre-oviposition Weibull model fit were employed for sexual maturation as outlined in the text.

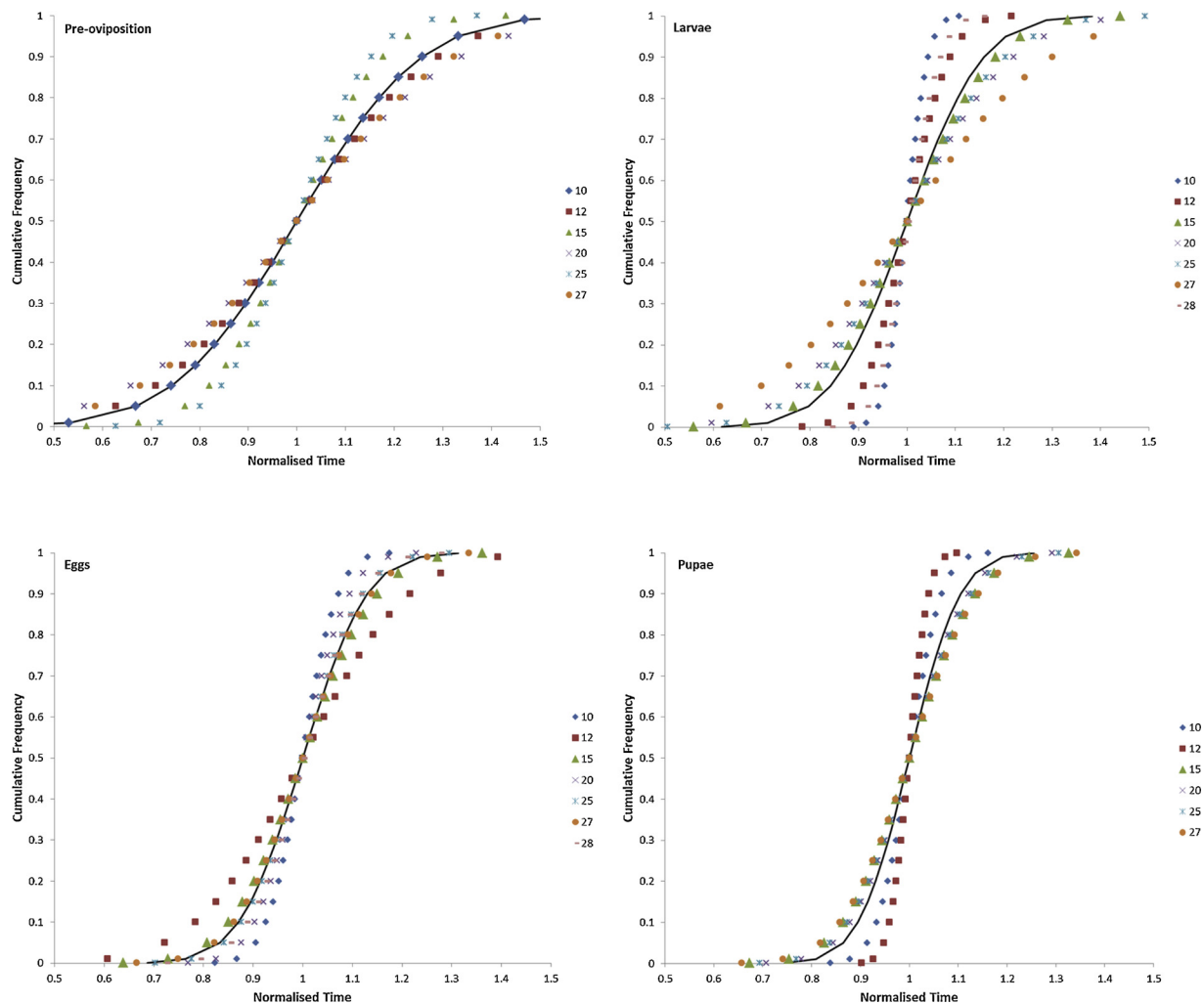| Parameter	Pre-oviposition	Oviposition	Eggs	Larvae	Pupae
γ	0.7207 ± 0.0190	−0.0716 ± 0.0394	0.5730 ± 0.0323	0.8652 ± 0.0027	0.4990 ± 0.0778
η	0.3517 ± 0.0201	0.5117 ± 0.0434	0.4706 ± 0.0328	0.1661 ± 0.0029	0.5335 ± 0.0782
β	1.7918 ± 0.1324	1.6997 ± 0.1708	3.5592 ± 0.2821	1.7224 ± 0.0393	5.3502 ± 0.8538

Fig. 5. Cumulative frequency of development completion for *Phratora vulgatissima* for the different constant temperatures (symbols) and normalised time of post-diapause pre-oviposition, eggs, larval and pupal development times (line).

only start to increase after the middle of the year. When coupled with an earlier date of budburst, temperatures are insufficient for significant development to occur in the pre-oviposition stage. For example, the estimated T_L (Lactin model) for the pre-oviposition stage is 7.19°C, below which no development takes place. Fig. 11 shows the accumulated thermal units for three base temperatures, namely 5, 7 and 9 °C, and the daily mean temperature from Casement from 2005, one of the warmest years on record over the period 1964–2018. Daily mean temperatures at this site only start to increase above T_L after day 160. A further examination of the data but with the daily mean temperature shifted by +4 and +6 °C, respectively, resulted in a greater impact on the timing of the subsequent life cycle stages suggesting that the low sensitivity to changes in bud burst evident at this site are related to the Lactin T_L threshold (i.e. low development rates at low temperatures) and the generally low temperatures experienced in Ireland during spring.

Sensitivity of the model simulated life cycle completion dates based on sampling the Lactin parameters was assessed within the range of ± 10% of the parameter estimated values (Table 4), shown in Fig. 12; other ranges were also examined (e.g. 5%, 20%, 30%). Based on this evaluation, the model was found to be sensitive to changes in the Lactin parameters, ranging from a difference of 83 days for post diapause stage completion between the 2.5 and 97.5% range simulated at ± 5%, to a difference of 130 (between the 2.5 and 97.5% range simulated) days for the ± 10% sampling range. These differences

increased with higher specified sampling ranges. This is not unexpected; changing the Lactin parameters alters the rate of development and consequently the time taken to complete a particular life cycle stage.

The Weibull estimated parameters (Table 6) were also varied with ± 10% range, which resulted in small differences in the median stage completion dates; up to a maximum of 10 days difference between the 2.5% and 97.5% range across all life cycle stages (Fig. 13). A ± 30% range in the Weibull parameters was also examined, with a maximum difference of 36 days between the 2.5% and 97.5% samples across all life cycle stages, confirming the low model sensitivity to this component of the phenology model.

An assessment of the critical day length threshold, CDL, was also performed. Here, we assessed the CDL that would result in a specified proportion of adult insects not progressing from the sexual maturation life cycle stage. On the basis of the specified CDL, 14.92 h, 50% of the 1st generation adults would complete sexually maturation on day 303; no proportion of 2nd generation adults completed sexual maturation (e.g. Fig. 8). Based on the outcome of the CDL sensitivity analysis, only 1% of emerging adults would complete sexual maturation at a CDL of 16.64 h; 99% of emerging adults would complete sexual maturation at 11.92 h CDL (Table 7). Within the range sampled, no proportion of second generation adults were simulated to complete sexual maturation.

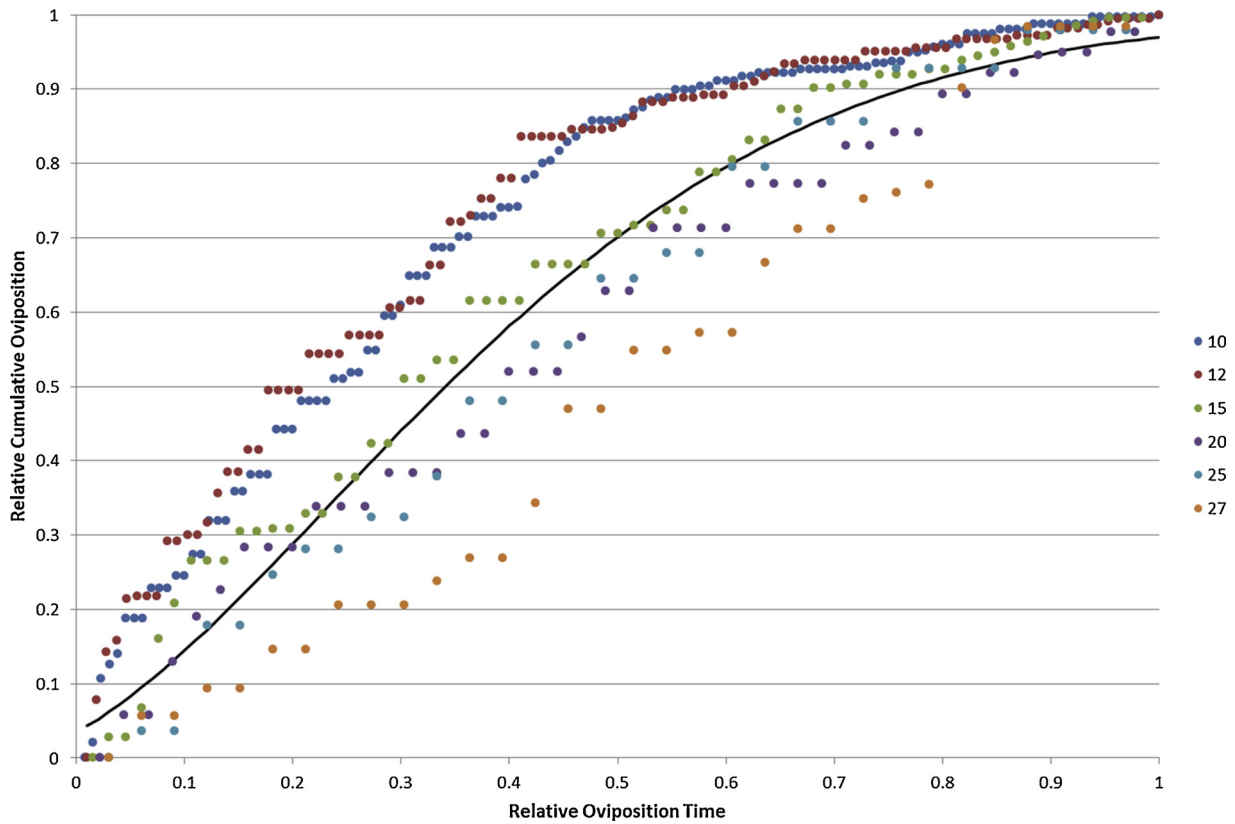Fig. 14 illustrates plots of model sensitivity to a change in the CDL

Fig. 6. Relative oviposition of *P. vulgatissima* described using Weibull (3 P) model. Colours represent the different temperature experiments. The black line is the fit of the Weibull function.

threshold (bottom axis) for different specified proportions, namely 0.1, 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, 0.95, 0.99, of emerging adult insects. At a lower CDL, less than the 14.92 h specified in the model and equivalent to later in the year, an increasing proportion of adult insects are simulated to complete sexual maturation and *vice versa*.

As a final test of the model components and how they interact over

time (e.g. potential for second generation etc.), a climate change experiment was performed with the phenology model for the 50% emergence proportion. A priori, warmer temperatures should result in an earlier date of budburst and shorter development times, assuming that warmer temperatures do not exceed the life cycle stage temperature optimum (T_{OPT}) or upper lethal threshold (T_U). Bias corrected daily
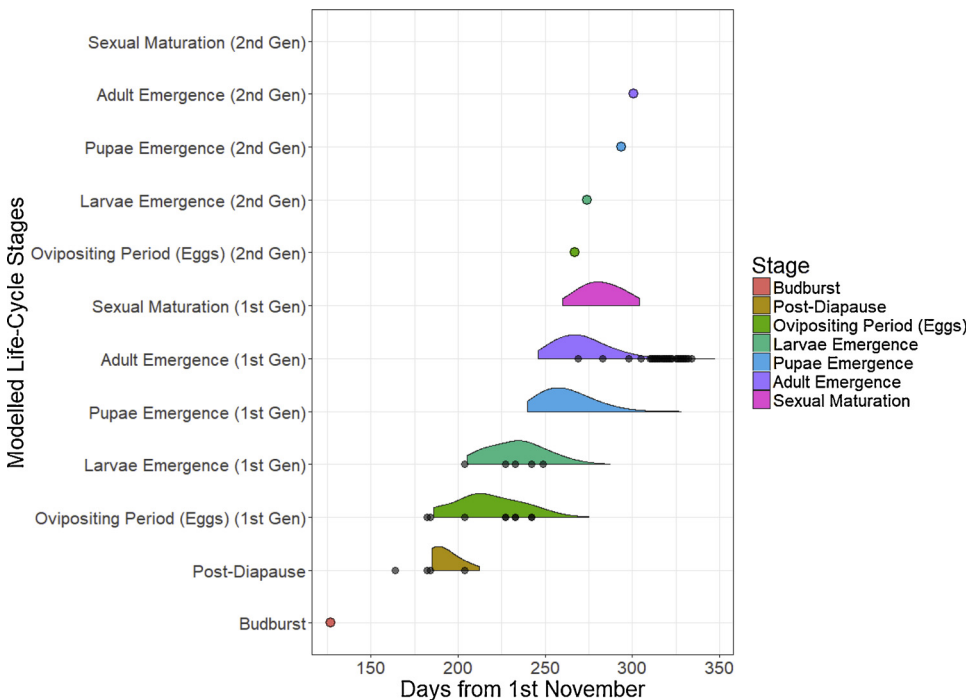

Fig. 7. Model simulated life cycle stages for *P. vulgatissima* based on temperature from Westonbirt, Gloucestershire, UK, from 1995. Black dots indicate field recorded observations of adults, eggs and larvae from SRC located in Long Ashton obtained by Kendall and Wiltshire (1998). The distributions represent the proportion of insects completing a life cycle stage on a particular day. Days are from the 1st November in the preceding year. Recorded observations of adults have been allocated to life cycle stage as outlined in the text.
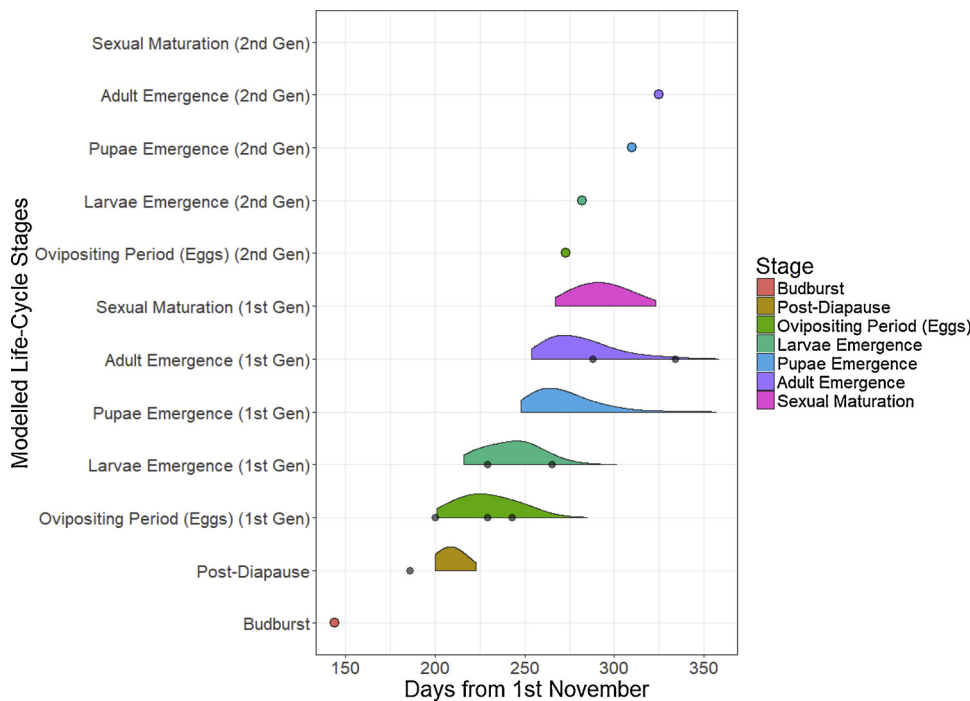
Fig. 8. Model simulated life cycle stages for *P. vulgatissima* based on temperature from Casement Aerodrome, Co. Dublin, IE, from 2013. Black dots indicate field recorded observations of adults, eggs and larvae from SRC located in Donard, Co. Wicklow, obtained by Pollard (2014). The distributions represent the proportion of insects completing a life cycle stage on a particular day. Days are from the 1st November in the preceding year. Recorded observations of adults have been allocated to life cycle stage as outlined in paper.

maximum and minimum temperature data for two RCPs, namely 2.6 and 8.5, were obtained for a model grid location approximating the location of Casement Aerodrome and used as input to the phenModel. The climate simulations do not account for model uncertainty, only the output from one climate model is employed, but are used here to explore if the simulated response of the phenology model to changes in temperature that are likely to occur over the course of the present century is consistent with expectation. The assessment also illustrates how the phenology model could be employed to assess the impact of increasing temperatures, due to climate change, on *P. vulgatissima*.

Depending on RCP, the average date of budburst is simulated to decrease from day 145 during the period 1951–1960 to day 126 (RCP2.6; Fig. 15a) and day 119 (RCP8.5; Fig. 15b), over the period 2090–2099 (Table 8). All subsequent life cycle stages are projected to occur earlier, with the greater changes evident with the warmer

scenario (i.e. RCP8.5 relative to RCP2.6). A second generation of adults reaching sexual maturity is not simulated to occur under either RCP; however, 50% of the insects are simulated to complete a second generation adult life cycle stage every year after the middle of the present century.

6. Discussion

Temperature and photoperiod are typically considered the prime factors that influence insect life-histories (Tauber et al., 1986; Porter et al., 1991; Bale et al., 2002), especially in the temperate latitudes where large seasonal changes in temperature and photoperiod occur (Tauber et al., 1998). Of these, temperature is a key factor influencing insects (Davidson, 1944; Messenger, 1959; Wigglesworth, 1972; Hoffmann, 1985). To establish a relationship between temperature and
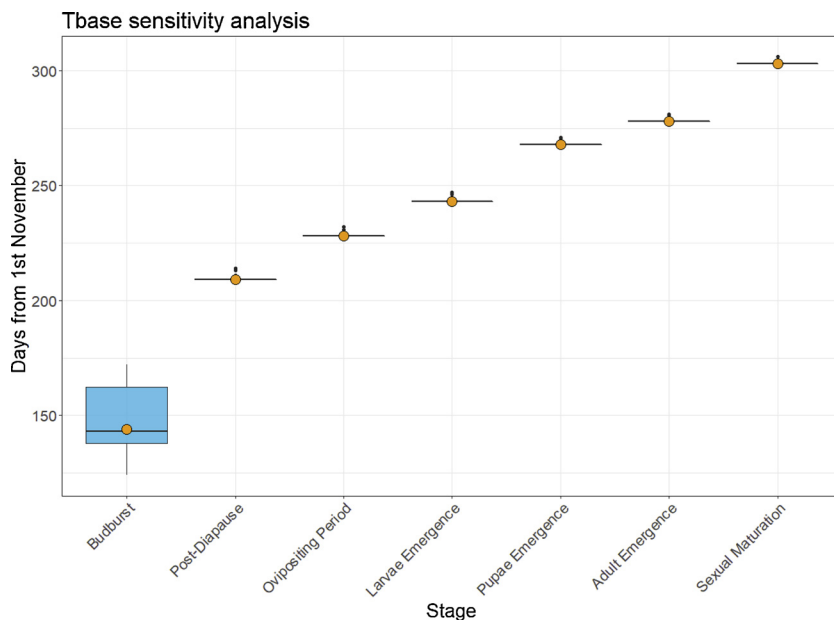

Fig. 9. Sensitivity analysis with the temperature threshold sampled from a range ± 30% of the specified value. Boxplots represent the median (50%) and upper and lower quartiles (25% and 75%). The orange dots represent the model output from original estimated parameter values, for comparison. Statistics are derived from 1000 runs. Data are based on model simulations run with Casement Aerodrome temperature for 2013.
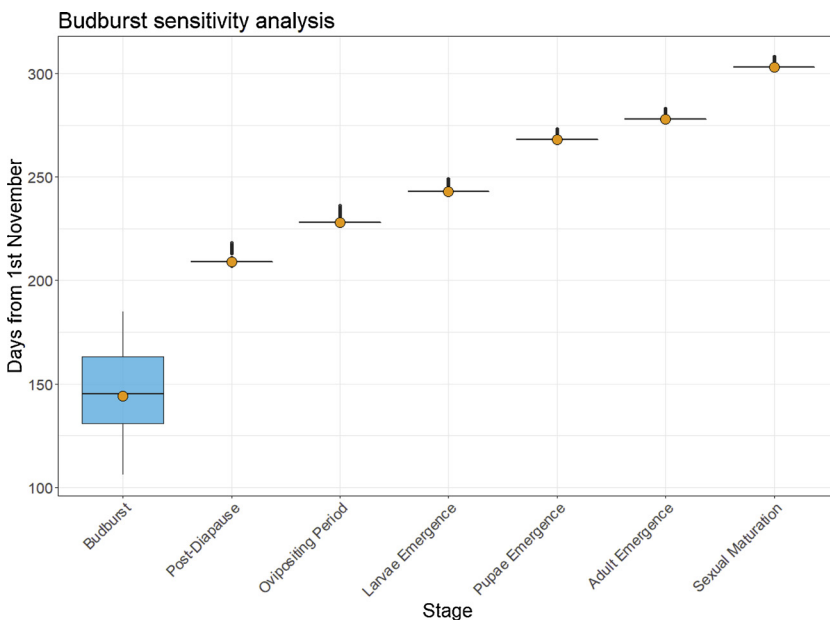
Fig. 10. Sensitivity analysis budburst parameters sampled from a range ± 30% of the specified values. Boxplots represent the median (50%) and upper and lower quartiles (25% and 75%). The orange dots represent the model output from original estimated parameter values, for comparison. Statistics are derived from 1000 runs. Data are based on model simulations run with Casement Aerodrome temperature data from 2013.
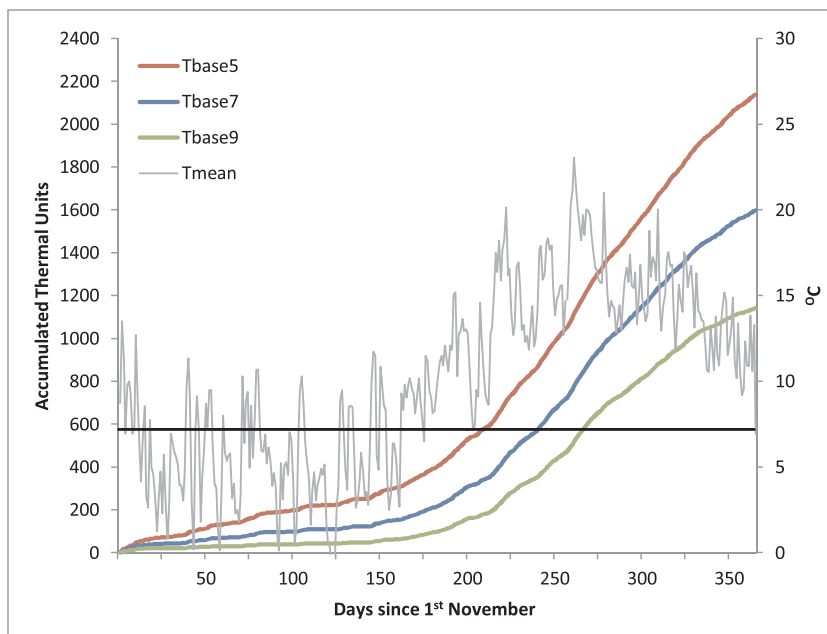

Fig. 11. Accumulated thermal units for base threshold temperatures of 5, 7 and 9 °C and daily mean temperature from Casement Aerodrome from 2005. The black line represents the estimated T_L (7.19 °C) from the Lactin equation for the Pre-oviposition stage. The daily mean temperature only begins to increase above T_L after day 150 (30 March).

P. vulgatissima development rates obtained from the laboratory experiments, a selection of widely used empirical and biophysical approaches were assessed, namely a linear model (Campbell et al., 1974) and three non-linear models, Briere (Briere et al., 1999), Lactin-2 (Lactin et al., 1995) and Schoolfield (Schoolfield et al., 1981) models. Campbell's et al. (1974) linear model is one of the most widely utilised in development rate studies, due to its ability to identify degree-day requirements for development as well as the lower temperature for development. For *P. vulgatissima,* the linear model indicated a temperature threshold of 7.5 °C for post-diapause pre-oviposition development, with a cumulative temperature requirement for oviposition of 100 °-days. These values differ substantially from the respective values of 5.5 °C and 222 DD calculated by Dalin (2011) for a Swedish population of *P. vulgatissima.* However, insects are adapted to local conditions (Chown, 2001) and frequently exhibit latitudinal clines in response to environmental factors such as temperature (Posledovich et al., 2014; Lehmann et al., 2015). As the temperature-development

relationship in poikilothermic organisms typically becomes non-linear at temperatures approaching the upper and lower critical values, non-linear models have a critical role in estimating the optimum temperature for development and the upper critical limit. Of the models assessed, the Lactin-2 model was ultimately selected for use in the phenology model when judged by the stated evaluation criteria: statistical fit of the model to the experimental data and realistic representation of the biology.

Linear and non-linear models are deterministic, they model insect development based on the mean or median of all individuals at each temperature. These functions do not account for intrinsic differences among individuals in a population. The necessity for integrating deterministic development rate equations with stochastic development time equations within phenology models has been espoused by a number of authors (e.g. Wagner et al., 1985; Ma and Bechinski, 2009) and more recently by Rebaudo and Rabhi (2018). For *P. vulgatissima,* the variation among individuals in development times was best
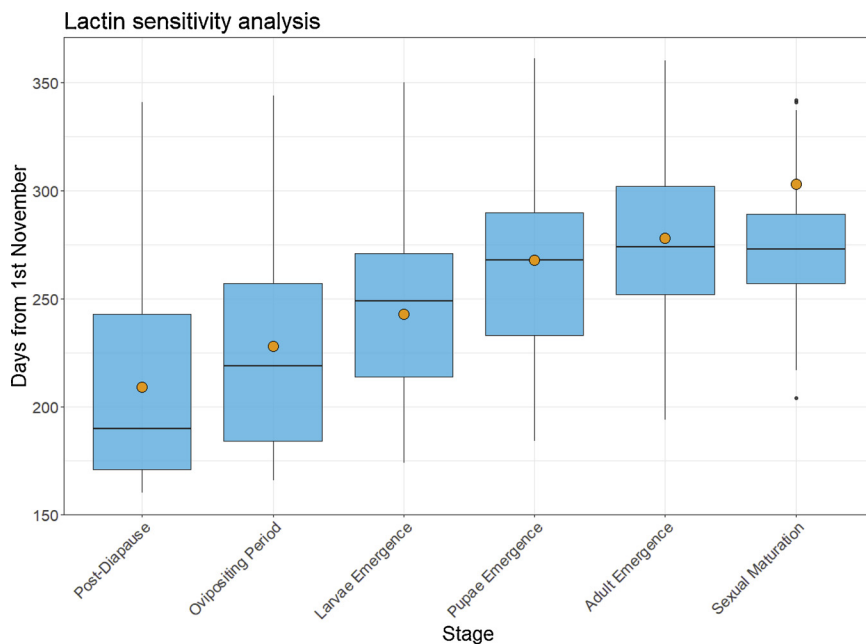
Fig. 12. Sensitivity analysis of the Lactin parameters sampled from a range ± 10% of the estimated values. Boxplots represent the median (50%) and upper and lower quartiles (25% and 75%). The orange dots represent the model output from original estimated parameter values for comparison. Statistics are derived from 1000 runs. Data are based on model simulations run with Casement Aerodrome temperature data from 2013.

described by the three parameter Weibull function (Wagner et al., 1984). The smaller value of the shape parameter (β) in the Weibull function for larvae suggests that the variation in development time is greater than for eggs and pupae. A similar pattern for larval or nymphal development to be more variable than for egg or pupal stages has been reported for other insects (Choi and Kim, 2014; Han et al., 2013; Son and Lewis, 2005b). Whether this serves an ecological function e.g. as a bet-hedging strategy (Hopper, 1999) caused by inter-individual sensitivity to temperature (Chuche and Thiéry, 2009) warrants further investigation, but is beyond the scope of the current study.

With regards to the specified model constants, the base temperature threshold (7 °C) for calculating thermal and chilling units for budburst, was found to have limited impact on the subsequent timing of the pre-oviposition life cycle stage and consequently the timing for all remaining life cycle stages. Similar results were obtained from varying the budburst equation parameter estimates. The timing of subsequent simulated life cycle stages was found to be insensitive to changes in

budburst between days 80 and 160 (mid-January – end of March). This is likely attributable to the specifics of the annual temperature cycle in Ireland, which is maritime influenced climate, resulting in an annual cycle of cooler temperatures experienced during winter and spring, followed by increasing temperatures after the middle of the year. The subsequent evaluation with daily temperatures increased by + 4 and + 6 °C, would seem to confirm the interaction between temperatures and the T_L parameter from Lactin, with impacts evident on the timing of all life cycle events for both scenarios. An additional contributing factor is likely associated with the swarming and dispersion of adult beetles in spring; the temperature threshold for swarming (e.g. Taylor, 1963) is typically higher than the thresholds for other life cycle stages (e.g. Baier et al., 2007; Jönsson et al., 2007). While the implementation of a threshold for swarming may contribute to an improved simulation of day of oviposition, no data were available to include this in the current model.

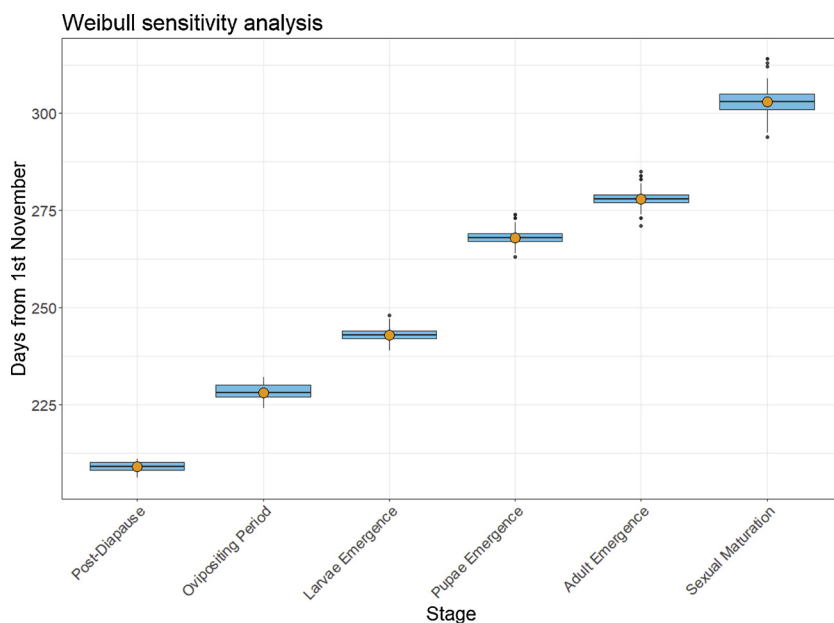Changes in the Lactin parameters were found to have the greatest

Fig. 13. Sensitivity analysis of the Weibull parameters sampled from a range ± 10% of the estimated values. Boxplots represent the median (50%) and upper and lower quartiles (25% and 75%). The orange dots represent the model output from original estimated parameter values for comparison. Statistics are derived from 1000 runs. Data are based on model simulations run with Casement Aerodrome temperature data from 2013.

Table 7

Proportion of adults that would complete the sexual maturation life cycle stage at various critical day length thresholds. Statistics are derived from 1000 runs. Data are based on model simulations run with Casement Aerodrome temperature data from 2013.

Proportion	0.01	0.05	0.1	0.25	0.5	0.75	0.9	0.95	0.99
CDL (hrs)	16.64	16.54	16.37	16.09	15.49	14.68	13.62	11.94	11.94

impact on the timing of the different life cycle stages; this is a finding that is not unexpected. While the sampled ranges were unlikely to be realistic or biologically informed estimated, the sensitivity analysis points to the importance in correctly fitting the temperature dependent development time model to the observed data when estimating model parameters. In contrast, alterations to the Weibull parameters were found to have a small effect on the timing of life cycle stages.

For the CDL sensitivity analysis, we assessed the 'cut off' CDL, or daylength above and below which adult insects would progress to oviposition or diapause, respectively, from the sexual maturation life cycle stage. Based on the limited available laboratory data which was employed to derive this parameter, Pollard (2014) estimated the CDL at 14.92 h (95% CI: 14.46–15.41 h). The model estimated value for CDL, the day length threshold inducing diapause in 50% of the population, was 15.49 h, approximately 5 min longer than the 95% confidence interval associated with the laboratory analysis. In terms of the impact of a change in the CDL on the simulated outcomes, the CDL value employed in the model was found to only impact on the proportion of first generation adult insects completing sexual maturation. Adaptation to local conditions (Chown, 2001), including temperature (Posledovich

et al., 2014) and photoperiod (Lehmann et al., 2015) probably explain the difference in critical day-length for diapause induction of *P. vulgatissima*, calculated as 18 h 10 min. in Sweden (Dalin, 2011) and 14 h 56 min for the populations reported on here. Based on the CDL analysis, less than 1% of adults would complete the sexual maturation stage at a CDL of 16.64 h, well below that of Dalin (2011).

At present, *P. vulgatissima* is typically univoltine in northern Europe (Björkman and Eklund, 2006; Kelly and Curry, 1991; Kendall and Wiltshire, 1998) although partial second generations have been recorded in some years (Dalin, 2011). Earlier spring emergence and faster development is expected to increase the probability of additional generations of various coleopterans from Italy to Scandinavia (Colombari et al., 2012; Jönsson et al., 2013). Under the present climate conditions, additional generation development for these species is currently limited by diapause-inducing photoperiod thresholds (Wilde et al., 1959; Gehrken, 1985; Doležal and Sehnal, 2007). *P. vulgatissima* has a facultative reproductive diapause induced by declining day-length (Dalin, 2011). Warmer temperatures, suggested to occur as a consequence of climate change, may have pronounced effects on earlier emergence and faster development, with oviposition for an additional generation(s)
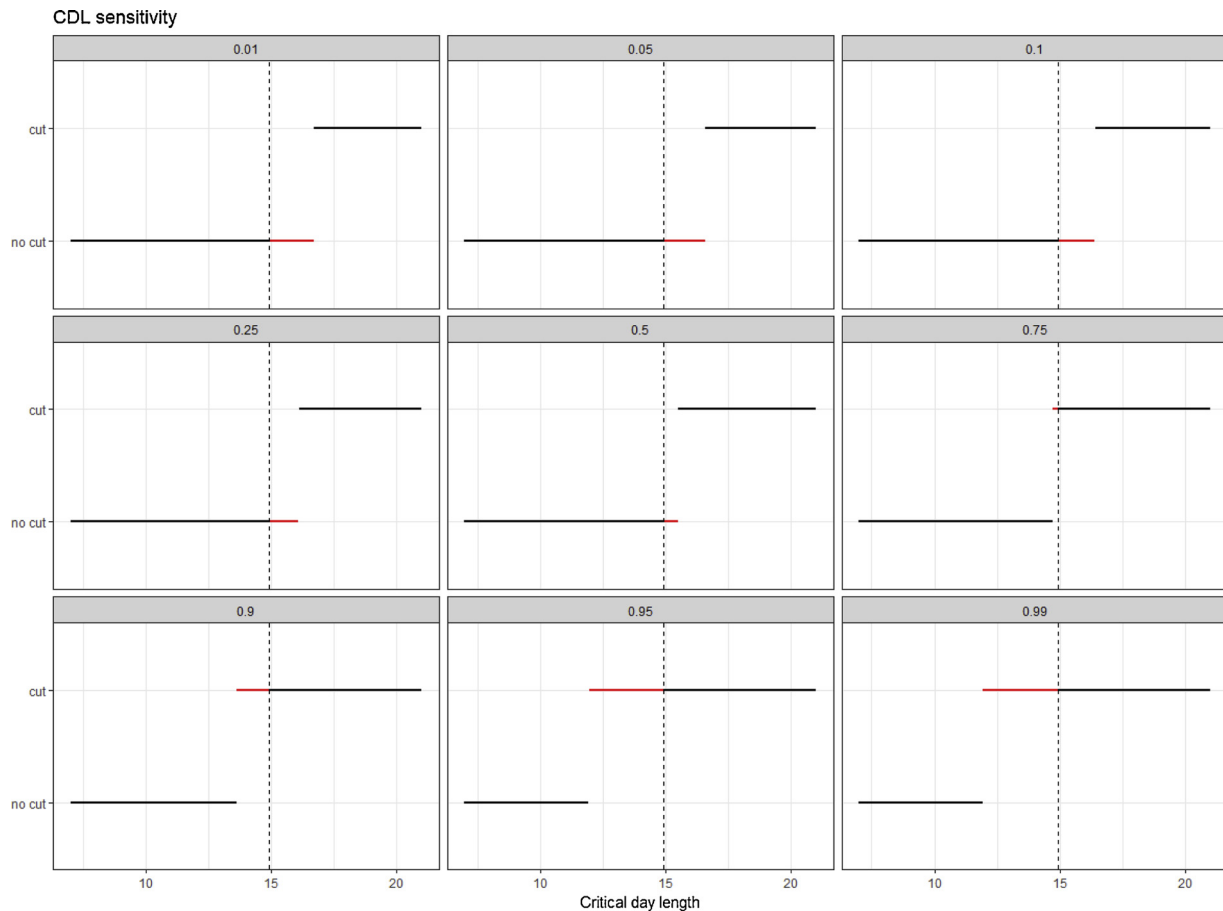

Fig. 14. Sensitivity analysis of changes to critical day length for different specified proportions (0.1, 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, 0.95, 0.99) of emerging adult insects. The vertical dashed line is the original CDL of 14.92 h. The length of the red section is directly proportional to how sensitive the model output would be to a change in the CDL threshold, i.e. no cut (advance to the sexual maturity stage) vs. cut (not advance). Statistics are derived from 1000 runs. Data are based on model simulations run with Casement Aerodrome temperature data from 2013.
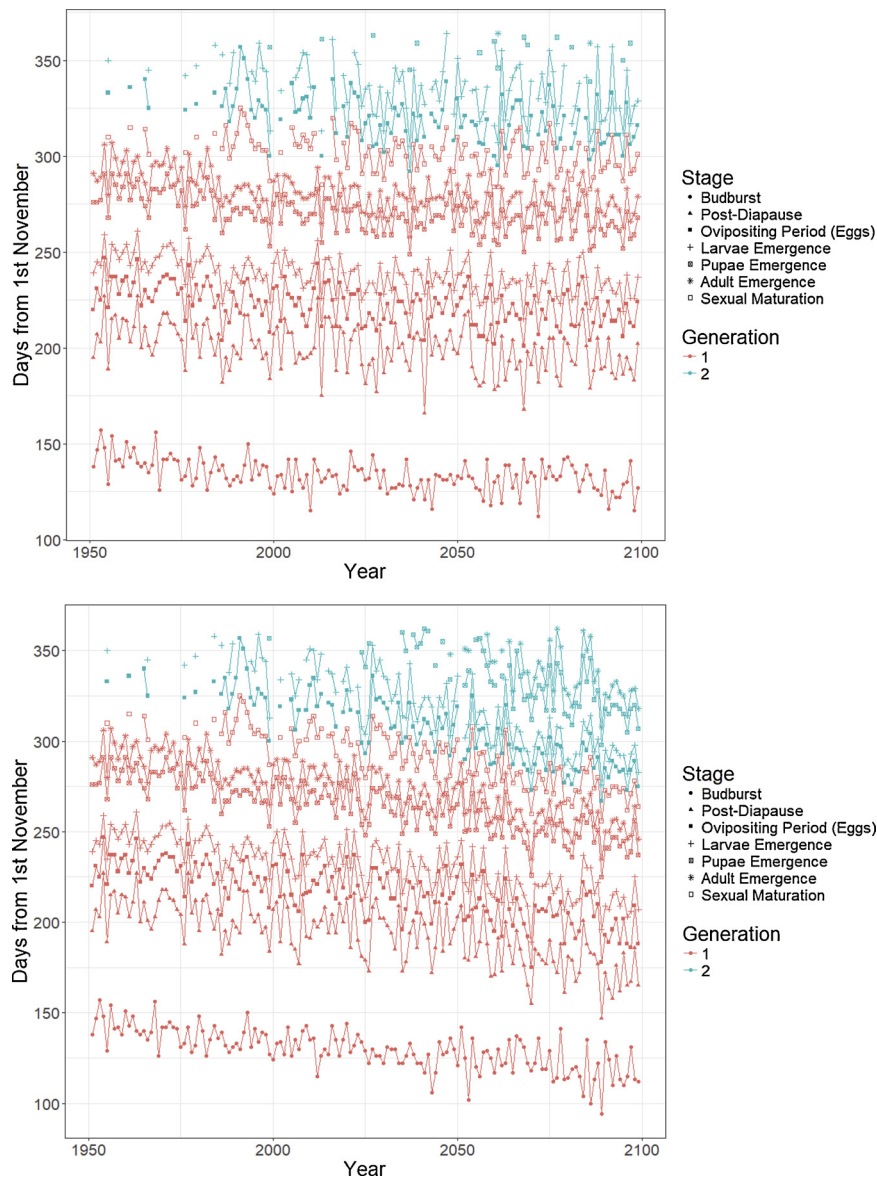
Fig. 15. Model simulations for a) RCP2.6 (top) and b) RCP8.5 (bottom) based on daily maximum and minimum temperature obtained from the WRF regional climate model for a grid box located over Casement Aerodrome for the period 1951-2100. The historical (1951–2005) and future climate simulations (2006–2100) are based on dynamically downscaled ICHEC EC-Earth earth system model for a European domain using the WRF regional climate model.

Table 8
Average day of budburst and of completion for 50% of the insects emerging from a life cycle stage. The averages are calculated over 10 year periods, 1951–1960 and 2090-2099, for two representative concentration pathways (RCPs), RCP2.6 and 8.5. The simulated day of emergence is based on bias corrected maximum and minimum temperature from the WRF regional climate model used to dynamically downscale the ICHEC EC-Earth earth system model for a location approximate to Casement Aerodrome. A critical day length (CDL) of 14.92 was employed for all the simulations.

Scenario	Period	Budburst	Post Diapause	Eggs	Larva	Pupa	Adult
Historical	1951–1960	145	209	232	248	282	295
RCP2.6	2090–2099	126	192	217	231	262	273
RCP8.5	2090–2099	119	170	194	211	243	252

more likely to occur prior to CDL. To evaluate the model's ability to simulate the timing of life cycle stages under altered climate conditions, temperature data was obtained from a regional climate model for two representative concentration pathways, namely RCP2.6 and 8.5, for the

period from 1951 to 2100 for a location proximate to Casement Aerodrome. While not undertaken as an assessment of the likely impacts of climate change on the life cycle of *P. vulgatissima,* as only one climate model was employed, the conditional findings indicate that warmer temperatures will likely result in a second generation of adults emerging every year by the end of the present century, under RCP8.5. The effects of this are likely to have consequences for SRC; namely, the likelihood a second generation of larvae and new adults will result in increased herbivory in autumn, and also the likelihood of a greater number of overwintering adults emerging to feed in the following spring.

7. Limitations

While temperature and photoperiod are considered the prime factors influencing insect life histories, other abiotic factors such as moisture (Tauber et al., 1998) and atmospheric greenhouse gas concentrations (Zvereva and Kozlov, 2006) and biotic factors such as host plant quality (Hunter, 2001; Peacock et al., 2004) and natural enemies

(Hance et al., 2007) may interact with temperature and photoperiod to directly or indirectly influence insect behaviour, ecology and physiology. For example, moisture, in the form of relative humidity, has been shown to affect coleopteran development rates (Howe, 1962; Shires, 1979; Zhou et al., 2010) and oviposition (Coombs, 1978; Jacob, 1996; Simmons et al., 2008). Moisture has also been identified as a seasonal cue during various diapause phases (Hodek, 2003). Although the combined phenology/voltinism model developed here incorporates temperature and photoperiod, elucidating the roles of other environmental variables in insect seasonal cycles could contribute to the development of more comprehensive combined phenology/voltinism models.

To more fully explore the likely impact of temperature and temperature change on *P. vulgatissima*, it would be necessary to include a survival function in the model. Although survival data is available for some life-cycle stages, a survival component was not incorporated in the current version of phenModel. Future versions of this model could be modified to take account of insect mortality, and in doing so, allow for a population dynamics analysis instead of a proportion based emergence assessment as outlined here.

Additional field data to evaluate the model presented would significantly aid in adding confidence in the model's abilities to produce meaningful 'timing of events' within the species lifecycle. The absence of long term field data to enable further evaluation of the model is an area that merits further work. In spite of the potential shortcomings, the phenology model was found to largely replicate the timing of life cycle stages observed at two sites, Long Ashton (UK) and Donard (IE), based on limited available field data. A limitation of the model is also attributed to the basis on which the parameters were derived, from constant temperature experiments. The pattern of exposure to critical temperatures has previously been found to influence survival in some insect species and some studies suggest that daily temperature cycles can play an important role in insect development (Rock, 1985; Roltsch et al., 1990; Fornasari, 1995). For example, *Plutella xylostella* (diamondback moth) development from egg to adult was recorded for constant temperatures within the range $8\,^{\circ}\text{C}-32\,^{\circ}\text{C}$ only but for alternating temperatures $4\,^{\circ}\text{C}-12\,^{\circ}\text{C}$ and $28\,^{\circ}\text{C}-38\,^{\circ}\text{C}$ at $12\,\text{L}{:}12\text{D}$, immature life-cycle development was completed also (Liu et al., 2002). Despite these findings, development times have been found to frequently mirror times recorded under fluctuating temperature regimes (Campbell et al., 1974) which validates their use here. Further examination of the effects of alternating temperatures on *P. vulgatissima* is merited in any future laboratory experiments for this species, but which were beyond the scope of the present study.

8. Conclusion

This study sought to account for the temperature dependent emergence patterns of *P. vulgatissima* through the development of a multi-component phenological/voltinism model, phenModel, which has been developed in the R programming language and is available for download as a CRAN R package (https://CRAN.R-project.org/package=phenModel). The model incorporates an alternating (forcing degree-days – chilling days) budburst model for *S. viminalis*; temperature-dependent development rate and temperature-independent time distribution functions for each life-cycle stage; an oviposition function and a reproductive diapause-inducing CDL to estimate the number of days, from 1 st November, required by selected proportions of beetles to complete a full generation of development. The model is structured in a way that it is modifiable; where a user has equivalent model parameters for a species exhibiting a similar life cycle these can be readily incorporated into the model, facilitating its use beyond the specifics of the population or species employed here. The empirical data outlined here, and in the supplementary material, will provide some new insights into the biology of *P. vulgatissima*, contributing to the existing, limited, information on this important pest species of SRC willow.

An improved understanding of the biology of this species and the associated phenology model could have a potentially significant role to play in informing and assisting managers to forecast and control pest outbreaks of *P. vulgatissima,* an economically important pest species of SRC willow in Europe and elsewhere. In addition, the model can simulate changes in the timing of life cycle events based on scenarios of past or future changes in temperature, associated with climate change, potentially assisting in the development of long term pest management strategies.

Other woody crops similar to willow such as eucalyptus, and non-woody crops such as hemp and miscanthus that have been proposed as renewable energy options have associated pests and diseases also such as *Paropsisterna selmani*, *Grapholita delineana* and *Diabrotica virgifera virgifera* respectively. Although these crops may appear to be economical and practical solutions in the short term, without knowledge of insect life-cycles under projected climate change conditions and their impact on these crops, such adaptation measures may falter.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2019.108910.

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